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福山地區維管束附生植物之物種組成及功能性狀

在垂直方向的變化趨勢

Species Composition and Functional Traits of

Vascular Epiphytes Show Vertical Trends in

Fushan Experimental Forest

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本論文係李先祐君 (R05625005) 在國立臺灣大學森林環境暨資源學系所完成之碩士學位論文，於民國 107 年 12 月 27 日承下列考試委員審查通過及口試及格，特此證明

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兩年半的時間匆匆而過，不知不覺間這篇碩士論文也即將要完成了，回想起來還真覺得有些不可思議。以前看別人的論文謝辭，總會覺得何必列這麼多名字。但等到自己真正開始做研究，才知道需要感謝的人真的太多了！

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中文摘要



在森林中包括光度、相對濕度及溫度等環境因子都會隨高度改變，形成垂直的環境梯度。維管束附生植物因為生長在其他植物之上，面對從林下層到樹冠層的多樣微環境，因此適合用來研究垂直環境梯度對生物的影響。本研究針對在臺灣東北部福山試驗林的附生植物，以釐清附生植物的物種組成以及功能性狀是否會隨著高度改變。本研究選定 24 棵樣樹，在每棵樣樹上劃設 5-6 個垂直分區，並透過雙索攀樹技術，在各分區內設立樣區進行物種調查。除了記錄樣區內的物種及豐度，亦採集個體量測功能性狀，包括葉厚度、比葉面積、葉乾物質重、單位葉面積葉含水率以及葉綠素含量（單位葉面積及單位葉質量）。

研究結果顯示，樣區的物種組成會隨離地高度而改變。各物種會佔據不同的高度範圍，形成垂直分層分布。此外，對於單葉的附生植物物種來說，葉厚度以及單位葉面積葉含水率會隨高度上升而增加，比葉面積和單位葉質量的葉綠素含量則會隨高度上升而減少。本研究指出離地高度確實對附生植物的分布以及功能性狀都具有顯著的影響。

【中文關鍵字】

維管束附生植物、垂直環境梯度、垂直分層分布、功能性狀、群落加權平均

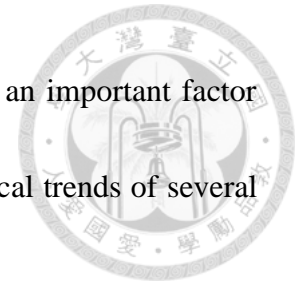
Abstract



Vascular epiphytes grow on other plants, facing various micro-environments from dark and humid understory to bright and dry canopy. Therefore, it is quite suitable to use epiphytes to analyze the effects of vertical environmental gradients on organisms. I studied vascular epiphytes in Fushan Experimental Forest (located in northeastern Taiwan) in 2018 and aimed to determine whether species composition and several functional leaf traits of vascular epiphytes change along vertical environmental gradients. I used doubled rope techniques to climb up 24 sampled trees and surveyed the epiphytes on them. I set 5-6 vertical zones within each sampled tree based on height above ground, and set sampling plots within each zone, recorded all species that appeared in the plots and their abundance. I also collected some epiphyte individuals to measure functional traits including leaf thickness, specific leaf area, leaf dry matter content, leaf water content (per unit area) and leaf chlorophyll content (per unit area and per unit mass).

The results show that epiphyte species composition changed significantly with height, and epiphyte species differentiated in their height distribution. Angle differences between aspects of plots and the south direction were also suggested to have effects on epiphyte species composition. Besides, several functional leaf traits show vertical trends. Leaf thickness and leaf water content (per unit area) of simple-leaved epiphytes significantly increased with height, while specific leaf area and chlorophyll content (per

unit mass) decreased with height. This study reveals that height is an important factor which not only structures species composition but also creates vertical trends of several functional leaf traits.



Keywords

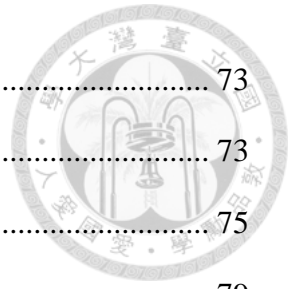
Vascular epiphytes, vertical environmental gradients, vertical stratification, functional traits, community weighted mean

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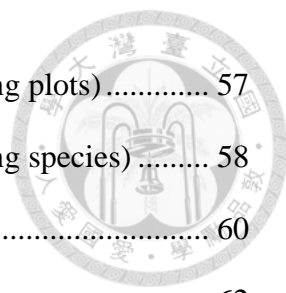


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Introduction

1. Vascular epiphytes and their importance

Epiphytes are those plants that germinate and grow on other plants (i.e., host plants) without taking nourishments from them (de Mirbel, 1815; Zotz, 2016). In other words, they are not parasitic and can survive on photosynthesis by their own. In a taxonomic perspective, epiphytes can be classified as vascular epiphytes and non-vascular epiphytes. Vascular epiphytes include those epiphytic species belonging to ferns, fern allies, basal angiosperms, monocots and eudicots, while non-vascular epiphytes refer to epiphytic lichens, mosses and liverworts. Due to large differences between the morphology, physiology, life history characteristics and adaptive strategies of vascular and non-vascular epiphytes, these two types of epiphytes are usually studied separately (Affeld *et al.*, 2008). In this study, only vascular epiphytes were considered. All of the terms “epiphytes” used in this study refer to vascular epiphytes unless there is an additional notation.

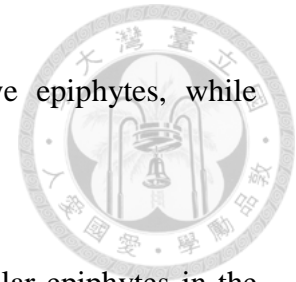
The definition of epiphytes mentioned in previous paragraph is quite simple, while it is difficult to apply this simple definition under some circumstances because the life history characteristics and the life forms of plants in real world are much more complicated. Those species of which all individuals are epiphytic and not connected to the ground during all stages of life history belong to epiphytes without question. Actually,



these species are also called “true epiphytes” or “holoepiphytes” (Kress, 1989; 徐嘉君, 2007). On the other hand, hemiepiphytes refer to those species which have connections to the ground at some of their life history stages, and can be further classified as primary hemiepiphytes and secondary hemiepiphytes (Kress, 1989). Primary hemiepiphytes grow on other plants during early stages but finally reach the ground and become terrestrial plants, such as some *Ficus* species. Secondary hemiepiphytes germinate from the soil, but they lose the connection to the ground sooner or later, such as *Pothos chinensis* (in Araceae). There are also some species of which some individuals are epiphytic while the other individuals are terrestrial or lithophytic. These species are usually called “facultative epiphytes” (Benzing, 2004; Burns, 2010).

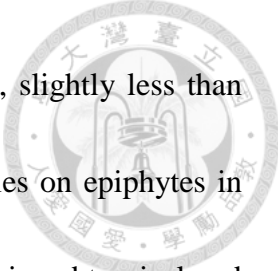
True epiphytes, primary and secondary hemiepiphytes and facultative epiphytes were all viewed as epiphytes when Kress (1989) described the systematic distribution of vascular epiphytes in the world. When 徐嘉君 (2007) summarized the species list of vascular epiphytes in Taiwan, she also adopted this general definition. However, there are still some debates about the definition of epiphytes. For example, Zotz (2013) suggested that secondary hemiepiphytes should not be considered as epiphytes because they are quite similar to climbing plants (vines) physiologically. In this study, I used a more general definition of epiphytes like Kress (1989) and 徐嘉君 (2007), that including true

epiphytes, primary and secondary hemiepiphytes, and facultative epiphytes, while excluding accidental epiphytes and climbing plants.



According to Zotz (2013), there were 27614 species of vascular epiphytes in the world, approximately equaling to 9% of all vascular plant species. At a local perspective, this proportion (also called “epiphyte quotient”) may be even higher. In some tropical montane cloud forests, epiphytes may account for up to 30% of all vascular plant species (Küper *et al.*, 2004). For such high proportions, it seems that epiphytes should not be ignored when studying regional or local plant communities. However, due to the paucity of efficient methods to reach forest canopies, not much emphasis were put on epiphytes in canopies until 1980s (Lowman *et al.*, 2012), causing a research gap that should be filled.

Vegetation ecologists have observed and surveyed terrestrial plants for a long time. However, it seems that the principles summarized from these studies cannot be applied to epiphyte assemblages directly (Zotz, 2016). For example, interspecific competition and herbivory are important factors shaping the structures and dynamics of tree communities, while their influences on epiphytes are much more subtle (Zotz and Hietz, 2001). The three-dimensional distribution patterns of epiphytes are also quite different from the planar distribution of terrestrial plants. Hence, there is a need to study the vegetation structure of epiphytes.



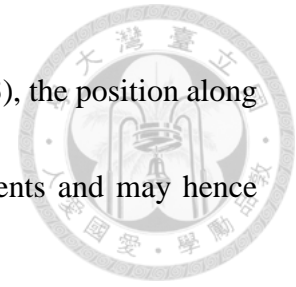
In Taiwan, the epiphyte quotient is about 8% (徐嘉君, 2007), slightly less than epiphyte quotient in the world (9%). Although there are many studies on epiphytes in tropical regions, especially in Central and South America, epiphytes in subtropical and temperate regions get less attention (Zotz, 2016). Studies on epiphytes of Taiwan can fill this research gap.

2. Environmental gradients that epiphytes experience

Large scale environmental gradients such as latitudinal or elevational gradients may have some effects on the distribution or diversity of epiphytes. For example, species richness of epiphytic ferns declines from tropical to temperate regions, and the trend is much sharper than terrestrial ferns (Zotz, 2016). It is also suggested that the abundance and species richness of epiphytes are hump-shaped distributed along elevational gradient, reaching maximum values in cloud forest zone which is typically at intermediate elevation (e.g., Krömer *et al.*, 2005).

At a local scale, epiphytes may also experience various microenvironments. Growing on other plants, epiphytes are actually distributed in a three-dimensional space, and the microenvironments may change a lot in both horizontal and vertical directions. In horizontal direction, there are many factors that may influence microenvironments, causing complicated structures. For example, the distance to forest edge (Davies-Colley

et al., 2000), the distance to water source (Chilpa-Galván *et al.*, 2013), the position along the slope (Werner *et al.*, 2012) all have effects on microenvironments and may hence influence epiphyte assemblages.



On the other hand, the environmental gradients along vertical direction are much more stable and predictable. Solar radiation is suggested to decline dramatically from outer canopy to understory (Petter *et al.*, 2016). In a lowland forest in Panama, the mean daily illuminance at 20 m high was about 22% of the illuminance in outer canopy, and the ratio dropped to only 6% in understory layer (Wagner *et al.*, 2013). In other tropical forests, the ratio of illuminance in understory relative to that in outer canopy may be even lower (Richards, 1996). Air humidity also changes along vertical direction, which becomes higher and more stable from outer canopy to understory (Wagner *et al.*, 2013). It should be noticed that both vertical light and humidity gradients only exist during daytime. Illuminance and air humidity have been suggested to have nearly no difference between understory and canopy during night (Wagner *et al.*, 2013; Zotz, 2016). There is also a pronounced vertical temperature gradient, but this gradient is more complicated. Temperature may increase, decrease or nearly not change from understory to canopy, depending on season or time in a day (Christy, 1952). However, daily temperature fluctuation is typically larger in higher places (Wagner *et al.*, 2013). Besides, wind speed usually increases from understory to outer canopy (Oliver, 1971), and diameter, stability



and longevity of growing substrates (trunks, branches and twigs) also change along vertical direction (Cabral *et al.*, 2015).

In summary, many environmental variables, including solar radiation, air humidity, temperature fluctuation and wind speed, all change along vertical direction (Figure 1).

What effects these vertical environmental gradients have on vascular epiphyte assemblages is the main question that this study was aimed to answer.

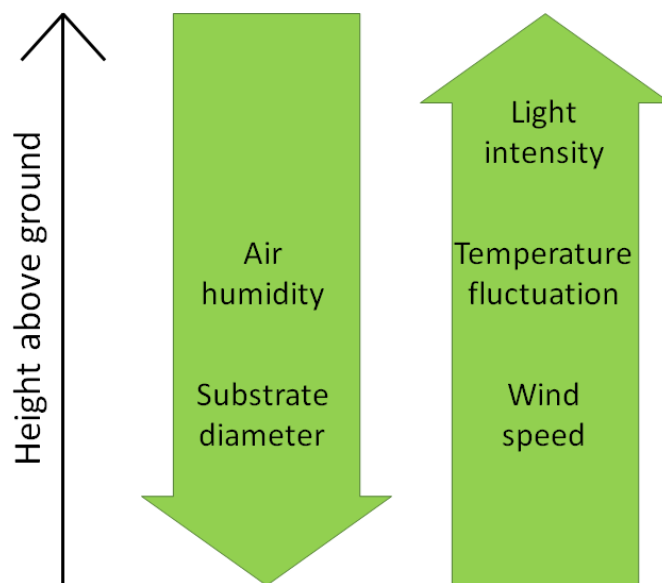



Figure 1. Common vertical environmental gradients in forests

Light intensity, temperature fluctuation and wind speed typically increase with height, while air humidity and diameter of growing substrates (trunks or branches) decrease with height. (modified from Petter *et al.*, 2016)

3. Effects of vertical environmental gradients on species composition



Explaining species composition of local communities is a central theme in ecology (Weiher and Keddy, 1995). A set of species which may potentially colonize a site is usually called the “species pool” of that site (Pärtel *et al.*, 2011), and several mechanisms have been proposed to filter a species pool into observed species composition of a local community. Three types of filtering mechanisms are usually mentioned, including dispersal filter, abiotic environmental filter and biotic interaction filter (Cadotte and Tucker, 2017) (Figure 2). Dispersal filter first excludes those species unable to arrive at the site due to limitations of dispersal abilities. Environmental filter excludes those species not capable of establishing and persisting in such environmental conditions (Bazzaz, 1991), and biotic interactions such as competition and predation may furthermore filter out some species (Hardy *et al.*, 2012). Although these three types of filtering mechanisms are usually described as sequential and discrete processes, they actually interact with each other in complex ways in reality (Cadotte and Tucker, 2017).

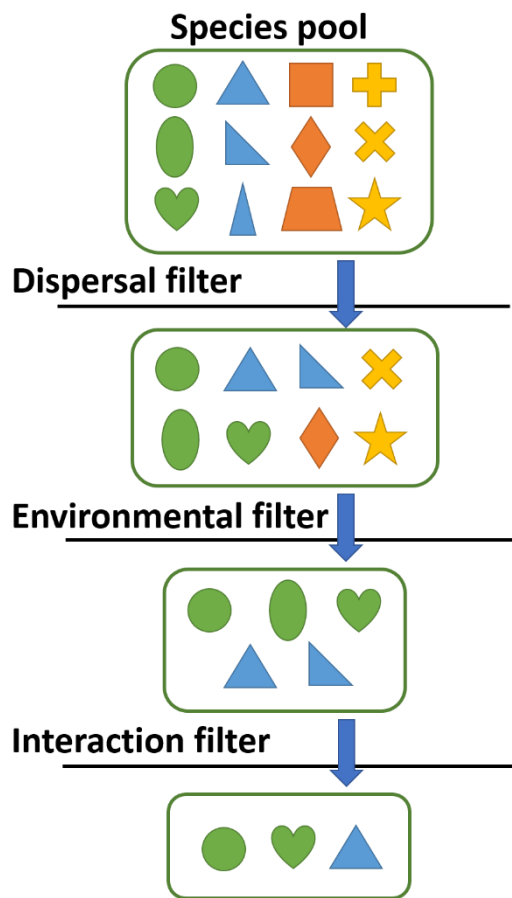
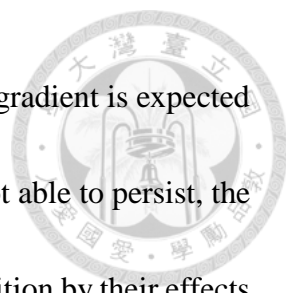


Figure 2. Three types of filtering mechanisms

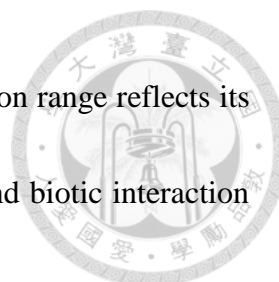
These three types of filtering mechanisms were proposed to explain species composition of a local community. Each symbol in this figure represents a species within species pool of the community. Dispersal filter excludes those species cannot disperse to the site, environmental filter excludes those species cannot persist in that abiotic environment, and interaction filter excludes those species cannot persist because of biotic interactions like competition. (modified from Cadotte and Tucker, 2017)

These filtering mechanisms can also be applied to several local communities distributed along an environmental gradient. In this case, environmental filter is usually considered most influential (Kraft *et al.*, 2015). For gradual change of environmental conditions, the set of species which can pass environmental filter also changes. As a result,



a sequential change of species composition along the environmental gradient is expected (Laliberté *et al.*, 2014). Besides directly filtering out those species not able to persist, the environmental gradient may also indirectly influence species composition by their effects on biotic interactions. For example, competition ability of a species usually change along the environmental gradient, and a species may be absent in a local community not because of failure to survive in that abiotic environmental condition but because of lower competition ability relative to other coexisting species (Cadotte and Tucker, 2017) (Figure 3a & 3b).

The concept of these filtering mechanisms were proposed to explain species composition of local communities, while they can be linked to the niche concept of species. Hutchinson (1957) described the fundamental niche of a species as a state of abiotic environment which permits that species to exist, and can be viewed as an “n-dimensional hypervolume” of which each dimension represent one environmental variable. However, he also pointed out that a species usually only utilize a subset of its fundamental niche because of biotic interactions, and this subset was called “realized niche”. From this point of view, environmental filter actually filter out those species whose fundamental niche do not encompass the environmental condition of the site, so environmental filter is also called a “niche-based” process (Püttker *et al.*, 2015). The other way around, the distribution range of a species after considering the effects of



environmental filter reflects its fundamental niche, and the distribution range reflects its realized niche after considering the effects of both environmental and biotic interaction filter (Figure 3c).

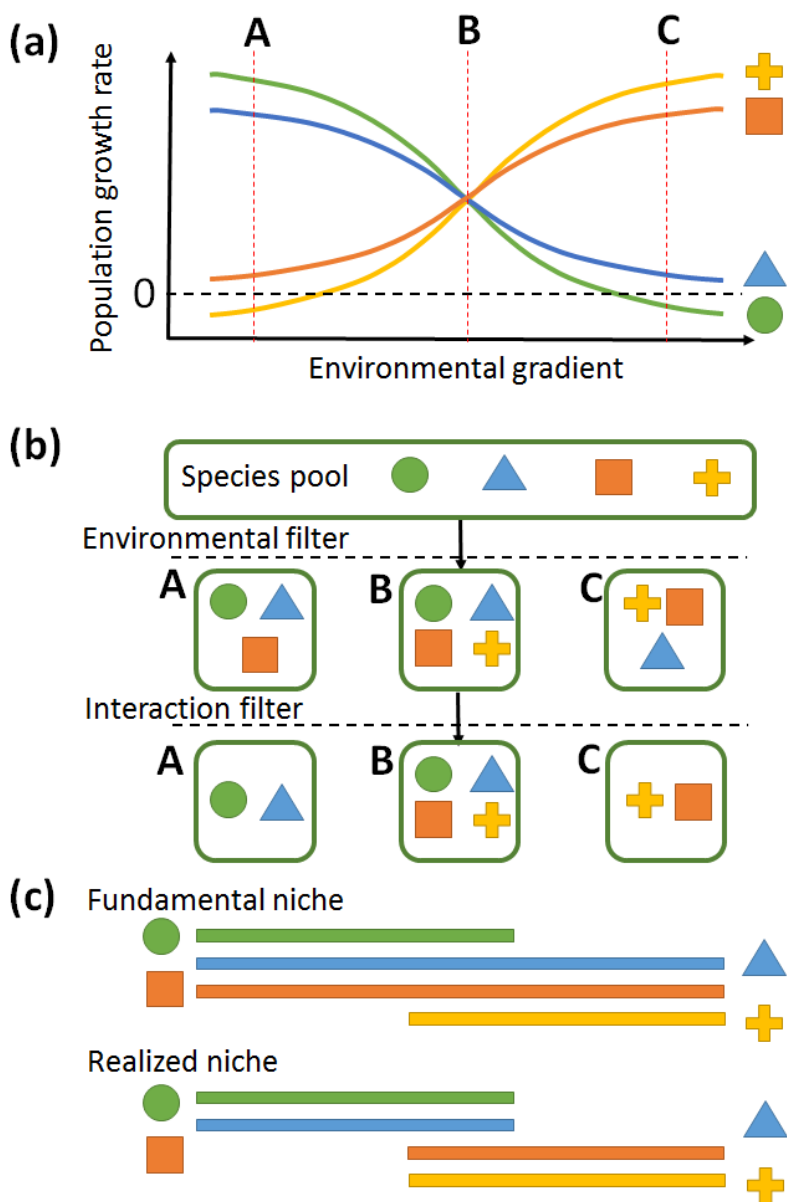
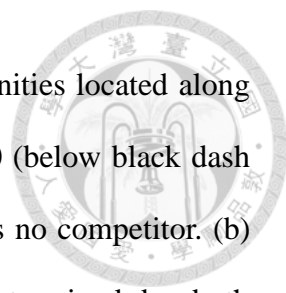


Figure 3. Filtering mechanisms, species composition and the niche concept

(a) Population growth rate of a species can reflect its fitness or competition ability, and usually change along environmental gradients. Four symbols showed in the right



represent four different species. A, B and C represent three communities located along this environmental gradient. If population growth rate is less than 0 (below black dash line), that species cannot persist in that environment even if there is no competitor. (b) Species composition in three communities (A,B and C) are determined by both environmental and interaction filters. The environmental filter excludes those species with population growth rate less than 0 (e.g. yellow cross species in community A), while the interaction filter excludes those species with population growth rate larger than 0 but not large enough to compete with other species (e.g. orange square species in community A). (c) Distribution range of a species after considering environmental filter reflects its fundamental niche, while the range after considering both environmental and interaction filters reflect its realized niche. (partly modified from Cadotte and Tucker, 2017)

As mentioned in previous section, solar radiation, air humidity, temperature fluctuation and wind speed all change along vertical direction in a forest. All of these environmental variables are influential to physiology of plants. For example, net primary productivity of a leaf usually increases with the amount of photosynthetically active radiation (PAR) received until reaching saturation (Ögren and Evans, 1993). Air humidity directly influences vapor pressure deficit between a leaf and the air, and hence has strong effects on transpiration rate (Lambers, 2008). A moderate increase in temperature usually causes an increase in primary productivity (Sage and Kubien, 2007), while usually accompanied by increasing vapor pressure deficit and transpiration rate (Lambers, 2008). Therefore, these vertical environmental gradients are expected to have strong direct or

indirect effects on species composition. A sequential change of species composition along these gradients as well as a differentiation of niches occupied by each species are expected as a result.




Many previous studies have reported that different epiphyte species occupied different height ranges on host trees just as the expectation above, and this phenomenon was called “vertical stratification” (Johansson, 1974; Nieder *et al.*, 2000; Krömer *et al.*, 2007; Zotz, 2007; Parra *et al.*, 2009). However, most of these studies were done in tropical forests, especially in Central and South America. Whether vertical stratification of epiphyte species also exists in subtropical forest in Taiwan is one of the questions that this study was aimed to answer.

4. Effects of vertical environmental gradients on functional traits


Functional traits are measurable attributes of an organism, which strongly influence its performance or fitness (McGill *et al.*, 2006). These attributes may be morphological, physiological, biochemical, phenological or behavioral (Violle *et al.*, 2007). Functional traits usually reflect how organisms respond to environments, that is, their adaptive strategies (Nock *et al.*, 2016).

Analyzing the relationships between functional traits and environmental gradients can be helpful to better understand the mechanisms structuring communities (Ackerly and



Cornwell, 2007; Petter *et al.*, 2016). As mentioned in previous section, environmental gradients may cause a change in species composition by direct or indirect effects. However, competition alone or even stochastic process may also lead to similar patterns even if environmental gradients have no effect on performances of species (Kraft *et al.*, 2015). Hence, it is difficult to infer the influences of environmental gradients simply by observed patterns of species composition. Functional traits, on the other hand, can reveal more information about how organisms respond to environments. Therefore, if a change in species composition is accompanied by strong relationships between functional traits and environmental gradients, it is suggested with more confidence that this change was caused, at least partly, by environmental gradients (Cadotte and Tucker, 2017). Besides, analysis of functional traits can also reveal potential trade-offs when organisms adapt to environments (Wright *et al.*, 2004; Gotsch *et al.*, 2015).

For vascular epiphytes, the ratio of leaf mass to whole plant mass are usually high (Zotz and Asshoff, 2010), so leaf traits received more attention in previous studies (Petter *et al.*, 2016). Several functional leaf traits are suggested to reflect how plants adapt to environments with different levels of solar radiation or moisture, and hence are expected to change along vertical environmental gradients in forests. For example, specific leaf area (SLA), defined as leaf area divided by leaf dry mass, is related to light-capturing efficiency, and tends to be larger in shaded understory environment (Wright *et al.*, 2004).



Leaf thickness (LT), on the other hand, is predicted to be larger in sunnier and drier environments to reduce water loss by transpiration and prevent overheating (Pérez-Harguindeguy *et al.*, 2016). Other leaf traits such as leaf dry matter content, leaf water content (per unit area) and leaf chlorophyll content (per unit area or per unit mass) are also expected to change along vertical environmental gradients (Petter *et al.*, 2016).

If a functional trait of all epiphyte individuals in a site is observed to change along vertical direction, this changing pattern may come from two different mechanisms. The first one is species turnover along vertical gradients, and the other is change in functional trait value along vertical gradients within each species (i.e., intraspecific trait variation) (Cornwell and Ackerly, 2009). These two mechanisms may work alone or work together, and give rise to very similar patterns (Figure 4). In order to determine what mechanism causes observed pattern, a further analysis of intraspecific trait variation is necessary.

Although vertical stratification of epiphytes were frequently reported, few studies have analyzed functional traits of epiphytes (see Cavaleri *et al.*, 2010 and Petter *et al.*, 2016). This study was aimed to analyze the relationships between several leaf functional traits of all epiphytes and vertical environmental gradients, and also tried to figure out whether these relationships exist within each species.

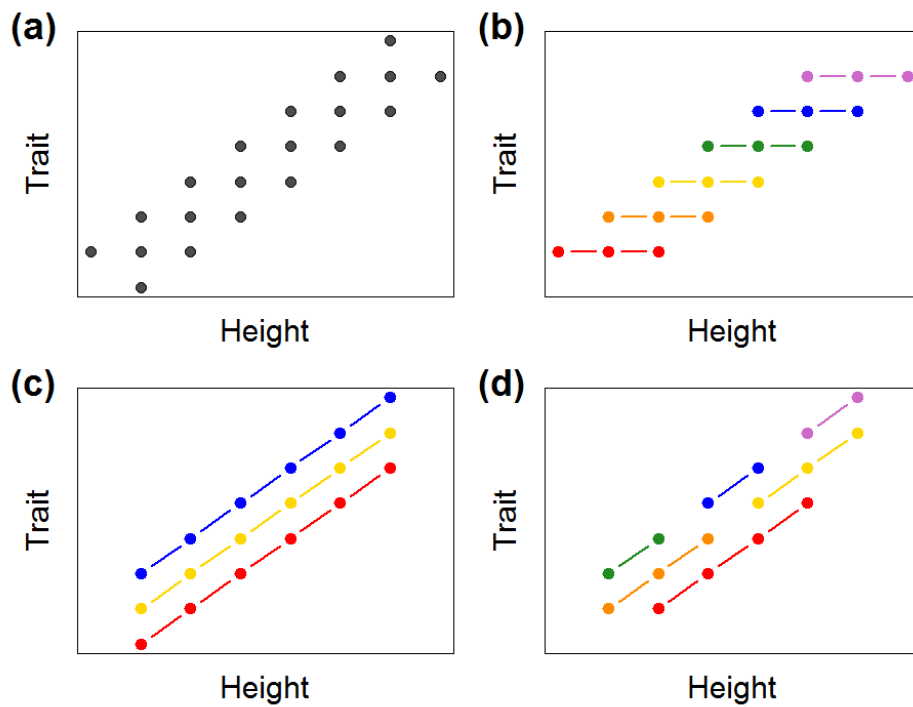


Figure 4. A trait-height relationship and underlying mechanisms

- (a) Trait values of individuals are observed to change with height. (b) This pattern may be caused by species turnover alone. (Each color in the figure represents one species.)
- (c) This pattern may be caused by intraspecific trait variation alone. (d) This pattern may also be caused by both species turnover and intraspecific trait variation.



5. Purposes of this study

From the introduction in previous sections, there are obvious vertical environmental gradients within forests, and these gradients are expected to have effects on both species composition and functional traits of vascular epiphytes. Therefore, this study was aimed to:

- (1) determine whether height is an important factor that influences epiphyte species composition, and identify other significant factors;
- (2) describe the vertical distribution patterns of different epiphyte species in the study area;
- (3) examine the trends of functional leaf traits of all epiphytes with height and other factors;
- (4) determine whether functional leaf traits of individuals of the same epiphyte species change significantly with height.

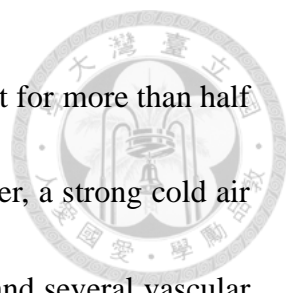


Methods

1. Study site

This study was conducted in Fushan Experimental Forest which is located in northeastern Taiwan, just at the border between New Taipei City and Yilan County (Figure 5). Fushan Experimental Forest belongs to the north part of Snow Mountain Range geographically. The altitude range is from 400 m to 1400 m. It belongs to Northeastern Inland Climate Zone defined by 蘇鴻傑 (1985) or Montane Subtropical Wet-Hot-Summered Climate Zone defined by 梁玉琦 (2004). This type of climate zone is characterized by high precipitation during the whole year, with nearly no dry season. According to weather data collected by two weather stations (Fushan Nursery Weather Station and Hapen Weather Station) located within the study site during 1988 to 2011, the mean annual temperature was about 18.4 °C, and annual precipitation was 3787.3 mm. There were 206 rainy days per year on average, and mean annual relative humidity could be as high as 93.3 %, supporting that this area is rainy and humid all year round (陸象豫及黃惠雪, 2013) and hence providing ideal weather for epiphytes to grow.

The natural vegetation in Fushan Experimental Forest belongs to *Machilus-Castanopsis* belt defined by 蘇鴻傑 (1984) or *Machilus-Castanopsis* type defined by 林建融 (2009). Dominant tree species in this vegetation type include species of Lauraceae, Fagaceae and Theaceae. Based on previous surveys, there are more than 200



species of vascular epiphytes in Fushan Experimental Forest, account for more than half of the vascular epiphyte species in Taiwan (徐嘉君, 2013). However, a strong cold air mass passed through Fushan Experimental Forest in January 2016, and several vascular epiphyte species, especially epiphytic orchids, were killed by cold weather (林建融, personal communication).

Fushan Experimental Forest was divided into three districts—Water Source Reserve, Fushan Botanic Garden and Hapen Nature Reserve from north to south (Figure 5). Most of the sampled trees surveyed in this study were located in Fushan Botanic Garden, while the others were within Water Source Reserve. However, all of them were within the same watershed (Hapen Creek Watershed).

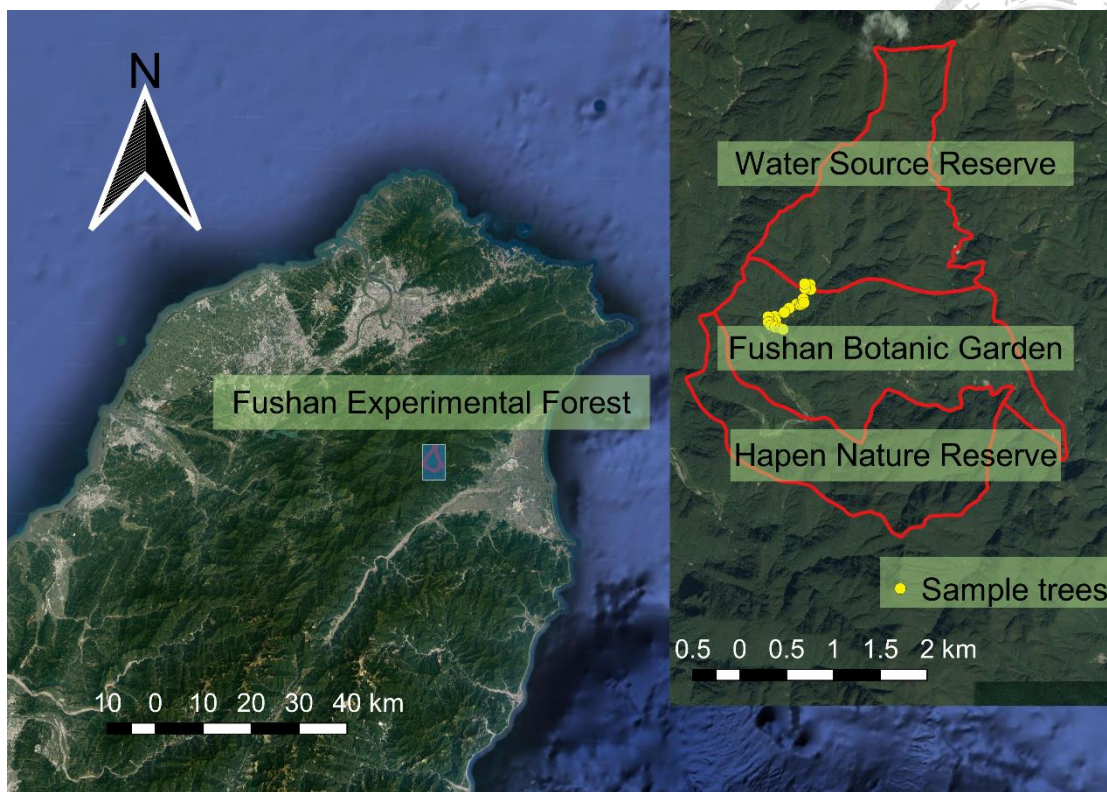


Figure 5. The location of Fushan Experimental Forest

Fushan Experimental Forest was located in northeastern Taiwan, and it was divided into three districts—Water Source Reserve, Fushan Botanic Garden and Hapen Nature Reserve. Most of the sampled trees surveyed in this study were within Fushan Botanic Garden, while the others were within Water Source Reserve. (The background images of this figure were obtained from Google, 2018)



2. Vertical environmental gradients within the study site

As mentioned in the introduction, many environmental variables including are suggested to change along vertical direction. In order to confirm vertical environmental gradients in the study site, I used HOBO MX2301 data loggers (Onset Computer Corporation, Bourne, MA, USA) to measure temperature and relative humidity at different height in the forest.

One erect big tree (sampled tree T010) with closed surrounding canopy was selected to hang the HOBO data loggers. I considered canopy closure because measured data may be biased if the logger is directly exposed to sunlight. Five HOBO data loggers were hung and fixed on the trunk at 1, 3, 5, 7 and 9 m height separately. All of the data loggers were hung at similar aspect of the trunk, with aspect range from 220° to 260° , and they were hung at positions where were seldom directly illuminated by sunlight. I also used a white plastic box to shield each HOBO data logger to prevent strong impact by sunlight, rain or falling debris (Figure 6). From August 22 to September 10 in 2018 (20 days in sum), ambient temperature and relative humidity were measured and recorded every 10 minutes for each HOBO data logger.

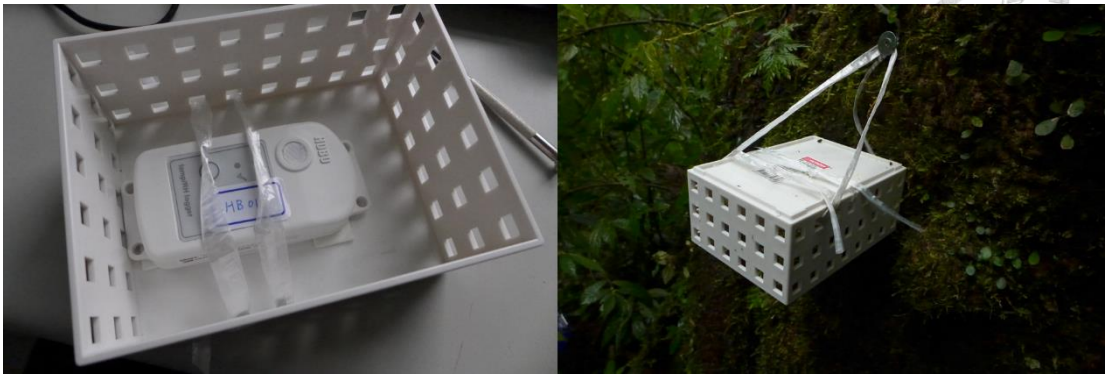


Figure 6. A HOBO data logger hung on the trunk

HOBO MX2301 data loggers were used to measure ambient temperature and relative humidity at different height in this study. The device showed in the left is a HOBO MX2301 data logger. The logger was attached to a white plastic box using double-sided tape and nylon rope, and then was hung on the trunk using screws. The plastic box could protect the logger from direct impact by sunlight, rain or falling debris.

Ambient temperature and relative humidity measurements of the 20 days recording period were averaged and plotted against time of day (Figure 7 and Figure 8). Ambient temperature variation fluctuated widely during the day, lowest around 6 AM and peaked between 12 AM and 1 PM (Figure 7). However, ambient temperature of higher positions was higher than that of lower positions during daytime, especially around noon; but this trend reversed after sunset, temperature of higher positions became lower (Figure 7). This means ambient temperature of higher positions had greater variation within a day, while lower positions had relatively stable ambient temperature. On the other hand, relative humidity showed different patterns (Figure 8). During nights, all positions were quite humid, with relative humidity close to 100%. After sunrise, RH dropped and had obvious

differences between positions. Higher positions were drier than lower ones during daytime.

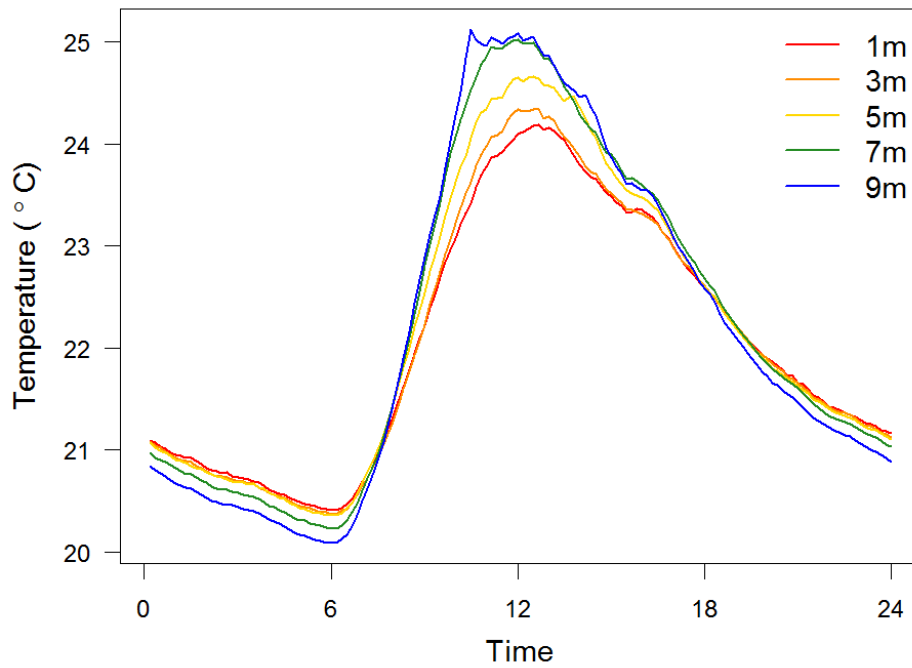
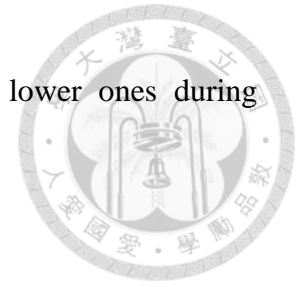


Figure 7. Ambient temperature variations within a day of positions at different heights
Ambient temperature values showed in the figure are mean values of 20 days. Daily ambient temperature variations of higher positions were larger.

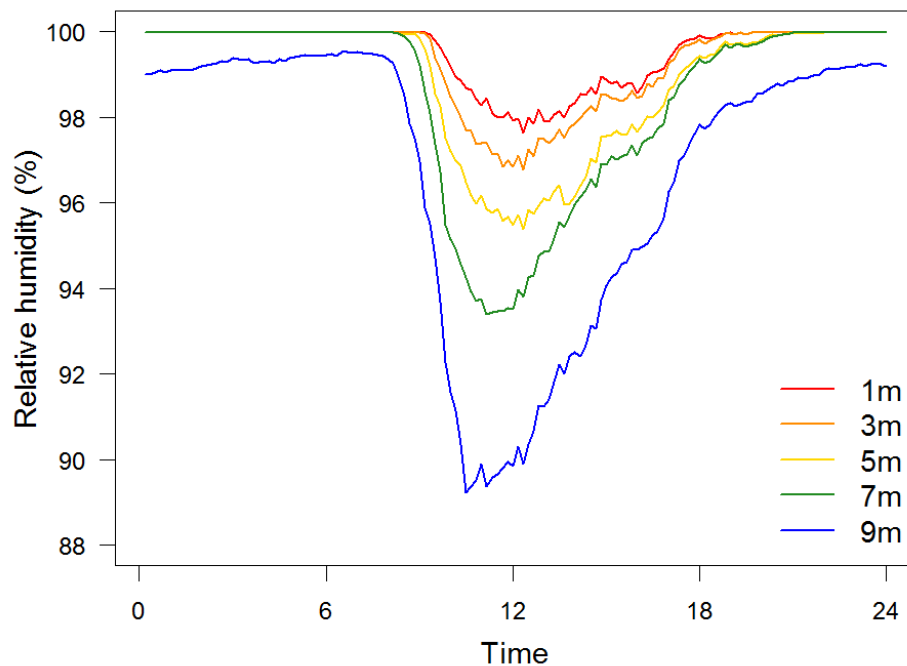
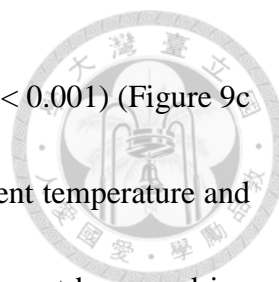


Figure 8. Relative humidity variations within a day of positions at different heights

Relative humidity values showed in the figure are mean values of 20 days. During night, all positions were quite humid, with relative humidity close to 100%, while relative humidity of higher positions became obviously lower during daytime.

Daily mean values and daily standard deviation (SD) of ambient temperature and relative humidity of each position were calculated, and a nonparametric Friedman test was used to test the differences between positions (setting position as an explanatory variable and date as a block factor). There were no large differences between daily mean temperature values of different positions (Figure 9a). Nonetheless, daily SD of temperature increased significantly with height (Friedman test, $p < 0.001$) (Figure 9b). For relative humidity, daily mean values decreased significantly with height (Friedman



test, $p < 0.001$) while the SD increased with height (Friedman test, $p < 0.001$) (Figure 9c & 9d). The results confirm vertical environmental gradients of ambient temperature and relative humidity existed in the study site. Higher on a tree, environment became drier, and fluctuations of both temperature and relative humidity became more dramatic. This pattern is also consistent to previous studies (Richards, 1996; Wagner *et al.*, 2013).

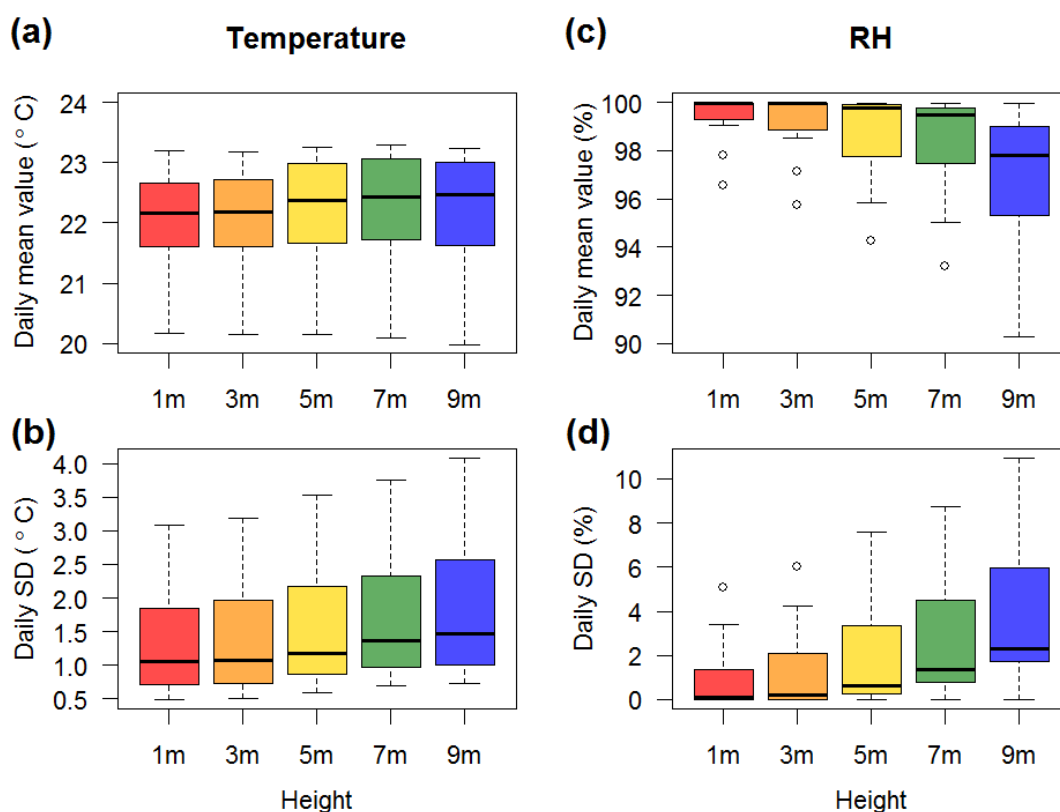
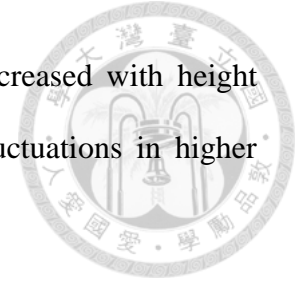


Figure 9. Daily mean values and standard deviation (SD) of ambient temperature and relative humidity (RH) at different heights

The box plots were drawn based on measurements of a 20-day period. (a) Daily mean ambient temperature didn't increase or decrease with height. (b) Daily SD of ambient temperature increased with height (Friedman test, $p < 0.001$), indicating larger temperature fluctuations in higher positions. (c) Daily mean relative humidity decreased with height

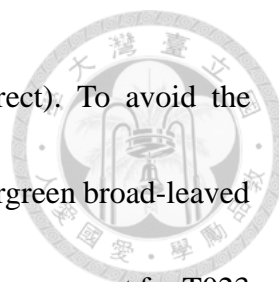
(Friedman test, $p < 0.001$). (d) Daily SD of relative humidity increased with height (Friedman test, $p < 0.001$), indicating larger relative humidity fluctuations in higher positions.



3. Plot survey for recording epiphyte species

Plot survey method was used in this study to investigate species composition at different microenvironments, as well as the distribution pattern of each species. The first step of survey was choosing sampled trees. Afterwards, I divided each sampled tree into different vertical zones, then set one or more plot(s) within each vertical zone. For each plot, I recorded all plant species appearing inside the plot and their abundance.

There were some considerations when choosing sampled trees. This study mainly focused on the effects of different microenvironments within trees, not the effects of large-scale environmental variables such as elevation or topography. Hence, I selected 24 sampled trees in similar environments. All of them were located in Fushan Botanic Garden and Water Source Reserve, and besides Hapen Creek (Figure 10). The geographic positions and altitudes of these sampled trees were similar. The altitudes of all sampled trees ranged from 600 m to 700 m. The sizes and architectures of trees were also under consideration. Only big canopy trees with heights over 14 m and diameters at breast height (DBH) over 50 cm were chosen (except for sampled tree T003). Besides, all the sampled trees did not incline too much. The inclination angles at breast height were all



smaller than 20° (inclination angle is 0° if trunk is absolutely erect). To avoid the influences of some tree attributes that related to tree species, only evergreen broad-leaved tree species were chosen. All of the 24 sampled trees belong to Lauraceae except for T023, which belongs to Fagaceae. The detailed information of all sampled trees is shown in Appendix 1.

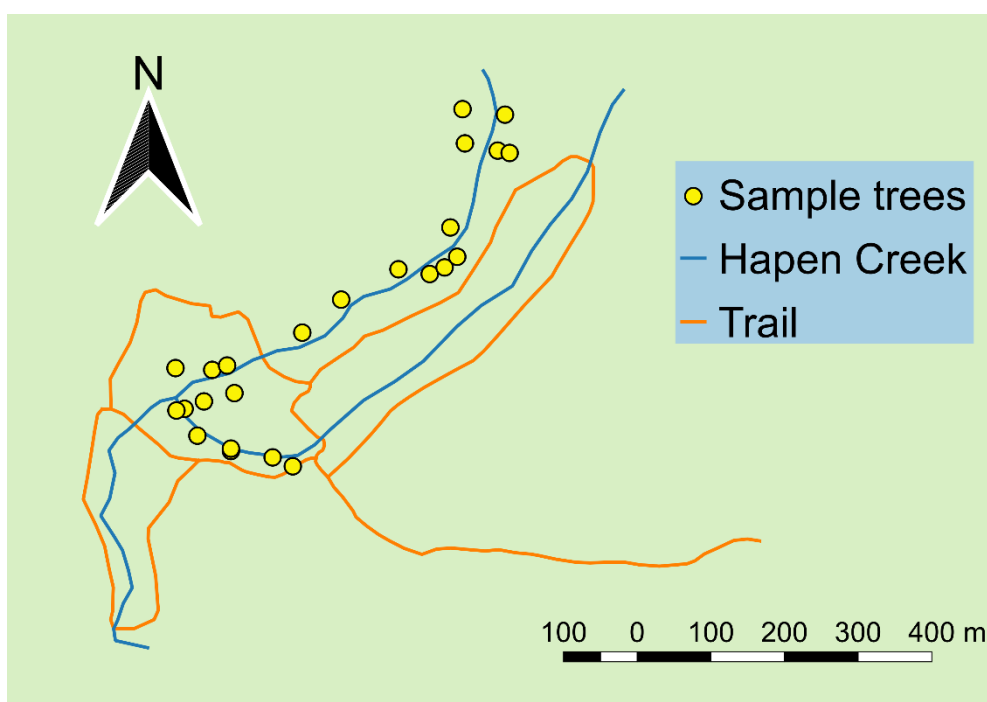
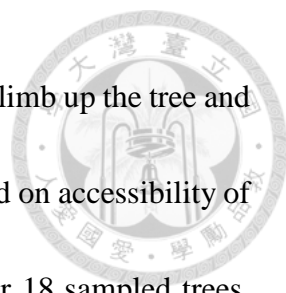


Figure 10. The locations of sampled trees

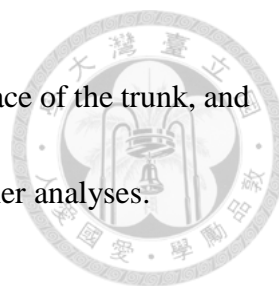
There were 24 sampled trees in total. All of them were located besides Hapen Creek.

Each sampled tree was divided into several vertical zones based on height above ground, and each vertical zone was 2 m high. Therefore, zone 1 was from the ground to 2 m high, zone 2 was from 2 to 4 m high, and so on (Figure 11). For those vertical zones



higher than human height, I used doubled rope technique (DdRT) to climb up the tree and survey. The number of vertical zones that could be surveyed depended on accessibility of sampled trees. Therefore, only five vertical zones were surveyed for 18 sampled trees, and only six sampled trees had six vertical zones surveyed.

Within each vertical zone, one or two plot(s) was set to survey epiphytes species composition. When setting a plot, I chose a position where epiphytes species richness was high and the species composition was as representative as possible for that vertical zone. Each plot was 40×50 cm surface area on trunk or a branch of the sampling tree, and it was further divided into 20 10×10 cm grids. When surveying a plot, all vascular plant species within the plot were recorded as well as the number of grids that each species occupied. The latter was an estimation of species abundance (Figure 12). For all species recorded in the plot, one individual was collected as a voucher which could be used for species identification. Considering accessibility, all of the plots were set on the trunk or erect main branches, not on those branches or twigs growing outward. Some positional variables of each plot were recorded, including the height of plot center, the inclination angle of plot surface, the aspect of the plot relative to the trunk and the diameter of the growing substrate (the trunk or the branch) (Figure 13). The inclination angle was 0° if the plot was absolutely perpendicular to ground surface. The inclination angle was positive if the plot surface inclined toward the sky, and was negative if inclined toward



the ground. The aspect of the plot was 0° if the plot set on the north face of the trunk, and ranged from 0° to 359° . These positional variables were used in further analyses.

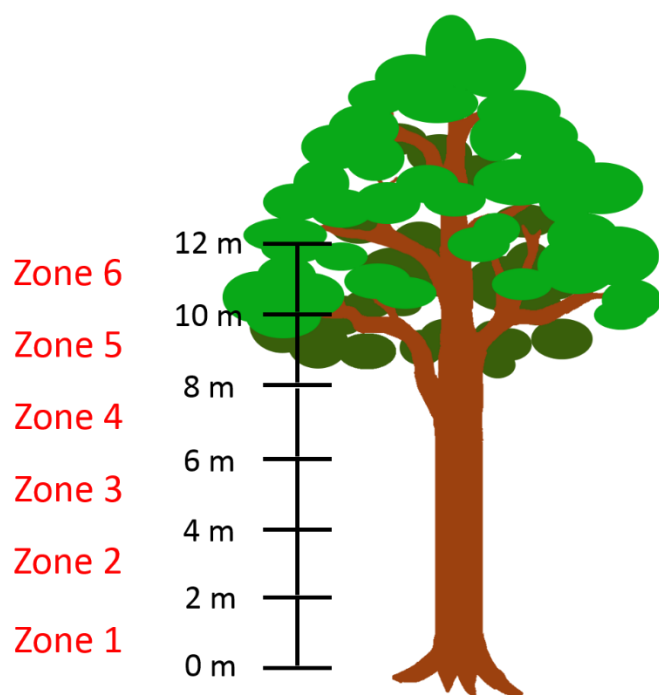


Figure 11. Vertical zones of a sampled tree

Each vertical zone was 2 m high. Five to six vertical zones were surveyed for each sampled tree.

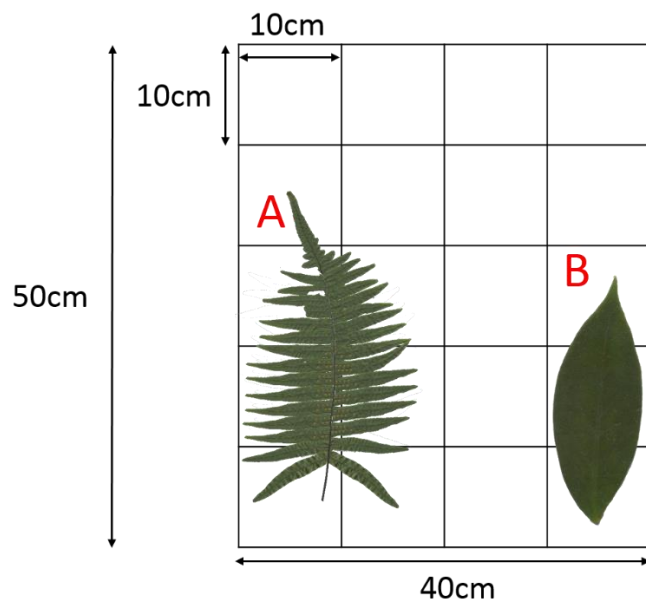


Figure 12. A sampling plot used to survey epiphytes

Each plot was 40×50 cm, and it was divided into 20 grids which was 10×10 cm. All vascular plant species within the plot and the number of grids they occupied were recorded. For the case shown here, it is recorded that species A occupies seven grids and species B occupies three grids.

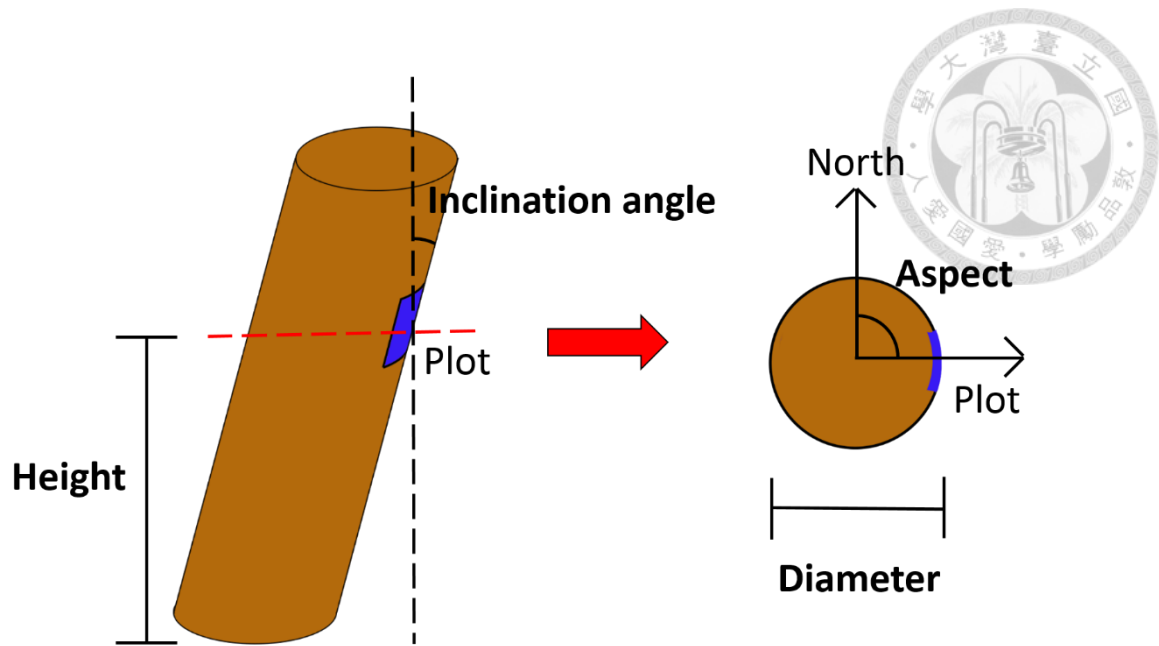
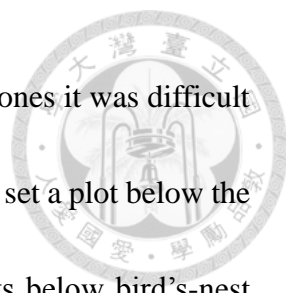


Figure 13. Positional variables recorded for each plot

Four positional variables were recorded for each plot, including height, inclination angle, aspect and diameter of the growing substrate (the trunk or the branch). Height was the distance between plot center and the ground. Inclination angle was the angle difference between plot surface and vertical direction. Inclination angle was 0° if the plot was absolutely perpendicular to the ground. It was positive if the plot inclined toward the sky, while was negative if the plot inclined toward the ground. Aspect was the angle difference between the direction plot facing and the north direction, ranging from 0° to 359° .

There were some large bird's-nest ferns growing on trees in the study area. They actually belonged to two different species, *Asplenium antiquum* and *Asplenium nidus*, but sharing quite similar morphology. These bird's-nest ferns may have some influences on other epiphytes species, and the species compositions of the places below bird's-nest ferns were usually different from other places based on observation. Hence, I avoided setting

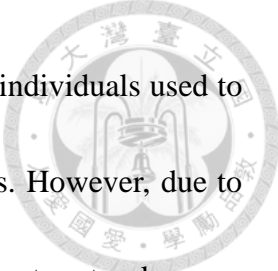


plots below bird's-nest ferns if possible. However, in some vertical zones it was difficult to find a place not influenced by bird's-nest ferns. For that case, I still set a plot below the bird's-nest fern, but a special note was taken. There were nine plots below bird's-nest ferns in total.

All of the plot surveys in this study were done during January to April, 2018. In total, 24 sampled trees and 139 plots on them were surveyed. There were 52 vascular plant species recorded in these plots, and 39 of them were epiphytes. This study used a general definition of epiphytes, which includes true epiphytes, hemiepiphytes and facultative epiphytes, and life forms of recorded species were determined basically based on the epiphyte species list summarized by 徐嘉君 (2007). The information of all recorded species is shown in Appendix 2.

4. Measurements of functional traits

In order to analyze variation of functional traits along micro-environmental gradients, I collected some epiphyte individuals for measurements. There were some criteria when collecting these individuals. First, only mature individuals were collected. Whether an individual was mature or not was judged based on morphology and appearance. For fern species, the existence of reproductive structures (e.g., sori) could be used to judge. The leaves of these individuals should be healthy, not wilted or rolled, and without any spot,



wound, gall or other signs indicating disease or herbivory. All of the individuals used to measure functional traits were collected from those 24 sampled trees. However, due to the limitation of tree-climbing method, small twigs located away from tree trunks were difficult to access. Therefore, only those individuals growing on trunks or vertical main branches were collected. During collecting, dominant species within each vertical zones were collected if its individuals met the criteria of collection mentioned above. To prevent bias in analyses, number of collected individuals of each species was roughly proportional to their relative abundance in each vertical zone. In a way similar to plot surveys, the positional variables of all collected individuals were recorded for further analyses. These variables included height above ground, inclination angle and aspect of the growing surface and diameter of the substrate.

One mature and healthy leaf was chosen from each collected individual to undergo the measuring procedures below:

(1) Measurement of leaf thickness (LT)

Leaves collected from the field may dehydrate to some degree. Hence, I put each leave in a hermetic plastic bag, sprayed some water inside and made the bag close tightly. Then the plastic bag was placed in cool and shaded place for at least 12 hours to make the leaf rehydrate. After rehydration, the leaf thickness of each leaf was measured using a

digital thickness gauge (precision = 0.001 mm) (Digital Micrometers Ltd, Sheffield, UK).

Each leaf was measured four times at different positions, typically at the top left, top right, bottom left and bottom right part separately. Measuring thickness at midrib, primary veins or leaf border was avoided. The thickness values of four positions were averaged to represent the thickness of the whole leaf.

(2) Measurement of chlorophyll content

A SPAD-502 chlorophyll meter (Konica Minolta, Osaka, Japan) was used to measure leaf chlorophyll content. This is a non-destructive method, and the procedure is easier and quicker than leaf extraction approach. Each leaf was measured six times at different positions, typically three times at the left part and other three times at the right part. It was ensured that the sensor of the meter was fully covered by leaf lamina when measuring. Measuring at midrib, veins, spots or sori was avoided. The number read from SPAD-502 chlorophyll meter is called SPAD value. However, SPAD value is a relative index without unit and not easy to interpret from ecological or physiological perspectives. Hence, SPAD values were converted to chlorophyll content per unit area and chlorophyll content per unit mass based on the formula presented by Coste *et al.* (2010).



(3) Scanning the leaf and calculating leaf area

After measuring thickness and SPAD value, the leaf was scanned using a scanner (Epson America, Long Beach, CA, USA). Before scanning, the petiole was cut off. The leaf was expanded and flattened when scanning. A length scale and a note that indicated the ID and species of the leaf was scanned along with the leaf. For those species with small simple leaves, two to three leaves were scanned simultaneously. On the other hand, each leaf was divided into several parts and those parts were scanned separately for those species with large leaves or compound leaves (Figure 14). In this way, overlap or extension outside the range of scanner were prevented. The axes and leaflets (parts with green expanded lamina) of compound leaves were divided and then scanned separately. For those compound leaves difficult to separate all axes and leaflets (e.g., tripinnate leaves), at least the main axis (rachis) and secondary axes were separate from other parts.

The images produced by scanner were then analyzed with Adobe Photoshop CS6 software (Adobe, San Jose, CA, USA). The conversion ratio was first set based on the length scale. After that, the leaf was selected using selection tool, and the area was calculated by image-analyzing tool. For compound leaves, only the leaflets were selected to calculate leaf area. Area of axes were not viewed as part of leaf area in this study.



Figure 14. Leaf-scanning procedures

A length scale and a note indicating ID and species were scanned along with the leaf. Two to three small simple leaves were scanned simultaneously (left), while compound leaves had to be divided into several parts (right). For a compound leaf, at least the main axis and secondary axes were separate from other parts, and these axes were excluded when calculating leaf area.

(4) Measurement of fresh mass

Fresh mass of the leaf was measured using an electronic balance (precision = 0.0001 g) (Ohaus, Parsippany, NJ, USA). It was ensured that the leaf underwent rehydration procedure mentioned above before measuring. For those large leaves or compound leaves which were divided into several parts when scanning, different parts were weighted separately and their fresh mass were summed up to compute total leaf fresh mass. To be

consistent with leaf area, only the leaflets were used to compute total fresh mass for compound leaves.



(5) Measurement of dry mass

After measuring fresh mass, the leaf was wrapped with a paper envelope and put into oven, then was toasted at 70°C for 72 hours (Pérez-Harguindeguy *et al.*, 2016), and the dry mass was measured afterwards. Once taken out from the oven, the dried leaf would quickly absorb water from the air, so it was put into a hermetic plastic bag as soon as possible before weighting. The leaf was put into a paper envelope again and kept in safe place afterwards so that it could be examined if necessary.

After undergoing all the procedures above, the leaf thickness, SPAD value, leaf area, fresh mass and dry mass were determined for each leaf. These values were further used to calculate other important functional traits. The calculation formulas of different traits are listed below. Six functional traits were used in data analyses (listed in Table 1).

$$\text{Specific leaf area (SLA)} = \text{Leaf area} / \text{Leaf dry mass}$$

$$\text{Leaf dry matter content (LDMC)} = \text{Leaf dry mass} / \text{Leaf fresh mass}$$



Leaf water content per unit area (LWC_area)

$$= (\text{Leaf fresh mass} - \text{Leaf dry mass}) / \text{Leaf area}$$

Chlorophyll content per unit area (Chl_area)

$$= (117.1 \times \text{SPAD value}) / (148.84 - \text{SPAD value})$$

(Coste *et al.*, 2010)

Chlorophyll content per unit mass (Chl_mass)

$$= \text{Chl_area} \times \text{SLA}$$

Table 1. Six functional traits used in data analyses

Functional traits	Abbreviation	Unit
Leaf thickness	LT	mm
Specific leaf area	SLA	cm ² /g
Leaf dry matter content	LDMC	g/g
Leaf water content (per unit area)	LWC_area	g/m ²
Chlorophyll content (per unit area)	Chl_area	µg/cm ²
Chlorophyll content (per unit mass)	Chl_mass	mg/g



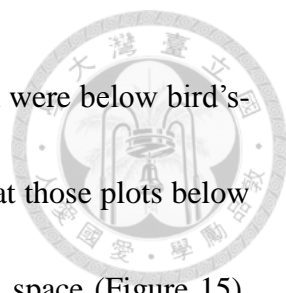
5. Data analyses

(1) Variation of species composition

Ordination methods were used to analyze variation of species composition.

Ordination is a kind of multivariate analysis. There are two types of ordination—unconstrained ordination and constrained ordination. In this study, unconstrained ordination was first used to show the differences between species composition of plots, as well as the differences between distribution patterns of species. Then constrained ordination was used to find out those factors that could explain significant proportion of species composition variations of plots.

There are several different ordination methods which can be used in different situations. For example, principal component analysis (PCA) is a linear method, and it is suitable to analyze data whose plots are located in homogeneous environment. In contrast, correspondence analysis (CA) and detrended correspondence analysis (DCA) are unimodal methods, more proper to analyze data with highly heterogeneous plots. Lepš and Šmilauer (2003) suggested that a DCA can be done in advance to decide which method is more suitable. If the length of first DCA axis is shorter than 3 SD, a linear method is suggested. In contrast, if the length of first DCA axis is longer than 4 SD, a unimodal method would be more proper.



There were 139 plots surveyed in this study, while nine of them were below bird's-nest ferns. I conducted a DCA to analyze all 139 plots, and found that those plots below bird's-nest ferns located away from most of the other plots in DCA space (Figure 15). This result suggests that there were differences in species composition between plots below and not below bird's-nest ferns. Some epiphytes species, such as *Vittaria zosterifolia*, *Asplenium neolaserpitiifolium* and *Ophioglossum pendulum*, were observed to prefer to grow below bird's-nest ferns. These species were located close to those plots below bird's-nest ferns in DCA space (Figure 15). Some previous studies also indicated that bird's-nest ferns may have some positive effects on other epiphytes (簡珮瑜, 2011). Therefore, only those plots that are not below bird's-nest ferns were used in further analyses.

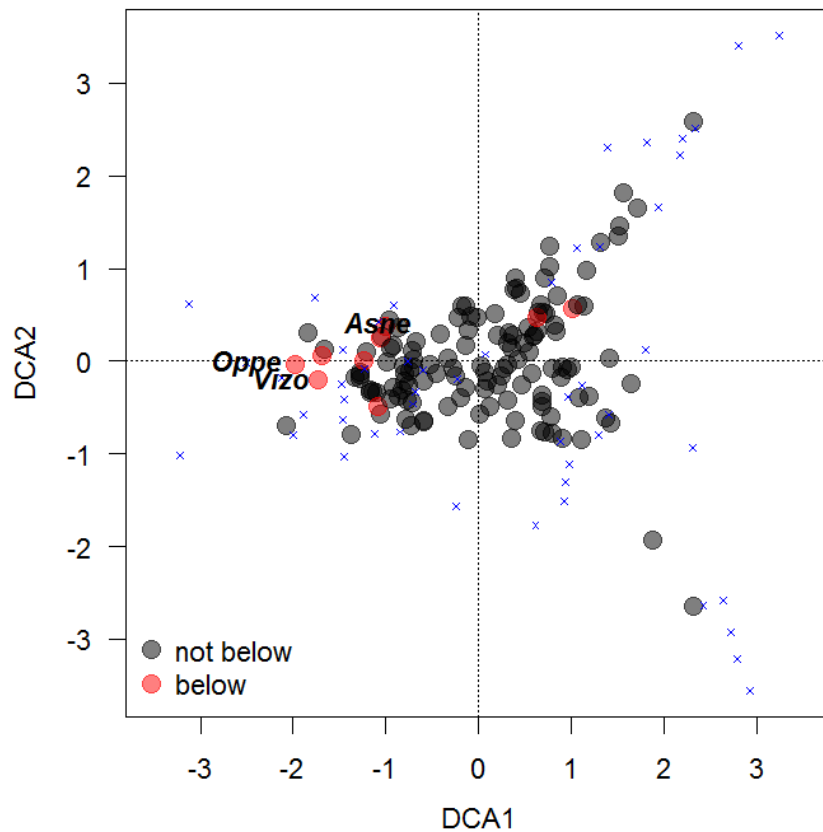


Figure 15. Plots below and not below bird's-nest ferns in DCA space

Red dots represent plots below bird's-nest ferns, while black dots represent the others. Most of red dots are located near the left end of first DCA axis, away from most of black dots. This indicates differences between species composition of these two types of plots. Three species that preferred to grow below bird's-nest ferns are labeled with text, including *Asne* (*Asplenium neolaserpitiifolium*), *Vizo* (*Vittaria zosterifolia*) and *Oppe* (*Ophioglossum pendulum*). Other species are only shown as blue crosses.

After excluding those plots below bird's-nest ferns, there were 130 plots remained.

The number of plots from zone 1 to zone 5 was similar, while number of plots in zone 6 was much less than others (Figure 16). This was due to limitation of the survey method.



For most of the sampled trees, it was difficult to climb up to zone 6. I conducted a DCA on species abundance data of these 130 plots (abundance was transformed using natural logarithm in advance). The length of first DCA axis was 4.85 SD, so unimodal methods (CA or DCA) were suggested. I finally chose DCA, not CA, to analyze and present data because the result of CA showed strong artefacts. Besides, these plots were set basically along one environmental gradients (height above ground), and this type of data was suitable for DCA.

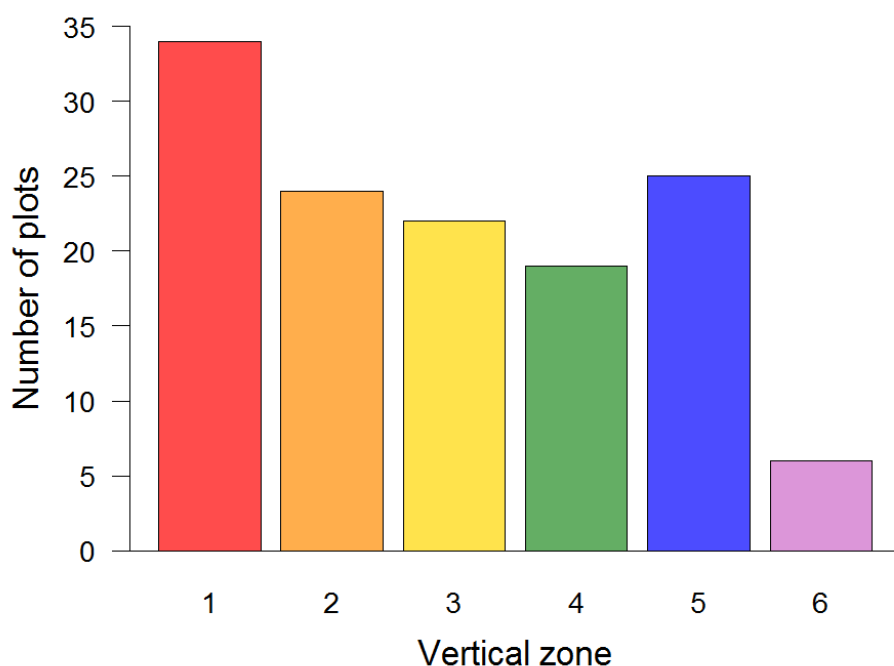

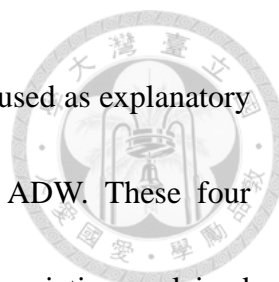


Figure 16. Number of plots in different vertical zones

Number of plots in zone 1 is more than the others due to high accessibility. There were not large differences from zone 2 to zone 5. Number of plots was the least in zone 6 because it was difficult to climb up.



After using DCA to quantify and visualize the variation of species composition, it was tested whether some positional variables could explain the variation using a constrained ordination method—canonical correspondence analysis (CCA). As mentioned in previous part, positional variables including height, inclination angle, aspect and diameter of the substrate were recorded for each plot. However, there would be some problems if these variables were directly used to explain variations of species composition. Aspect, for example, was a value ranging from 0° to 359°, but the meaning of this value was difficult to interpret. Therefore, aspect was converted to two more meaningful variables—angle difference for sunlight and angle difference for water. Angle difference for sunlight (ADS) is the angle difference between the aspect of the plot and the south direction (180°), ranging from 0° to 180° (Figure 17). Because the study site was located north of Tropic of Cancer, the south face of the trunk received most sunlight. Hence, ADS could indicate how much sunlight the plot received. The larger its value, the less sunlight received by the plot. Angle difference for water (ADW) is the angle difference between the aspect of the plot and the aspect facing nearest water source (Figure 17). This value could indicate the amount of moisture the plot received to some degree. Besides, there was a strong negative correlation between height above ground and diameter of the substrate (Pearson correlation coefficient (r) = -0.68, $p < 0.001$) (Figure 18). Therefore, diameter of the substrate was excluded in further analyses to avoid strong collinearity



among explanatory variables. Finally, four positional variables were used as explanatory variables in CCA, including height, inclination angle, ADS and ADW. These four variables were first used in CCA separately to calculate proportion of variation explained and test the significance. Then a forward selection using permutation test was conducted to determine the optimal CCA model. All the ordination analyses were conducted using R 3.5.0 (R Core Team, 2018) and the *vegan* (v2.5-2.; Oksanen *et al.*, 2018) package.

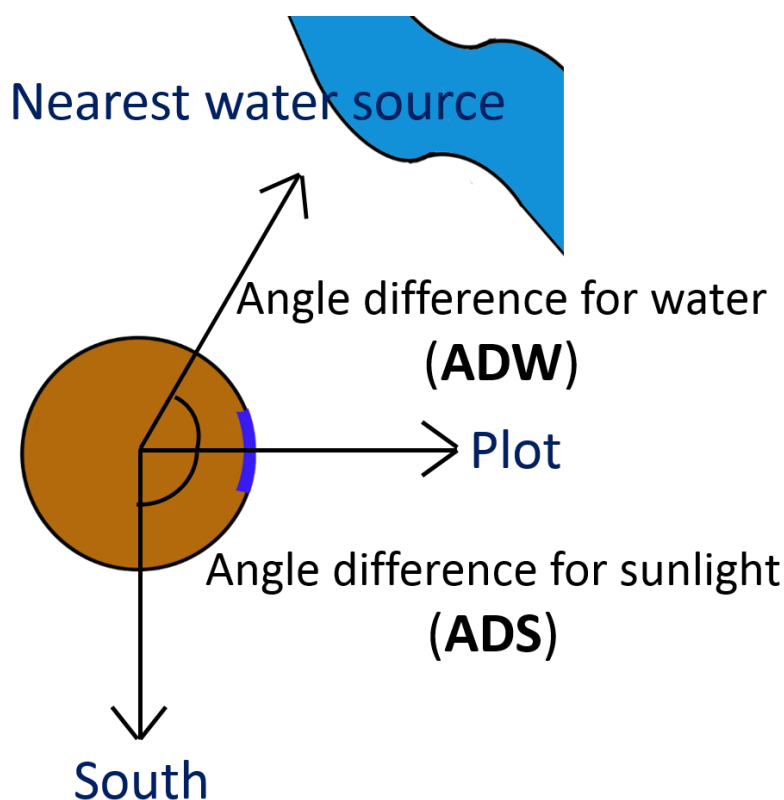


Figure 17. Definition of two positional variables calculated from aspect

Angle difference for sunlight (ADS) is the angle difference between the aspect of the plot and the south direction. ADS could indicate the amount of sunlight that the plot received. On the other hand, angle difference for water (ADW) is the angle difference between the aspect of the plot and the aspect facing nearest water source, which could reflect the

amount of moisture around the plot. These two variables were used in further analyses instead of aspect.

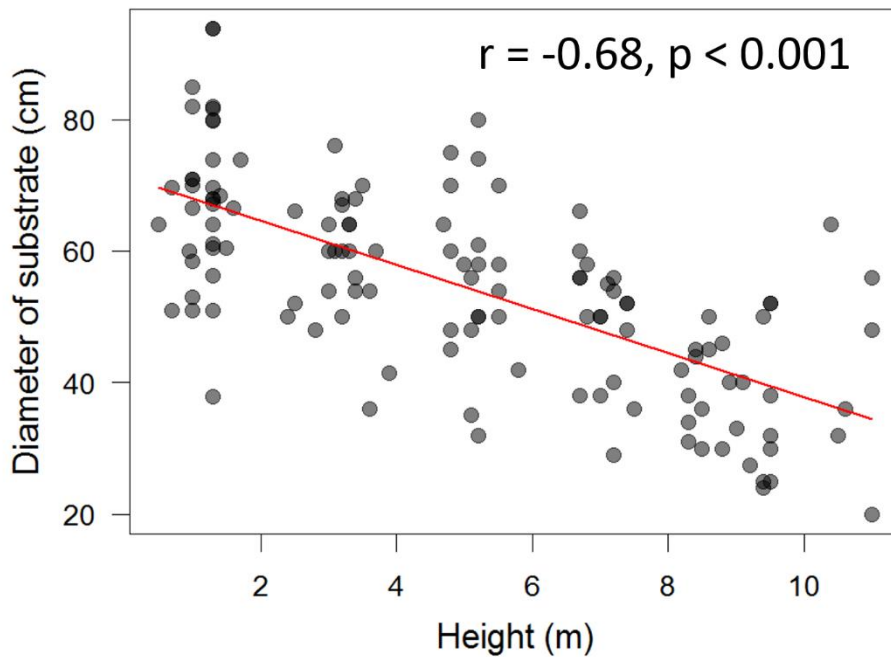


Figure 18. Negative correlation between height and diameter of substrate

The Pearson correlation coefficient of height and diameter of the substrate was -0.68 ($p < 0.001$), indicating strong negative correlation. The red line shown in the figure was the regression line based on a simple linear model.

(2) Distribution patterns of different species

There were 52 plant species in total recorded during plot survey. This study mainly focused on epiphytes, so only those species belonging to epiphytes (39 species) in a general definition were considered when describing distribution patterns. Besides, some epiphyte species were quite rare, only recorded in few plots. There was no sufficient

information to describe the distribution patterns of these rare species. Hence, I defined those epiphyte species that recorded in five or more plots as “abundant epiphyte species” and only the distribution patterns of these abundant epiphyte species were described.

Based on the definition above, there were 23 abundant epiphyte species in this study.

Most of them (19 species) were true epiphytes, while there were three secondary hemiepiphyte species and one facultative epiphyte species (Figure 19a). Eleven species were pteridophytes (ferns and fern allies), including species in Polypodiaceae, Vittariaceae, Aspleniaceae and others. Seven species were eudicots, including species in Gesneriaceae, Apocynaceae and others. Besides, there were three species belonging to monocots (Orchidaceae and Araceae) and two species belonging to basal angiosperms (Piperaceae) (Figure 19b). More details about the information of recorded species are shown in Appendix 2 and Appendix 3.

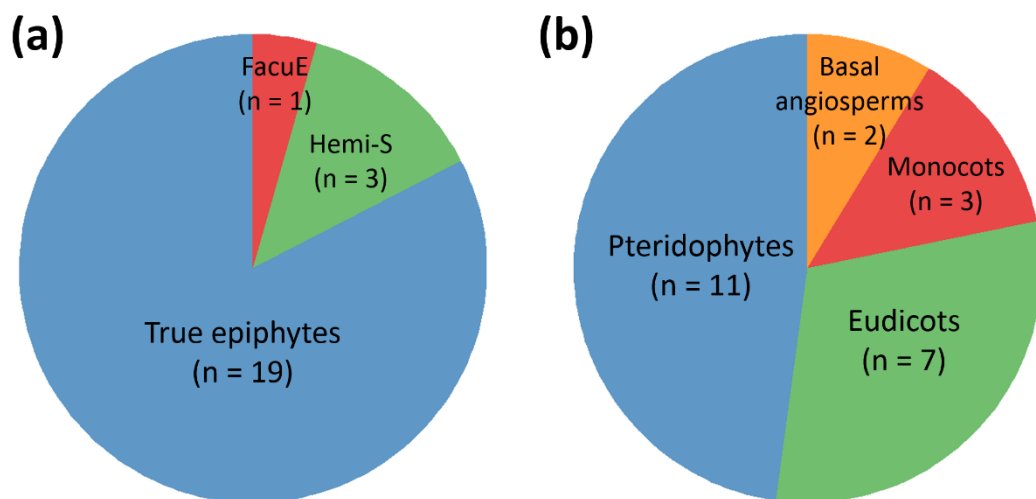


Figure 19. Epiphytic types and taxonomy groups of abundant epiphyte species

(a) There were 23 abundant epiphyte species which were recorded in five or more plots. Most of them (19 species) were true epiphytes, while three species were secondary hemiepiphytes (Hemi-S) and one species was facultative epiphyte (FacuE). (b) Eleven species were pteridophytes (ferns and fern allies), seven species were eudicots, three species were monocots and two species belonged to basal angiosperms.

Height above ground was assumed as an important variable that shape species distributions, so I first tried to describe the distribution patterns associated with height (i.e., vertical distribution patterns). A box plot was drawn to show the height distribution of each abundant epiphyte species, and this could help to judge whether vertical stratification existed. Then I calculated the Φ (phi) coefficient of each abundant epiphyte species in each vertical zone. Φ coefficient is an index that can reflect the fidelity of a species to a group of plots, and it is calculated from the formula below.



Setting

a = the number of plots **within** the group and **containing** the species

b = the number of plots **out of** the group and **containing** the species

c = the number of plots **within** the group and **not containing** the species

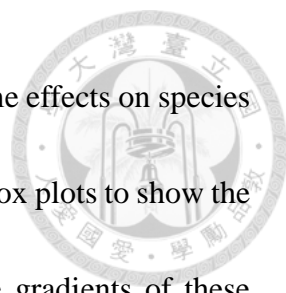
d = the number of plots **out of** the group and **not containing** the species

Then,

$$\Phi = \frac{(ad - bc)}{\sqrt{(a + b)(c + d)(a + c)(b + d)}}$$

(Tichý and Chytrý, 2006)

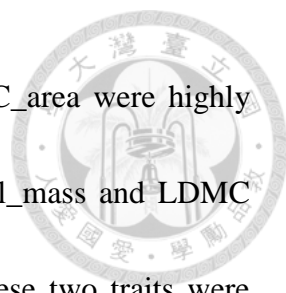
Φ coefficient ranges from -1 to 1. The higher the value is, the higher fidelity a species shows to that group of plots, and the significance of Φ coefficient can be test by Fisher's exact test. In this study, I viewed those species with a Φ coefficient which was significant and higher than 0.2 to a vertical zone as a representative species of that zone. A synoptic table was made to show those representative species of each vertical zone. Furthermore, I also calculated the relative frequency, which is the proportion of plots containing the species in a certain vertical zone, of each abundant epiphyte species in each zone. Φ coefficients and relative frequency were calculated using JUICE software (v7.0.102; Tichý, 2002). Bar plots were made to show the differences of relative frequency between vertical zones for some species, which could tell more information about the distribution patterns.



For other positional variables which were suggested to have some effects on species distribution based on the result of CCA in previous part, I also drew box plots to show the range each abundant epiphyte species was distributed in along the gradients of these variables.

(3) Variation of functional traits of all epiphytes

Before analyzing the effects of height and other positional variables on functional traits of epiphytes, something should be considered. First, the six functional traits measured in this study (including LT, SLA, LDMC, LWC_area, Chl_area and Chl_mass) may be correlated with each other. The relationships between them should be analyzed in advance in order to better interpret the relationships between traits and positional variables. Second, species using different strategies may have different functional trait syndromes (combination of six functional traits), and may be improper to analyze together. For example, functional traits may differ between simple-leaved species and compound-leaved species, and the effect of leaf type may shade the effects of positional variables on traits. Therefore, I calculated mean values of each functional trait for those epiphyte species having three or more measured individuals (25 species in total), and then conducted a PCA on species-trait data (trait values were standardized in advance). This could show not only the relationships between traits but also the difference of trait



syndromes between species. The result indicates that LT and LWC_area were highly positive correlated, while they were negatively correlated with Chl_mass and LDMC (Figure 20). SLA was negatively correlated with Chl_area, but these two traits were almost independent to other four traits. Besides, it seems that chlorophyll content calculated based on area (Chl_area) or based on mass (Chl_mass) had different meaning in an ecological perspective, because they were nearly independent to each other on PCA space. Moreover, the result of PCA also indicates that trait syndrome of simple-leaved species and compound-leaved species were rather different (Figure 20). Compound-leaved species usually had leaves with higher SLA and Chl_mass but lower LT and LWC_area compared to simple-leaved species. This difference were considered in further analyses.

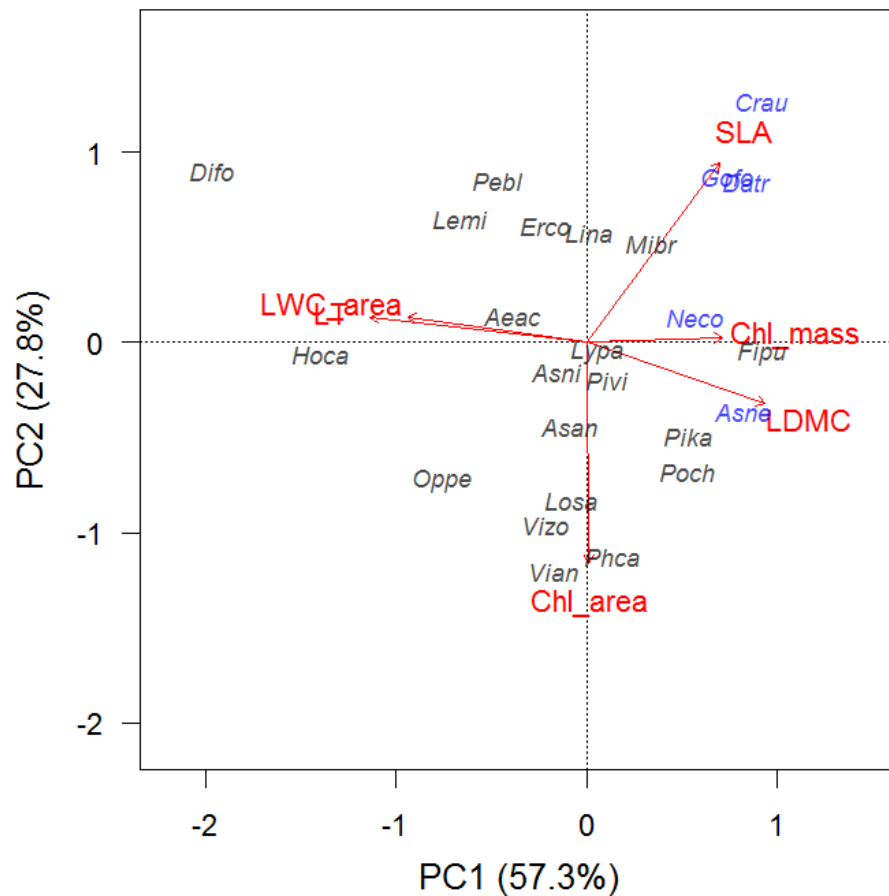
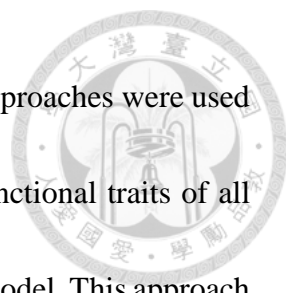
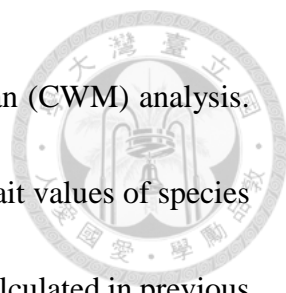


Figure 20. Result of the PCA on mean trait values of 25 epiphyte species

Functional traits were labeled with red text and their directions were shown using arrows. Leaf thickness (LT) and leaf water content per unit area (LWC_area) were highly positively correlated, while they were negatively correlated with leaf dry matter content (LDMC) and chlorophyll content per unit mass (Chl_mass). Specific leaf area (SLA) was negatively correlated with chlorophyll content per unit area (Chl_area), but these two were almost independent to the others. The differences between trait syndromes (combination of six traits) of species are also shown in this figure. Trait syndromes of compound-leaved species (labeled with blue text) are rather different from those of simple-leaved species (labeled with grey text). Complete scientific names of all the species abbreviations are listed in Appendix 2.

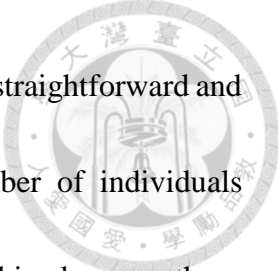


After analyzing the relationships between traits, two different approaches were used to analyze the effects of height and other positional variables on functional traits of all epiphytes in the study site. The first one was individual-based linear model. This approach directly used the individual-based data. Functional trait values (including LT, SLA, LDMC, LWC_area, Chl_area and Chl_mass) of all individuals were response variables, while positional variables were explanatory variables (Figure 21a). Trait values were transformed using square root or natural logarithm in advance to make their distribution meet the assumptions of linear model. The positional variables used in linear model were the same as those used in CCA, including height, inclination angle, angle difference for sunlight (ADS) and angle difference for water (ADW). A forward selection procedure using partial F-test was conducted to find optimal linear model for each functional trait and determine what explanatory variables had significant influences. To include some marginal significant results, the threshold of p-value was set as 0.1 when conducting forward selection. As mentioned in previous paragraph, trait syndromes of simple-leaved species and compound-leaved species were rather different, so these two types of species were analyzed separately. For simple-leaved species, there were 221 individuals belonging to 28 species analyzed, while there were 68 individuals belonging to 7 species with compound leaves.



The second approach was plot-based community weighted mean (CWM) analysis. Species abundance of plots, positional variables of plots and mean trait values of species were all needed in this approach. Mean trait values of species were calculated in previous work when analyzing relationships between traits, but in this approach only the mean trait values of simple-leaved species were used (20 species in total). Afterwards, community weighted mean (CWM) trait values was calculated for each plot by averaging the mean trait values of each species within the plot and using species abundance (transformed with natural logarithm in advance) as weights. Then the relationships between CWM trait values and positional variables of plots were examined using linear model and the significance was tested using p_{\max} permutation test (Dray and Legendre, 2008; ter Braak *et al.*, 2012) (Figure 21b). This testing method actually included two permutation tests. One permutes the rows (plots) of plot-species abundance matrix (number of permutations = 999), calculation the p-value of F-test, that was the proportion of F statistics from permutations larger than F statistics from real data, and the other permutes the columns (species) and then also calculated p-value. The larger p-value of this two permutation tests (p_{\max}) is a reliable index to test the relationships between functional traits and positional variables and determine the significance.

Both of these two approaches were used to analyze the effects of height and other positional variables on functional traits. I conducted both of them because they both have



some advantages and disadvantages. Individual-based linear model is straightforward and easy to understand, while the result largely depends on the number of individuals measured for each species and for each vertical zone, and may be bias because those individuals were not collected in a completely random way. Plot-based CWM analysis suffers less from sampling bias, while intraspecific trait variations are not considered because it uses mean trait values of each species. In addition, the number of species that can be used in CWM analysis is fewer (only 20 species). As a result, I conducted both approaches and compared their results to make conclusions. All the statistical analyses in these two approaches were done using R 3.5.0 (R Core Team, 2018) and the *weimea* (v0.1.10; Zelený, 2018) package.

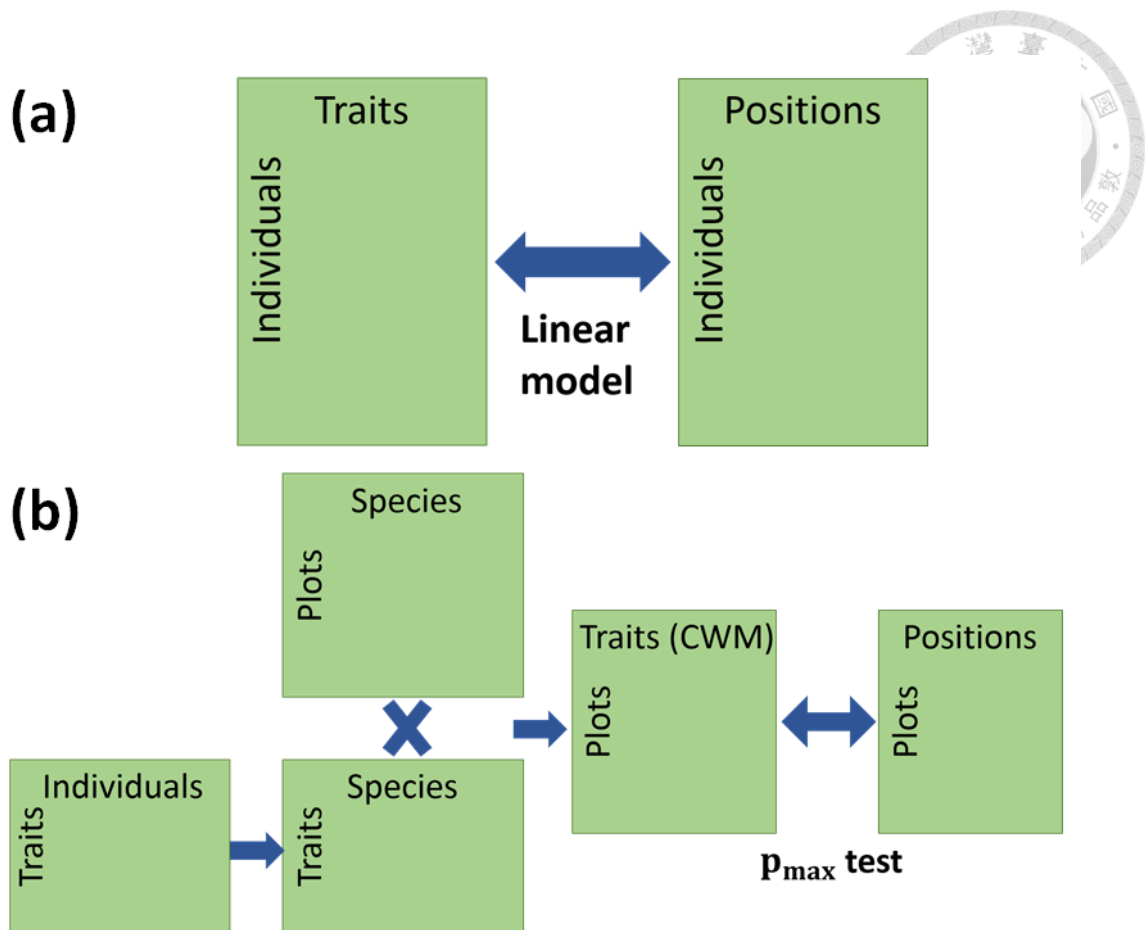
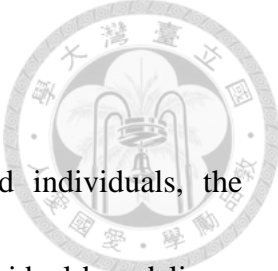


Figure 21. Two approaches used to analyze relationships between functional traits and positional variables

(a) First approach was individual-based linear model, which directly linked functional traits and positional variables by individual-based data. (b) Second approach was plot-based community weighted mean (CWM) analysis. Trait values of individuals were first used to calculate mean trait values of species, and then mean trait values of different species were averaged using species abundance as weights to calculate CWM trait values for each plot. Finally, CWM trait values of plots were linked to positional variables of plots using linear model and the significance was tested by p_{\max} permutation test.

(4) Variation of functional traits within species



For those epiphyte species that have 20 or more measured individuals, the intraspecific variation of functional traits was analyzed using individual-based linear model. There were four species with sufficient number of measured individuals, including *Lemmaphyllum microphyllum* (n = 35), *Goniophlebium formosanum* (n = 31), *Hoya carnososa* (n = 23) and *Aeschynanthus acuminatus* (n = 22). Same as the procedure mentioned in previous section, six functional traits were first transformed if necessary and then were used as response variables in linear model using R 3.5.0 (R Core Team, 2018). However, with such a small sample size, it is not proper to use multiple explanatory variables. Hence, only height was used as an explanatory variable. It is difficult to use this analysis to make strong conclusions, while the result may still tell some information.



Results

1. Variation in species composition

Species composition of the 130 plots not below bird's-nest ferns varied between vertical zones based on the result of DCA (Figure 22). The plots within the same zone were closer to each other than to plots in different zones. Besides, plots in zone 1 to zone 6 were roughly distributed from right to left along first DCA axis. This indicates that species composition of plots within the same vertical zone was more similar, and species composition changed gradually from lower zones to higher ones.

Those species located near the left end of DCA space, including *Pyrrosia lingua* (*Pyli*), *Pholidota cantonensis* (*Phca*) and *Davallia trichomanoides* (*Datr*), preferred growing on higher places (Figure 23). On the other hand, species preferring growing on lower places were close to the right end of DCA space, including *Crepidomanes auriculatum* (*Crau*) and *Abrodictyum obscurum* (*Abob*) (Figure 23).

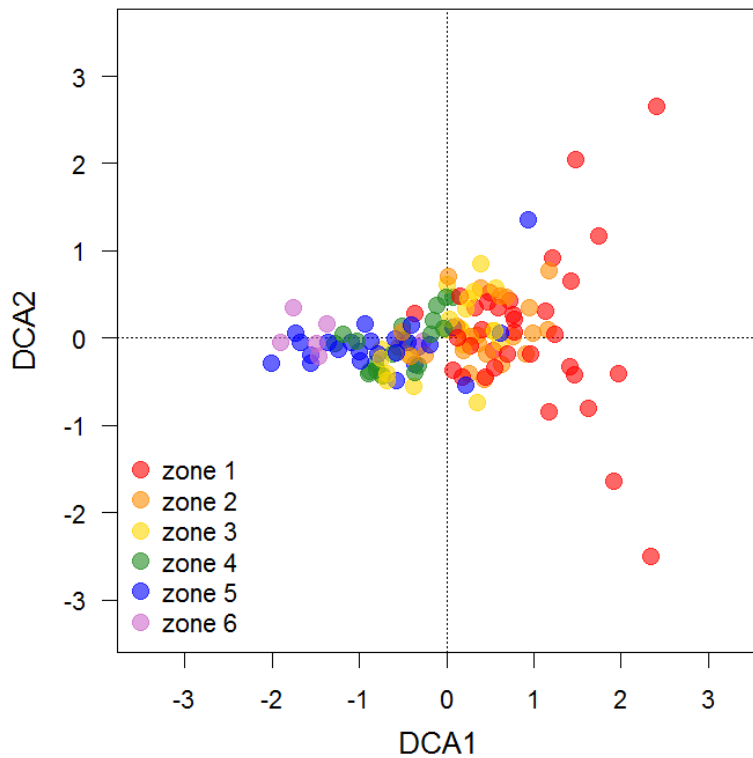


Figure 22. DCA analysis on plots not below bird's-nest ferns (showing plots)

Dots with six different colors represent plots located in different vertical zones. Plots in the same zone were close to each other, while the distances between plots in different zones were greater. Besides, plots in zone 1 to plots in zone 6 were roughly distributed from right to left along first DCA axis, indicating that species composition changed gradually from lower zones to higher ones.

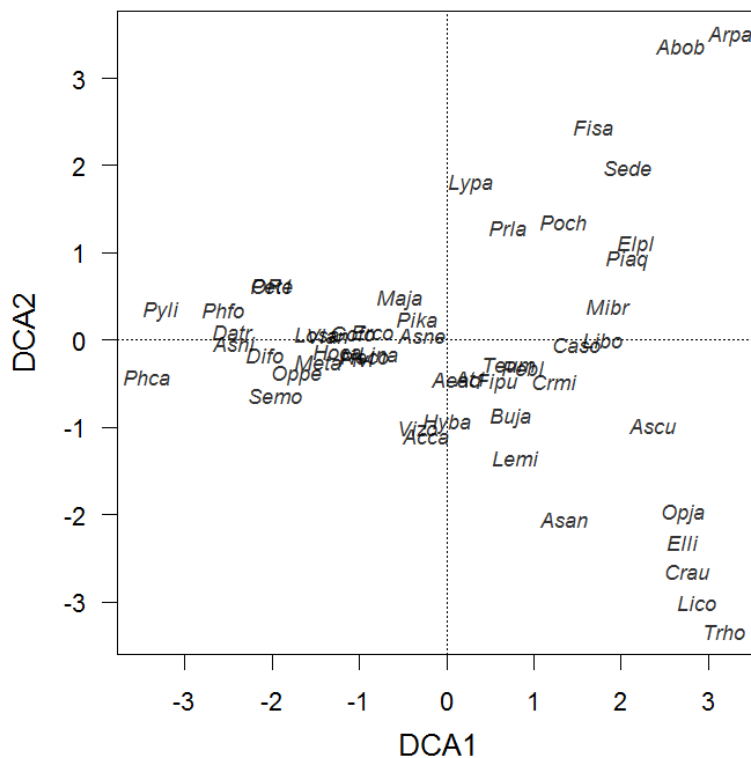


Figure 23. DCA analysis on plots not below bird's-nest ferns (showing species)
 Species located close to the left end of first DCA axis were those species preferred growing in higher zones. In contrast, species located in the right preferred growing in lower zones. The complete scientific names of these species abbreviations are shown in Appendix 2.

Four positional variables were used in CCA separately to calculate proportion of variation they can explain alone. The results are shown in Table 2. Height explained most variation of species composition (3.99%), and result of permutation test was significant ($p < 0.001$). Angle difference for sunlight (ADS) and angle difference for water (ADW) also explained significant variation if tested alone ($p = 0.015$ & 0.023).

Table 2. Positional variables and the proportion of variation they explained alone in CCA

Positional variables	Proportion of variation explained	p-value of permutation test
Height	3.99%	< 0.001***
ADS	1.17%	0.015*
ADW	1.09%	0.023*
Inclination angle	0.85%	0.277

When conducting forward selection, height was included into model first and followed by ADS, while ADW and inclination angle were not included. Hence, there were 2 variables, height and ADS, in the optimal CCA model and they explained 5.15% of variation together ($p < 0.001$) (Figure 24). Height was basically along first CCA axis, and ADS was along second CCA axis, indicating that the effects of height and ADS were nearly independent (Figure 24).

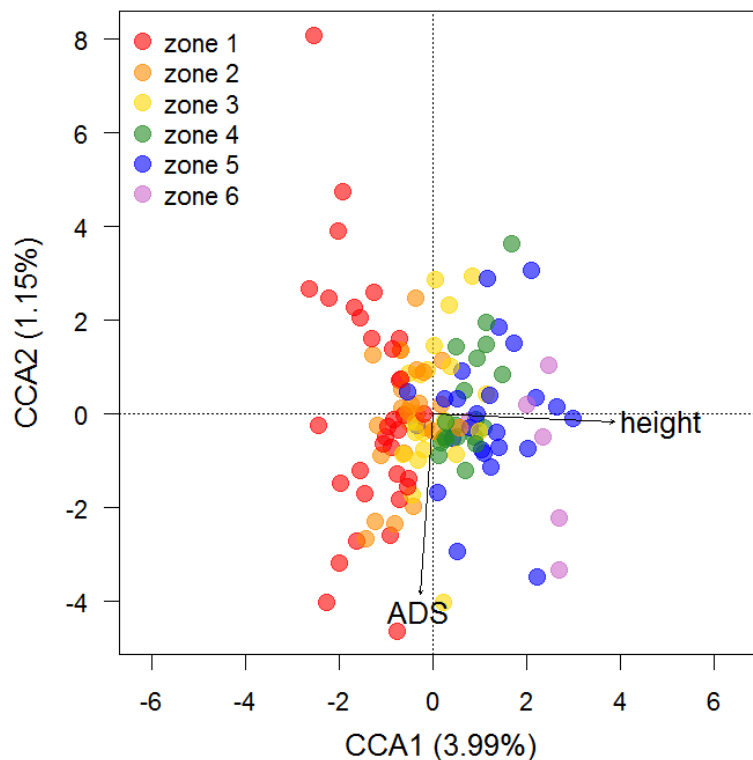
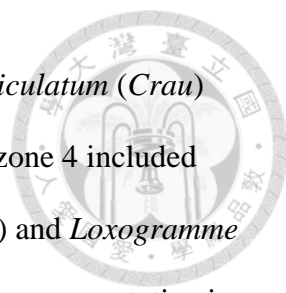


Figure 24. Optimal CCA model using two explanatory variables

Optimal CCA model was determined by a forward selection procedure using permutation test. There were two explanatory variables, height and ADS (angle difference for sunlight), in optimal CCA model, and they explained 5.15% of variation of species composition together. The directions of these two variables in CCA space were nearly perpendicular to each other, indicating that the influences of them on species composition were nearly independent.

2. Distribution patterns of different species

There were great variations in the height distribution of the 23 abundant species (Figure 25), indicating that these species used different niches. The synoptic table showing the significant Φ coefficient of each abundant epiphyte species in each vertical zone are shown below (Table 3). There were some unique representative species in zone 1 and



zone 4. Representative species in zone 1 included *Crepidomanes auriculatum* (Crau) and *Microsorium brachylepis* (Mibr), while representative species in zone 4 included *Vittaria anguste-elongata* (Vian), *Goniophlebium formosanum* (Gofo) and *Loxogramme salicifolia* (Losa). Those representative species in zone 5 were all also representative in zone 6, including *Davallia trichomanoides* (Datr), *Hoya carnosa* (Hoca) and *Dischidia formosana* (Difo). Relative frequency of all abundant epiphyte species in all vertical zones is shown in Appendix 4.

Relative frequency of four chosen species is shown below using bar plots (Figure 26). These four species were representative in zone 1 (*Microsorium brachylepis*), representative in zone 4 (*Vittaria anguste-elongata*), representative in zone 5 and zone 6 (*Davallia trichomanoides*) and not representative for all zones (*Lemmaphyllum microphyllum*), respectively. The distribution patterns of these four species were rather different (Figure 26).

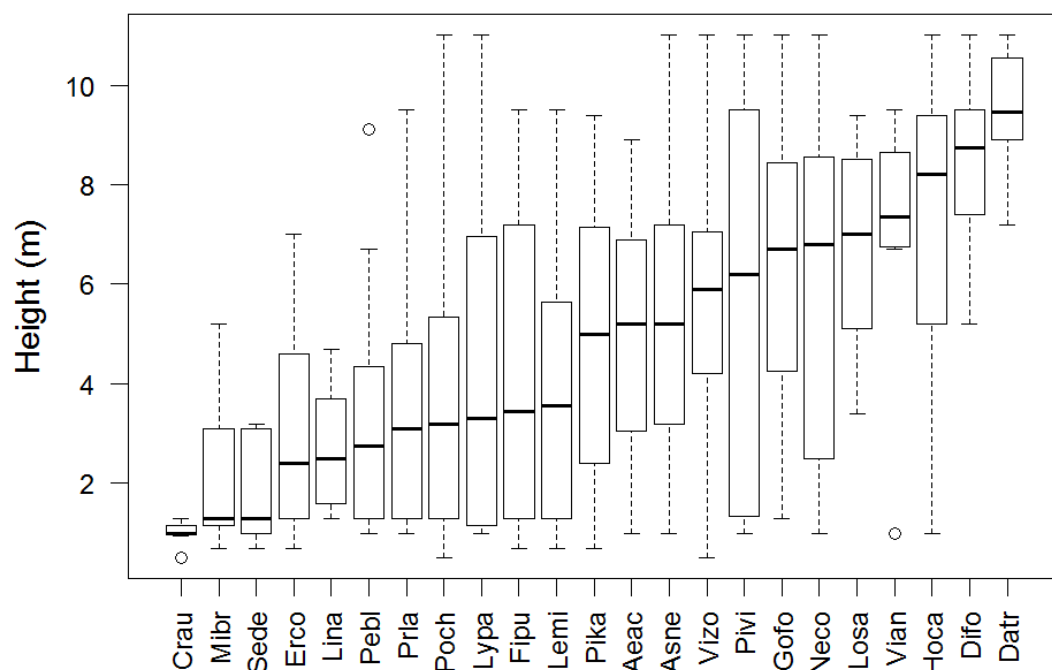


Figure 25. Height distribution of the 23 abundant epiphyte species

The box and whisker of each species was drawn based on the height of the plots containing that species. The lower and upper limits of the box were the first and the third quartiles. The black line inside the box indicated the median, and the species were sorted based on the medians. The whisker extended to the lowest or highest data point that still within 1.5 interquartile range (IQR) from limits of the box. Data points outside this range were viewed as outliers and shown as white dots. The height distribution of different species showed large differences, indicating niche differentiation. Complete scientific names of these species abbreviations are listed in Appendix 2.

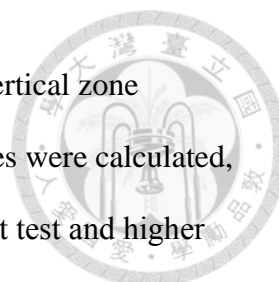


Table 3. The synoptic table showing representative species in each vertical zone. The Φ coefficient of all abundant epiphyte species in all vertical zones were calculated, but only those Φ coefficient that is significant based on Fisher's exact test and higher than 0.2 are shown in the synoptic table. Species with those significant and high enough Φ coefficient are viewed as representative species in those zones. Species in the table were sorted using Φ coefficient. Species representative in only 1 zone are listed first, followed by species representative in more than 1 zone, and those species not representative in all zones are not listed. The complete scientific names of these species abbreviations are shown in Appendix 2.

Species	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6
<i>Crau</i>	0.40					
<i>Mibr</i>	0.31					
<i>Vian</i>				0.26		
<i>Gofo</i>				0.22		
<i>Losa</i>				0.21		
<i>Poch</i>	0.30	0.26				
<i>Datr</i>					0.32	0.44
<i>Hoca</i>					0.25	0.23
<i>Difo</i>				0.21	0.20	0.34

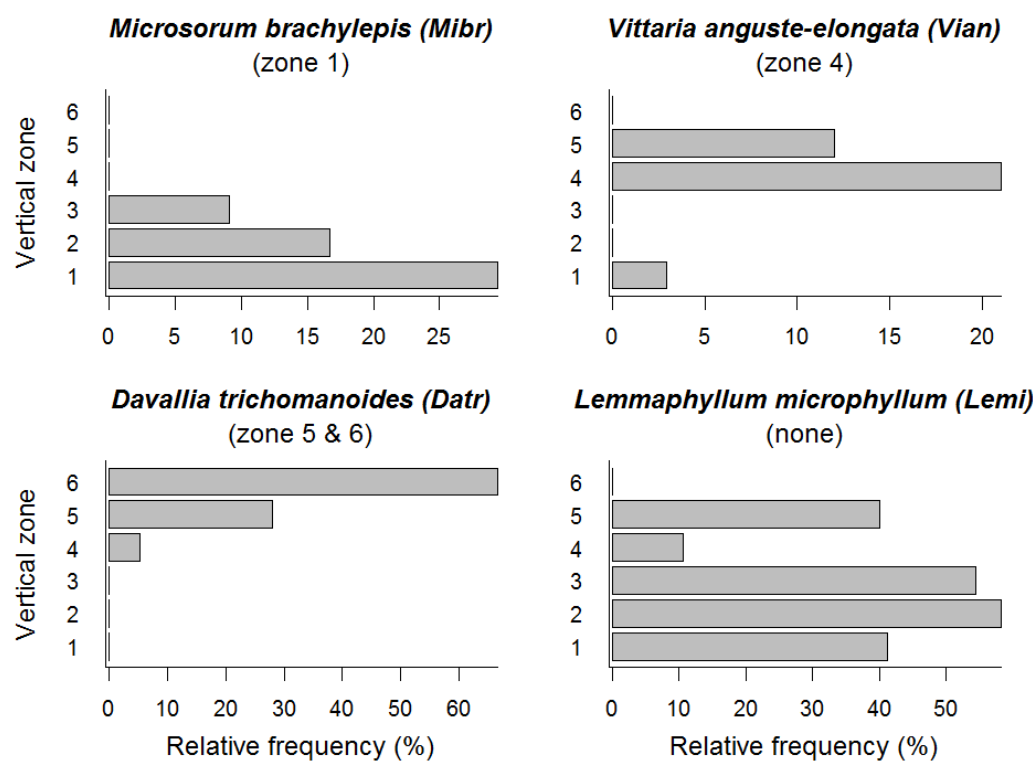


Figure 26. Relative frequency in each vertical zone for four species

Relative frequency is the proportion of plots containing that species in a certain vertical zone. The four species here were chosen based on the result of Φ coefficient analysis. *Microsorium brachylepis* was a representative species in zone 1. *Vittaria anguste-elongata* was a representative species in zone 4. *Davallia trichomanoides* was a representative species in both zone 5 and zone 6, while *Lemmaphyllum microphyllum* was not representative in all zones. The distribution patterns of these four species were rather different.

Because angle difference for sunlight (ADS) was correlated with species composition based on CCA, a box plot was made to show the range of ADS each abundant epiphyte species distributed (Figure 27). Compared to height, the ADS distribution of different species did not show large differences. Most of the species were distributed with



large range of ADS. Only few species had limited distribution, such as *Liparis nakaharae* (*Lina*) and *Microsorium brachylepis* (*Mibr*).

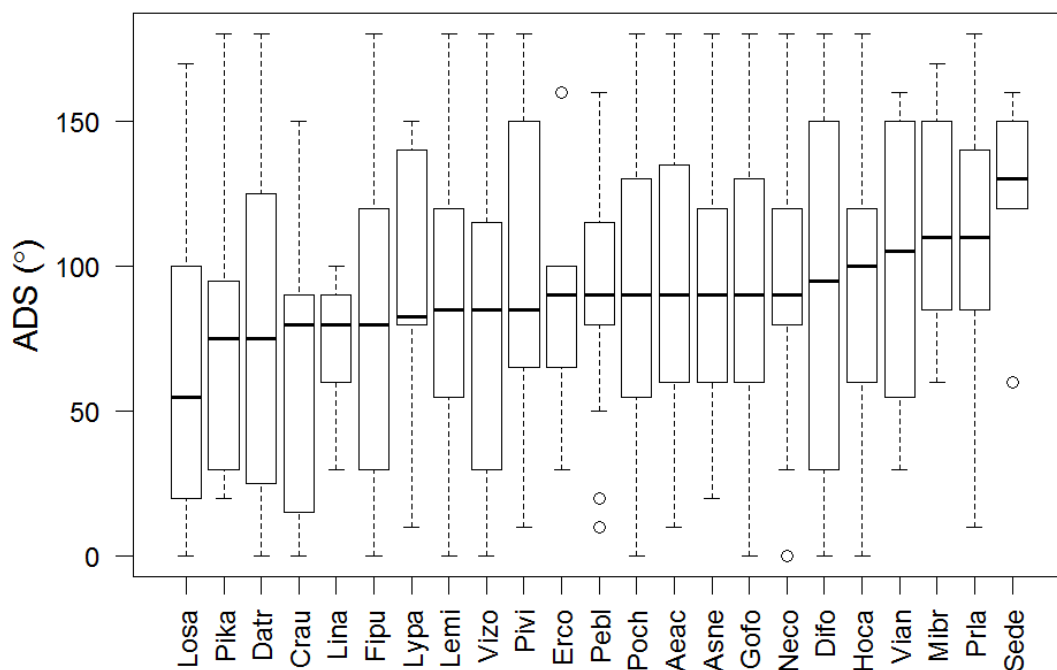


Figure 27. ADS distribution of the 23 abundant epiphyte species

The box and whisker of each species was drawn based on the angle difference for sunlight (ADS) of the plots containing that species. The lower and upper limits of the box were the first and the third quartiles. The black line inside the box indicated the median, and species were sorted based on the median. The whisker extended to the lowest or highest data point that still within 1.5 interquartile range (IQR) from limits of the box. Data points outside this range were viewed as outliers and shown as white dots. ADS distribution of different species did not show large differences. The complete scientific names of these species abbreviations are shown in Appendix 2.



3. Variation of functional traits of all epiphytes

Based on individual-based linear model (first approach), the relationships between all the six functional traits and all positional variables are summarized in Figure 28, and more details are shown in Appendix 5. For simple-leaved species, five functional traits had significant relationships with height. SLA ($p < 0.001$) and Chl_mass ($p < 0.001$) were negatively correlated with height, while LT ($p = 0.009$), LWC_area ($p = 0.012$) and Chl_area ($p = 0.045$) were positively correlated with height (Figure 28). LDMC only showed marginal significant relationship ($p = 0.082$) with height. The relationships between the six functional traits of simple-leaved epiphytes and height are shown more clearly using scatterplots and regression curves in Figure 29. On the other hand, for compound-leaved species, only LWC_area ($p = 0.002$) and LDMC ($p = 0.041$) showed significant relationships with height (Figure 28).

For positional variables except for height, only LT of compound-leaved epiphytes had a significant positive relationship with ADW ($p = 0.006$) (Figure 28). However, there were some marginal significant results. LT ($p = 0.098$), Chl_area ($p = 0.094$) and Chl_mass ($p = 0.062$) of simple-leaved epiphytes and Chl_area ($p = 0.095$) of compound-leaved epiphytes were marginal significantly correlated with inclination angle. Besides, LT of compound-leaved species was marginal significantly correlated with ADS ($p = 0.064$).

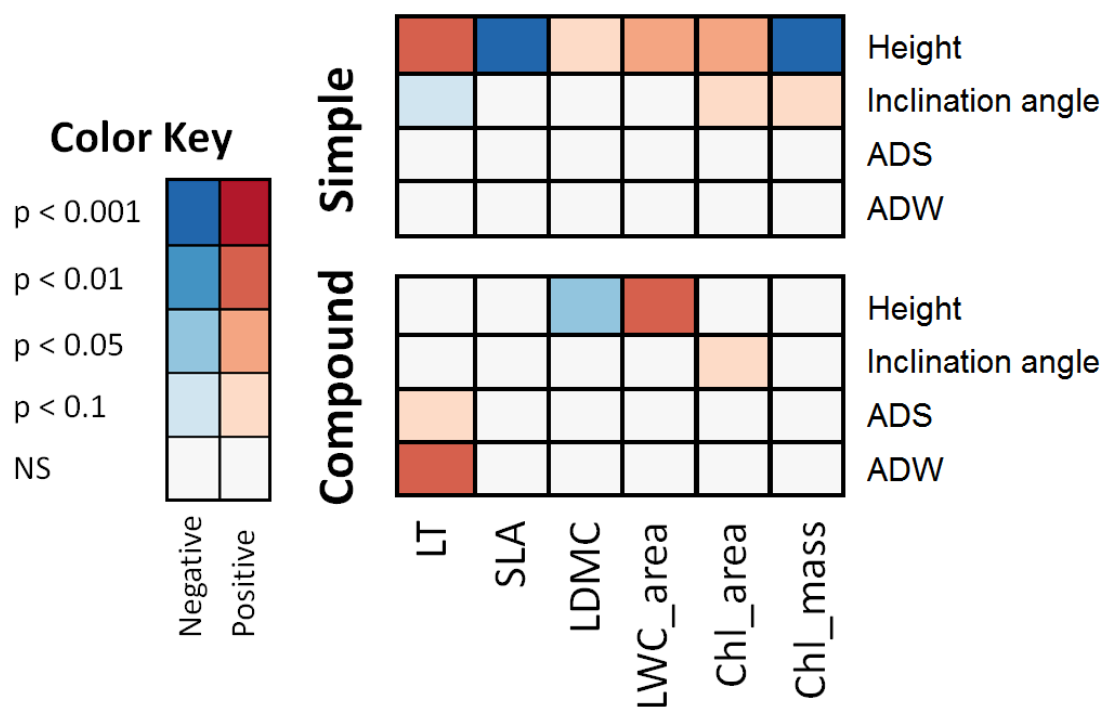


Figure 28. Relationships between functional traits and all positional variables based on individual-based linear model

Red colors in the figure indicate positive relationships between functional traits and positional variables, while blue colors indicate negative relationships. The densities of colors reflect the degree of significance based on partial F-tests in linear models. Those results with p-value between 0.05 and 0.1 were marginally significant. There were five traits of simple-leaved species and two traits of compound-leaved species were significantly correlated with height. LT of compound-leaved species was significantly correlated with ADW. Abbreviations: LT = leaf thickness; SLA = specific leaf area; LDMC = leaf dry matter content; LWC_area = leaf water content (per unit area); Chl_area = chlorophyll content (per unit area); Chl_mass = chlorophyll content (per unit mass); ADS = angle difference for sunlight; ADW = angle difference for water.

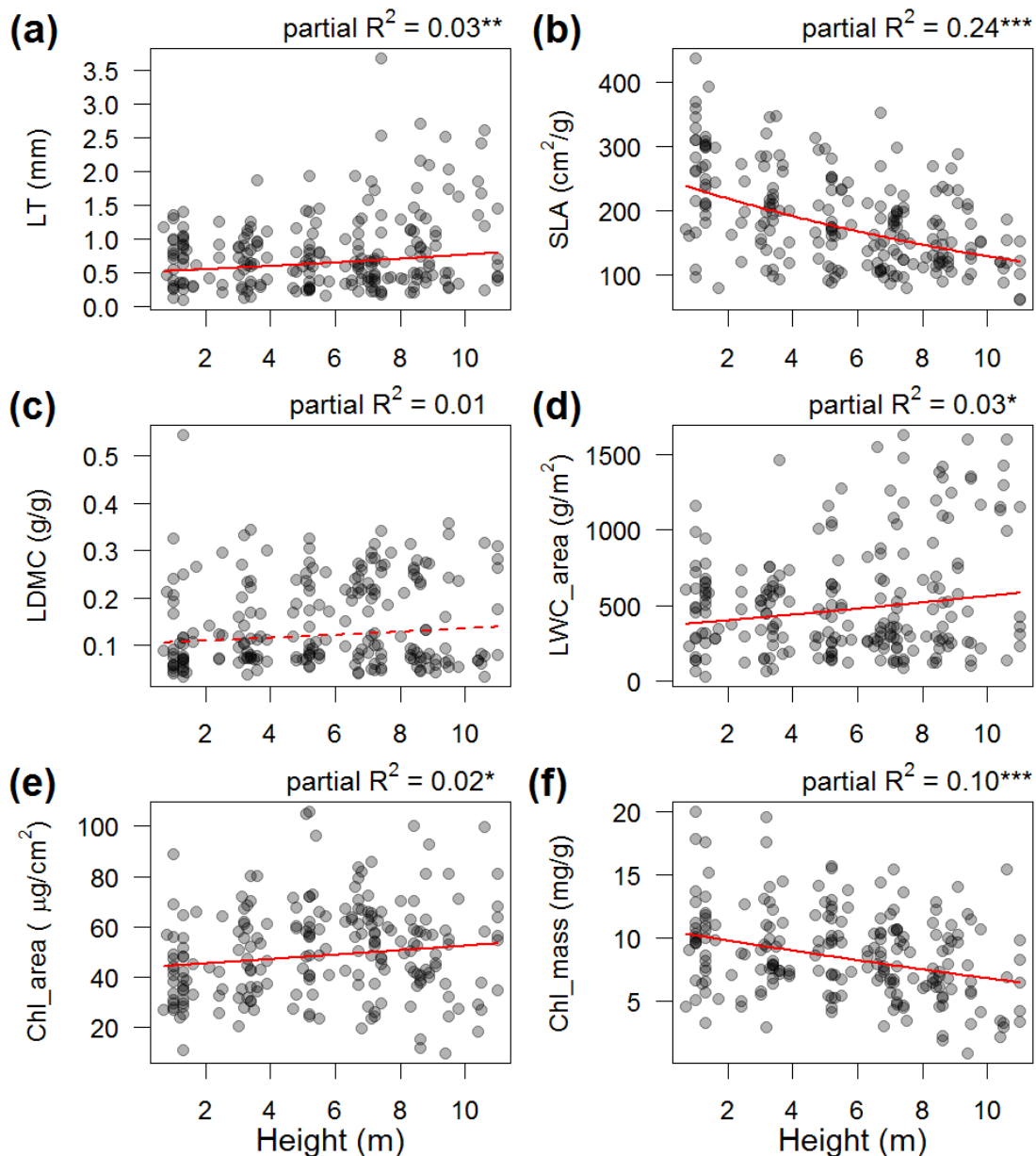
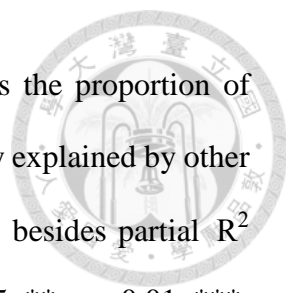


Figure 29. Scatterplots showing relationships between individual-based functional traits and height

The red curve in each plot shows the predicted values based on the optimal linear model. Dash line was used if the relationship was marginally significant. Because trait values were transformed using square root or natural logarithm when conducting linear model, the predicted values were retransformed to original trait units and shown in plots. If there were more than one explanatory variables in the optimal linear model, values of other variables were set at mean values when calculating predicted values. The partial R^2 of



height in the optimal linear model are shown. This value indicates the proportion of variation that height explained after excluding those variation already explained by other variables in the optimal linear model. The number of star signs (*) besides partial R^2 indicates the degree of significance based on partial F-test (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$). Abbreviations: LT = leaf thickness; SLA = specific leaf area; LDMC = leaf dry matter content; LWC_area = leaf water content (per unit area); Chl_area = chlorophyll content (per unit area); Chl_mass = chlorophyll content (per unit mass).

The results of plot-based community weighted mean (CWM) analysis (second approach) were summarized in Figure 30, and more details are shown in Appendix 6. Height was the only positional variable that had significant relationships with functional traits based on CWM analysis. LT ($p_{\max} = 0.019$) and LWC_area ($p_{\max} = 0.021$) were significantly and positively correlated with height, while SLA ($p_{\max} = 0.004$) and Chl_mass ($p_{\max} = 0.018$) were significantly and negatively correlated with height. The relationships between CWM functional traits and height are shown more clearly using scatterplots (Figure 31). For those traits having significant relationships with height based on CWM analysis, the relationships were consistent to the results of individual-based linear model.

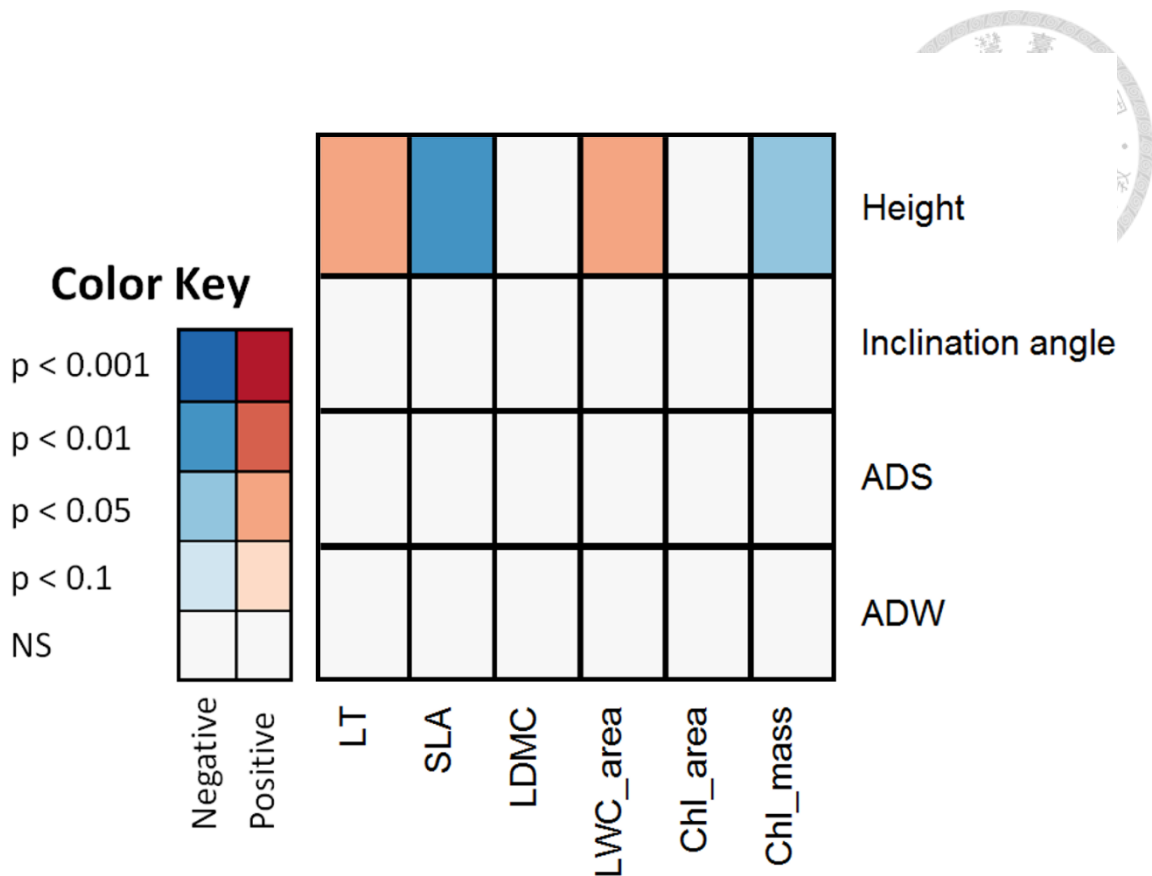


Figure 30. Relationships between all positional variables and functional traits based on plot-based CWM analysis

Red colors in the figure indicate positive relationships between community weighted mean (CWM) functional traits and positional variables, while blue colors indicate negative relationships. The densities of colors reflect the degree of significance based on p_{max} permutation tests. Height was the only positional variable that had significant relationships with functional traits. LT and LWC_area were significantly and positively correlated with height, while SLA and Chl_mass were significantly and negatively correlated with height. Abbreviations: LT = leaf thickness; SLA = specific leaf area; LDMC = leaf dry matter content; LWC_area = leaf water content (per unit area); Chl_area = chlorophyll content (per unit area); Chl_mass = chlorophyll content (per unit mass); ADS = angle difference for sunlight; ADW = angle difference for water.

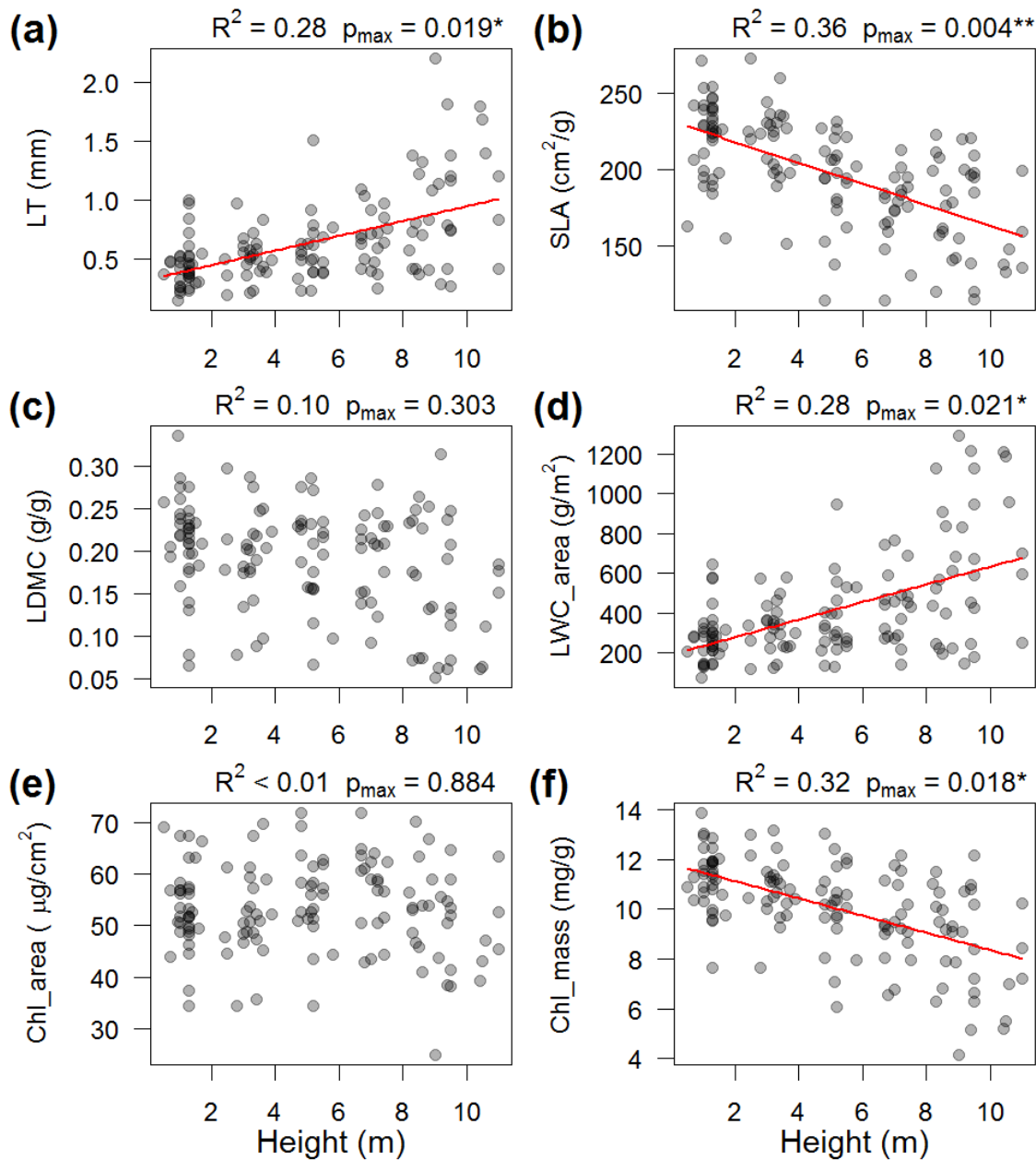
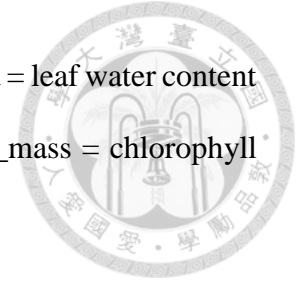


Figure 31. Scatterplots showing relationships between CWM trait values and height

The relationships between community weighted mean (CWM) trait values and height were examined using linear models and tested by p_{\max} permutation tests. The R^2 value indicates the proportion of variation that height explained. The p_{\max} value is a reliable index to test the significance of linear model in CWM analysis. The number of star signs (*) besides p_{\max} indicates the degree of significance (*: $p_{\max} < 0.05$; **: $p_{\max} < 0.01$; ***: $p_{\max} < 0.001$). For those traits with significant ($p_{\max} < 0.05$) relationships with height, the regression line were shown in the figure. Abbreviations: LT = leaf thickness;

SLA = specific leaf area; LDMC = leaf dry matter content; LWC_area = leaf water content (per unit area); Chl_area = chlorophyll content (per unit area); Chl_mass = chlorophyll content (per unit mass).



4. Variation of functional traits within species

The intraspecific variation of functional traits were analyzed for four species with sufficient measured individuals. There was no significant relationship between functional traits and height for all of these four species. However, for marginally significant results, SLA of *Lemmaphyllum microphyllum* is negatively correlated with height ($p = 0.093$), LDMC of *Lemmaphyllum microphyllum* is positively correlated with height ($p = 0.078$), and Chl_area of *Hoya carnosa* is negatively correlated with height ($p = 0.081$). The complete result of intraspecific functional trait analysis is shown in Appendix 7.

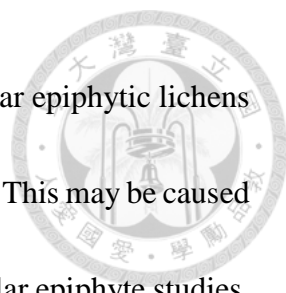


Discussion

1. Variation in species composition

The result of CCA confirms that height had significant influences on epiphyte species composition. Similar results were also reported in several previous studies (Krömer *et al.*, 2007; Zotz, 2007; Parra *et al.*, 2009). This result may come from close relationships between height and several environmental variables. Solar radiation, temperature fluctuation and wind speed typically increase with height while air humidity decrease in a forest (Richards, 1996; Wagner *et al.*, 2013). Vertical environmental gradients of temperature fluctuation and air humidity in the study site were also confirmed. These environmental variables are influential to physiology of epiphytes (Lambers, 2008; Zotz, 2016), and hence may influence epiphyte species composition by direct environmental filter or indirect effect via biotic interactions (Cadotte and Tucker, 2017). Besides, diameters, longevities and stabilities of growing substrates (trunks or branches) may influence epiphyte species composition, and they are also suggested to change with height (Cabral *et al.*, 2015).


Angle difference for sunlight (ADS) was also suggested to have effects on epiphyte species composition based on CCA. The effects of growing aspect on vascular epiphyte assemblages were seldom discussed, while aspect has been proposed to be related to microclimatic conditions, especially light intensity (Davies-Colley *et al.*, 2000), and has



been usually viewed as an influential factors in studies of non-vascular epiphytic lichens or bryophytes (Kantvilas and Minchin, 1989; Moe and Botnen, 2000). This may be caused by the difference of sampling scales between vascular and non-vascular epiphyte studies. Vascular epiphytes are usually surveyed by larger sampling unit, such as vertical zones or Johansson zones (Johansson, 1974), and these sampling methods are difficult to quantify the effects of micro-scale factors like aspect. The results of this study suggest that aspect of growing site should also be considered in vascular epiphyte studies if we are interested in micro-scale variation of epiphyte species composition.

Inclination angle of growing substrate has been proposed to have effects on epiphyte species composition (Zotz, 2007), while it was not significant in CCA in this study. The non-significant result of this study should not be simply interpreted as denying the importance of inclination angle. This study primarily focused on effects of height on epiphyte species composition and inclination angle of all the sampling plots were within a range from -20° to 20° except one plot (-30°). The non-significant result was possibly come from this small sampling range of inclination angle. I suggest that influences of inclination angle on epiphyte species composition should be further investigated using a more proper sampling scheme.

2. Distribution patterns of different species



The result of Φ coefficient analysis confirms that height distribution of different epiphyte species showed differentiation, consistent with many previous studies (Johansson, 1974; Krömer *et al.*, 2007; Zotz, 2007; Parra *et al.*, 2009). There were two unique representative species in zone 1—*Crepidomanes auriculatum* (Hymenophyllaceae) and *Microsorium brachylepis* (Polypodiaceae). Fern species in Hymenophyllaceae have been suggested to be sensitive to air humidity variation, and typically prefer to grow in very humid environment (Parra *et al.*, 2009). *Microsorium brachylepis* also grows in humid understory based on previous observations (郭城孟, 2008). There were up to three unique representative species in zone 4, suggesting that environmental conditions in zone 4 are different from the others. It was observed that height of the lowest branch of most sampled trees are within zone 4, and these branches may influence nearby microenvironment by blocking sunlight or accumulating organic matter, hence having unique species.

On the other hand, there was no unique representative species in zone 2, 3, 5 and 6. Zone 2 and zone 3 possibly served as transition zones for species turnover, so did not have unique representative species. All of the species representative in zone 5 were also representative in zone 6, suggesting that environmental conditions of these two zones were very similar. Besides, the species representative in zone 5 and 6 usually had some

drought-tolerant features, like scaled rhizomes of *Davallia trichomanoides* (Davalliaceae) and succulent leaves of *Hoya carnososa* (Apocynaceae) and *Dischidia formosana* (Apocynaceae).



In an epiphyte study in Bolivia, Krömer *et al.* (2007) classified epiphyte species into different ecological types including habitat generalists, trunk specialists, canopy specialists and hemiepiphytes. Among them, trunk specialists were similar to the representative species in lower zones in my study, and canopy specialists were similar to the representative species in higher zones. Krömer *et al.* (2007) also reported that most of trunk specialists were pteridophytes while most of canopy specialists were orchids. However, the results of my studies were somewhat different. Most of representative species in zone 1 to zone 4 were pteridophytes, and representative species in zone 5 and zone 6 were still pteridophytes and some species in Apocynaceae while there was no any representative orchid species. Compared with Neotropical forests, relative species richness and relative abundance of orchids to other epiphytes were much lower in my study site, and the canopy environment was occupied by species in Apocynaceae instead of orchids. The sparseness of orchids in my study site may come from the lower temperature in winter. Epiphytic orchids are suggested to be less tolerant to cold weather relative to other epiphytes (Zotz and Hietz, 2001), and their species richness and

abundance hence declined more dramatically from tropical to temperate regions (徐嘉君, 2007).



In this study, epiphytes were surveyed using vertical zones which were defined by absolute height, while many other studies used different sampling schemes. For example, Johansson (1974) divided each sampled host tree into 5 zones based on tree structure. Zone I and zone II represented lower part and upper part of tree trunk, while zone III to zone V represented inner to outer tree crown respectively (Figure 32). These zones are called Johansson zones and are frequently used in epiphyte studies (e.g., Krömer *et.al.*, 2007). I adopted vertical zoning scheme rather than Johansson's zoning scheme mainly because this study was aimed to analyze the effects of vertical environmental gradients, and also because outer tree crowns (Johansson zone V) were difficult to access through tree climbing. Vertical zoning scheme also helped to find out some information that might hardly be found by Johansson's zoning scheme. For example, results indicate that there were three unique representative epiphyte species in vertical zone 4. These species are supposed to prefer growing nearby the lowest living branch, while these kind of species can hardly be identified by Johansson's zoning scheme. On the other hand, the vertical zoning scheme in this study also had some disadvantages. This scheme did not consider tree structures at all, and was hence improper to be applied to trees with various tree height or tree structures. Moreover, outer tree crowns were not surveyed in this scheme

and therefore it was unable to examine whether there were representative species in outer tree crowns. Further studies using Johansson's zoning scheme or other sampling schemes may tell more information about distribution patterns of epiphytes that this study cannot tell.

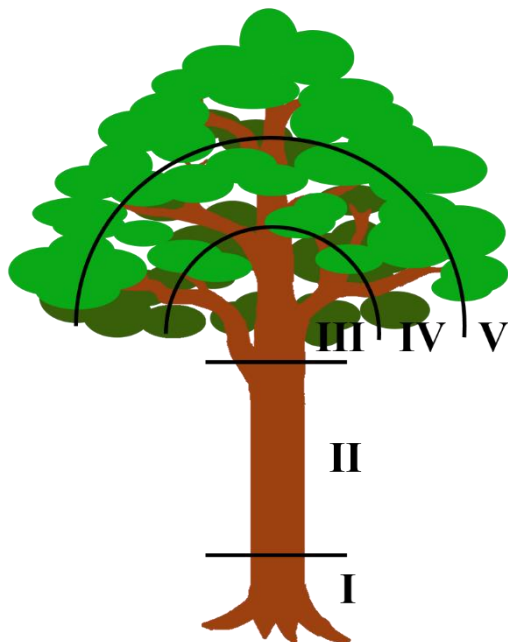


Figure 32. Johansson's zoning scheme

Zone I and zone II represent basal part and the other part of the tree trunk respectively.

Zone III, IV and V represent inner, middle and outer part of the tree crown respectively.

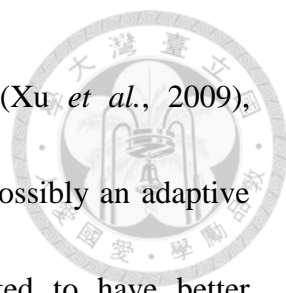
(modified from Johansson, 1974)



3. Variation of functional traits of all epiphytes

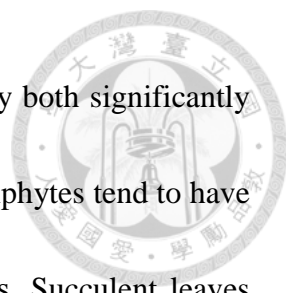
The results of individual-based linear model suggest that four functional leaf traits of simple-leaved epiphytes were significantly correlated with height, including LT, SLA, LWC_area and Chl_mass. The relationships between these four traits and height were also confirmed in plot-based community weighted mean (CWM) analysis. However, Chl_area of simple-leaved epiphytes was significantly correlated with height based on individual-based linear model, while it had no significant relationship with height based on plot-based CWM analysis. The difference between the results of these two approaches may come from effects of intraspecific trait variation, which was considered in individual-based linear model while ignored in plot-based CWM analysis. The difference was also possibly due to higher sensitivity to extreme trait values in individual-based linear model.

Compared with simple-leaved species, there were less functional traits (only LDMC and LWC_area) significantly correlated with height for compound-leaved species based on individual-based linear model. The difference in sample size between compound-leaved ($n = 68$) and simple-leaved species ($n = 221$) might have some effects. Besides, the result of PCA on species mean trait values suggests that trait variation among compound-leaved species was smaller (Figure 20), and smaller trait variation may lead to less significant relationships between traits and height. It was also reported in some previous studies that several leaf functional traits like leaf area of compound leaves were



more robust along environmental gradients than simple leaves (Xu *et al.*, 2009), somewhat consistent to my results. Growing compound leaves is possibly an adaptive strategy to drought environment. Compound leaves are suggested to have better efficiency of heat loss by convection, and therefore have lower leaf temperature and transpiration rate (Malhado *et al.*, 2010). Hence, it may be less necessary to adjust leaf morphology along vertical environmental gradients for compound-leaved species.

SLA of simple-leaved epiphytes was strongly negatively correlated with height in this study. SLA reflects light-capturing area per unit investment of dry mass, it is usually positively related to mass-based photosynthesis rate, while negatively related to leaf lifespan (Wright *et al.*, 2004; Pérez-Harguindeguy *et al.*, 2016). It is suggested that plants tend to have leaves with higher SLA in darker environment in order to enhance light-capturing efficiency and maximize total carbon gains over leaf lifespan (McMurtrie and Dewar, 2011). Because light intensity dramatically declines from outer canopy to understory (Wagner *et al.*, 2013), it is reasonable that epiphytes growing in understory have leaves with higher SLA, causing negative SLA-height relationship in this study. This negative relationship has also been reported in previous studies about vascular epiphytes (Cavaleri *et al.*, 2010; Petter *et al.*, 2016) or about sun leaves and shade leaves of tropical trees (Rozendaal *et al.*, 2006; Markesteijn *et al.*, 2007).



LT and LWC_area were closely correlated (Figure 20) and they both significantly increased with height for simple-leaved epiphytes, indicating that epiphytes tend to have thick and water-rich leaves (or “succulent leaves”) in higher zones. Succulent leaves usually have obvious hydrenchymal layers which can supply water for photosynthetically active cells and also have thick cuticle to reduce water loss (Gotsch *et al.*, 2015). The photosynthesis of succulent leaves is therefore less limited by drought. Succulent leaves may also benefit from preventing overheating in environment with strong light (Petter *et al.*, 2016). Besides, leaf thickness is suggested to be closely related to leaf physical strength (Onoda *et al.*, 2008), so having thick leaves may also help to resist strong wind in canopy. The increasing patterns of LT and LWC_area with height were also consistent to previous studies about epiphytes (Petter *et al.*, 2016) or trees (Markesteyn *et al.*, 2007).

Chl_mass of simple-leaved epiphytes was strongly negatively correlated with height, while the relationship between Chl_area and height was weaker, which was only significant in individual-based analysis. It is reported that shade leaves of trees have higher Chl_mass while their Chl_area are similar to sun leaves (Poorter *et al.*, 2000; Rozendaal *et al.*, 2006), consistent to the results of this study. Increase in Chl_mass in understory environment may be beneficial by increasing light absorption per unit biomass and hence increasing carbon gains per unit biomass (Poorter *et al.*, 2000). However, Chl_mass and Chl_area are related via SLA ($\text{Chl_mass} = \text{Chl_area} \times \text{SLA}$), so it seems

that the decreasing trend of Chl_{mass} with height was offset by decreasing trend of SLA, therefore leading to nearly no change in Chl_{area}.



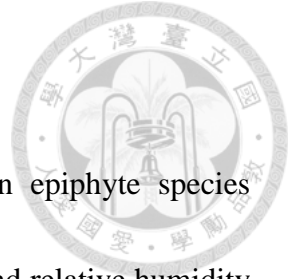
LDMC of simple-leaved epiphytes had no significant relationship with height, while LDMC of compound-leaved epiphytes was negatively correlated with height. Petter *et al.* (2016) also reported a negative relationship between LDMC and height, while the relationship was rather weak ($R^2 = 0.01$ for individual-based analysis). LDMC is actually in proportion to the inverse of SLA and LT if the density of leaf remains constant ($LDMC = 1 / (\text{Density} \times SLA \times LT)$) (Pérez-Harguindeguy *et al.*, 2016). Therefore, the decreasing trend of SLA with height may be offset by the increasing trend of LT, leading to rather weak relationship between LDMC and height.

There were few significant relationships between functional traits and other positional variables (inclination angle, ADS and ADW). It seems that these variables had less effects on functional traits of epiphytes. However, it should be noticed that these positional variables were designed and sampled as secondary factors, not the primary factor of this study. A better sampling scheme should be used if we want to further investigate their effects on functional traits.



4. Variation of functional traits within species

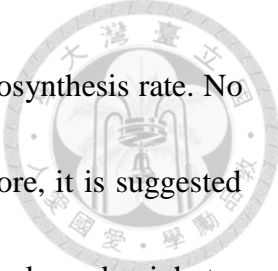
No significant relationship between functional traits and height was found within single epiphyte species in this study. Therefore, it seems that the significant relationships between functional traits and height in individual-based analysis for all epiphytes came from species turnover but not from intraspecific trait variation. However, the insignificant intraspecific trait variation might be caused by sparseness of analyzed species (four species) as well as small sample sizes ($n = 22-35$). Besides, epiphyte individuals growing on small twigs (that is, in outer tree crowns) were not collected and measured in this study due to limitation of tree-climbing method. Therefore, all of the measured individuals were collected from lower tree trunks to inner tree crowns, and the environmental gradient within this sampling range might be not strong enough to influence intraspecific functional traits. For the reasons above, the results should not be simply interpreted as denying intraspecific trait-height relationships in the study site. Petter *et al.* (2016) reported that 45.1% of studied epiphyte species had significant intraspecific SLA-height relationships, and 25.5% had significant LT-height relationships. Further studies with larger sample size and better sampling schemes which should include individuals in outer tree crowns are necessary to clarify intraspecific trait-height relationships of epiphytes in Taiwan.



Conclusions

Height was found to explain significant part of variation in epiphyte species composition based on CCA. Along with the results of temperature and relative humidity analysis, it is suggested that environmental variables changed with height and these vertical environmental gradients had effects on epiphyte species composition. It was also found that epiphyte species differentiated in their height distribution, and representative species in each vertical zone were identified by Φ coefficient analysis. There were unique representative species in zone 1 and zone 4, possibly because the environment in these two zones were different from the others. Zone 1 was closest to the ground and therefore was darkest and most humid, while zone 4 was typically influenced by lower living branches. On the other hand, angle differences between aspects of plots and the south direction also influence species composition, possibly due to differences in amount of sunlight received.

For functional traits analyses, it was found that leaf thickness (LT) and leaf water content (per unit area) (LWC_area) of simple-leaved epiphytes significantly increased with height, indicating that epiphytes prefer growing thicker and more water-rich leaves at higher positions, possibly because this type of leaves are more resistant to strong light and drought. On the other hand, specific leaf area (SLA) and chlorophyll content (per unit mass) (Chl_mass) of simple-leaved epiphytes significantly decreased with height,



possibly because these 2 traits are closely related to mass-based photosynthesis rate. No intraspecific trait-height relationship was found in this study. Therefore, it is suggested that these significant relationships between functional traits of simple-leaved epiphytes and height came from species turnover but not from intraspecific trait variation.

This study reveals that height is an important factor which not only structures epiphyte species composition but also have significant effects on several functional leaf traits of vascular epiphytes.



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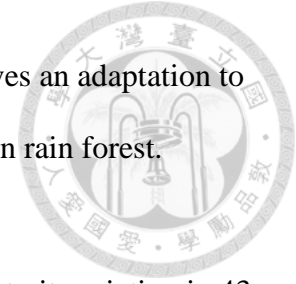
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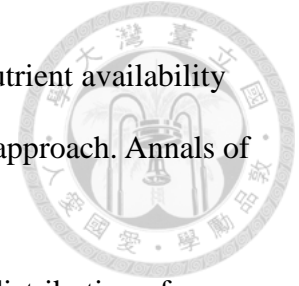
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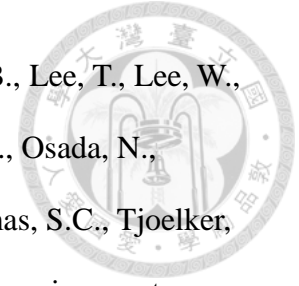
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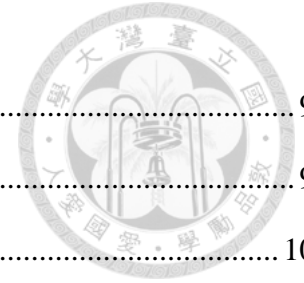
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Appendix 1. Information of all the 24 sampled trees

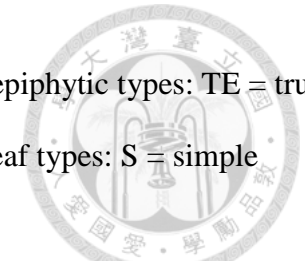
Tree ID	Species (scientific name)	Species (Chinese name)	Family	Altitude (m)	DBH (cm)	Tree height (m)	Number of zones
T001	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	658	60.0	19.8	5
T002	<i>Machilus zuihoensis</i>	香楠	Lauraceae	676	79.8	24.3	6
T003	<i>Litsea acuminata</i>	長葉木薑子	Lauraceae	646	37.9	11.8	5
T004	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	619	67.2	18.3	5
T005	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	622	56.3	18.3	5
T006	<i>Neolitsea konishii</i>	五掌楠	Lauraceae	655	60.4	17.0	5
T007	<i>Machilus japonica</i> var. <i>kusanoi</i>	大葉楠	Lauraceae	661	69.7	22.8	5
T008	<i>Machilus zuihoensis</i> var. <i>mushaensis</i>	霧社楨楠	Lauraceae	644	61.2	25.0	5
T009	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	647	81.6	24.0	5
T010	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	624	70.9	23.3	5
T011	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	619	66.5	15.4	5
T012	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	640	93.8	16.8	5
T013	<i>Machilus japonica</i> var. <i>kusanoi</i>	大葉楠	Lauraceae	635	68.4	24.1	6
T014	<i>Machilus zuihoensis</i> var. <i>mushaensis</i>	霧社楨楠	Lauraceae	635	73.9	24.0	6
T015	<i>Machilus zuihoensis</i> var. <i>mushaensis</i>	霧社楨楠	Lauraceae	673	80.0	20.7	6

Appendix 1. (continued) Information of all the 24 sampled trees

Tree ID	Species (scientific name)	Species (Chinese name)	Family	Altitude (m)	DBH (cm)	Tree height (m)	Number of zones
T016	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	641	82.0	14.1	5
T017	<i>Neolitsea konishii</i>	五掌楠	Lauraceae	651	51.0	25.3	5
T018	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	617	51.0	19.8	5
T019	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	644	58.5	19.6	6
T020	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	641	85.0	20.3	5
T021	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	652	70.0	17.5	5
T022	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	601	68.0	18.9	6
T023	<i>Castanopsis cuspidata</i> var. <i>carlesii</i>	長尾栲	Fagaceae	631	53.0	17.8	5
T024	<i>Phoebe formosana</i>	臺灣雅楠	Lauraceae	630	64.0	14.3	5

Appendix 2. List of all the 52 species recorded in plot surveys

Epiphyte species are listed first, followed by non-epiphytic species. Species are sorted based on taxonomy. Abbreviations of epiphytic types: TE = true epiphytes; Hemi-S = secondary hemiepiphytes; FacuE = facultative epiphytes; N = non-epiphytic species. Abbreviations of leaf types: S = simple leaves; PC = pinnately compound leaves; PAC = palmately compound leaves; PL = pinnately lobed leaves.



Species (scientific name)	Species abbreviation	Species (Chinese name)	Taxonomy group	Family	Epiphytic type	Leaf type
Epiphytes						
<i>Asplenium antiquum</i>	<i>Asan</i>	山蘇花	Pteridophytes	Aspleniaceae	TE	S
<i>Asplenium cuneatifforme</i>	<i>Ascu</i>	大蓬萊鐵角蕨	Pteridophytes	Aspleniaceae	TE	PC
<i>Asplenium neolaserpitiifolium</i>	<i>Asne</i>	大黑柄鐵角蕨	Pteridophytes	Aspleniaceae	TE	PC
<i>Asplenium nidus</i>	<i>Asni</i>	臺灣山蘇花	Pteridophytes	Aspleniaceae	TE	S
<i>Davallia trichomanoides</i>	<i>Datr</i>	海州骨碎補	Pteridophytes	Davalliaceae	TE	PC
<i>Crepidomanes auriculatum</i>	<i>Crau</i>	瓶蕨	Pteridophytes	Hymenophyllaceae	TE	PC
<i>Crepidomanes minutum</i>	<i>Crmi</i>	團扇蕨	Pteridophytes	Hymenophyllaceae	TE	S
<i>Hymenophyllum barbatum</i>	<i>Hyba</i>	華東膜蕨	Pteridophytes	Hymenophyllaceae	TE	PC
<i>Phlegmariurus fordii</i>	<i>Phfo</i>	福氏石松	Pteridophytes	Lycopodiaceae	TE	S
<i>Nephrolepis cordifolia</i>	<i>Neco</i>	腎蕨	Pteridophytes	Nephrolepidaceae	FacuE	PC
<i>Ophioglossum pendulum</i>	<i>Oppe</i>	帶狀瓶爾小草	Pteridophytes	Ophioglossaceae	TE	S

Appendix 2. (continued) List of all the 52 species recorded in plot surveys

Species (scientific name)	Species abbreviation	Species (Chinese name)	Taxonomy group	Family	Epiphytic type	Leaf type
<i>Goniophlebium formosanum</i>	<i>Gofo</i>	臺灣水龍骨	Pteridophytes	Polypodiaceae	TE	PL
<i>Lemmaphyllum microphyllum</i>	<i>Lemi</i>	抱樹蕨	Pteridophytes	Polypodiaceae	TE	S
<i>Loxogramme salicifolia</i>	<i>Losa</i>	柳葉劍蕨	Pteridophytes	Polypodiaceae	TE	S
<i>Microsorium brachylepis</i>	<i>Mibr</i>	波氏星蕨	Pteridophytes	Polypodiaceae	TE	S
<i>Pyrrosia lingua</i>	<i>Pyli</i>	石葦	Pteridophytes	Polypodiaceae	TE	S
<i>Selaginella delicatula</i>	<i>Sede</i>	全緣卷柏	Pteridophytes	Selaginellaceae	TE	S
∞ <i>Vittaria anguste-elongata</i>	<i>Vian</i>	姬書帶蕨	Pteridophytes	Vittariaceae	TE	S
<i>Vittaria zosterifolia</i>	<i>Vizo</i>	垂葉書帶蕨	Pteridophytes	Vittariaceae	TE	S
<i>Peperomia blanda</i>	<i>Pebl</i>	椒草	Basal angiosperms	Piperaceae	TE	S
<i>Peperomia tetraphylla</i>	<i>Pete</i>	小椒草	Basal angiosperms	Piperaceae	TE	S
<i>Piper kadsura</i>	<i>Pika</i>	風藤	Basal angiosperms	Piperaceae	Hemi-S	S
<i>Pothos chinensis</i>	<i>Poch</i>	柚葉藤	Monocots	Araceae	Hemi-S	S
<i>Bulbophyllum japonicum</i>	<i>Buja</i>	日本捲瓣蘭	Monocots	Orchidaceae	TE	S
<i>Eria corneri</i>	<i>Erco</i>	黃絨蘭	Monocots	Orchidaceae	TE	S
<i>Liparis bootanensis</i>	<i>Libo</i>	一葉羊耳蒜	Monocots	Orchidaceae	TE	S

Appendix 2. (continued) List of all the 52 species recorded in plot surveys

Species (scientific name)	Species abbreviation	Species (Chinese name)	Taxonomy group	Family	Epiphytic type	Leaf type
<i>Liparis cordifolia</i>	<i>Lico</i>	心葉羊耳蒜	Monocots	Orchidaceae	FacuE	S
<i>Liparis nakaharae</i>	<i>Lina</i>	長葉羊耳蒜	Monocots	Orchidaceae	TE	S
<i>Pholidota cantonensis</i>	<i>Phca</i>	烏來石山桃	Monocots	Orchidaceae	TE	S
Unknown	<i>Orl</i>	未知 (蘭科)	Monocots	Orchidaceae	TE	S
<i>Dischidia formosana</i>	<i>Difo</i>	風不動	Eudicots	Apocynaceae	TE	S
<i>Hoya carnosa</i>	<i>Hoca</i>	絨蘭	Eudicots	Apocynaceae	TE	S
♂ <i>Aeschynanthus acuminatus</i>	<i>Aeac</i>	長果藤	Eudicots	Gesneriaceae	TE	S
<i>Lysionotus pauciflorus</i>	<i>Lypa</i>	石吊蘭	Eudicots	Gesneriaceae	TE	S
<i>Pileostegia viburnoides</i>	<i>Pivi</i>	青棉花	Eudicots	Hydrangeaceae	TE	S
<i>Medinilla taiwaniana</i>	<i>Meta</i>	臺灣厚距花	Eudicots	Melastomataceae	TE	S
<i>Ficus pumila</i>	<i>Fipu</i>	薜荔	Eudicots	Moraceae	Hemi-S	S
<i>Ficus sarmentosa</i> var. <i>nipponica</i>	<i>Fisa</i>	珍珠蓮	Eudicots	Moraceae	Hemi-S	S
<i>Procris laevigata</i>	<i>Prla</i>	烏來麻	Eudicots	Urticaceae	TE	S

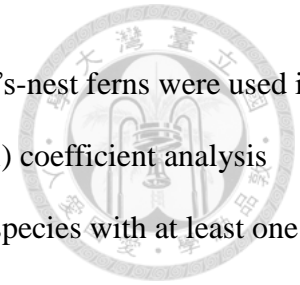
Appendix 2. (continued) List of all the 52 species recorded in plot surveys

Species (scientific name)	Species abbreviation	Species (Chinese name)	Taxonomy group	Family	Epiphytic type	Leaf type
Non-epiphytic species						
Unknown	<i>Atl</i>	未知 (蹄蓋蕨科)	Pteridophytes	Athyriaceae	N	PC
<i>Abrodictyum obscurum</i>	<i>Abob</i>	線片長筒蕨	Pteridophytes	Hymenophyllaceae	N	PC
<i>Selaginella moellendorffii</i>	<i>Semo</i>	異葉卷柏	Pteridophytes	Selaginellaceae	N	S
<i>Arthropteris palisotii</i>	<i>Arpa</i>	藤蕨	Pteridophytes	Tectariaceae	N	PC
<i>Carex sociata</i>	<i>Caso</i>	中國宿柱薹	Monocots	Cyperaceae	N	S
<i>Actinidia callosa</i> var. <i>discolor</i>	<i>Acca</i>	異色獼猴桃	Eudicots	Actinidiaceae	N	S
<i>Trichosanthes homophylla</i>	<i>Trho</i>	芋葉栝樓	Eudicots	Cucurbitaceae	N	S
<i>Maesa japonica</i>	<i>Maja</i>	山桂花	Eudicots	Primulaceae	N	S
<i>Ophiorrhiza japonica</i>	<i>Opja</i>	蛇根草	Eudicots	Rubiaceae	N	S
<i>Elatostema lineolatum</i>	<i>Elli</i>	冷清草	Eudicots	Urticaceae	N	S
<i>Elatostema platyphyllum</i>	<i>Elpl</i>	巒大冷清草	Eudicots	Urticaceae	N	S
<i>Pilea aquarum</i> ssp. <i>brevicornuta</i>	<i>Piaq</i>	短角冷水麻	Eudicots	Urticaceae	N	S
<i>Tetrastigma umbellatum</i>	<i>Teum</i>	臺灣崖爬藤	Eudicots	Vitaceae	N	PAC

Appendix 3. List of species used in different analyses

In this study, different species were used in different analyses. All vascular plants species recorded in the plots not below bird's-nest ferns were used in ordination (CA and DCA) of species composition (**Ordi**). Epiphyte species recorded in five or more plots were used in Φ (phi) coefficient analysis (**Phi**). Epiphyte species with three or more measured individuals were used in PCA of species-traits matrix (**PCA**). Epiphyte species with at least one measured individual were used in individual-based functional trait analysis (**Ind-trait**). Simple-leaved epiphyte species with three or more measured individuals were used in community weighted mean analysis (**CWM**). Epiphyte species with 20 or more measured individuals were used in the analysis of intraspecific trait variation (**Intra-trait**). Species used in different analyses (labeled with "T") are shown in this table.

Species	Ordi	Phi	PCA	Ind-trait	CWM	Intra-trait	No. of plots recorded	No. of individuals measured
No. of species	52	23	25	35	20	4		
<i>Pothos chinensis</i>	T	T	T	T	T		79	18
<i>Goniophlebium formosanum</i>	T	T	T	T		T	68	31
<i>Lemmaphyllum microphyllum</i>	T	T	T	T	T	T	52	35
<i>Ficus pumila</i>	T	T	T	T	T		48	4
<i>Asplenium neolaserpitiifolium</i>	T	T	T	T			42	11
<i>Aeschynanthus acuminatus</i>	T	T	T	T	T	T	39	22
<i>Nephrolepis cordifolia</i>	T	T	T	T			31	12



Appendix 3. (continued) List of species used in different analyses

Species	Ordi	Phi	PCA	Ind-trait	CWM	Intra-trait	No. of plots recorded	No. of individuals measured
<i>Hoya carnosa</i>	T	T	T	T	T	T	29	23
<i>Procris laevigata</i>	T	T		T			21	2
<i>Vittaria zosterifolia</i>	T	T	T	T	T		20	16
<i>Peperomia blanda</i>	T	T	T	T	T		20	10
<i>Selaginella moellendorffii</i>	T						19	0
<i>Dischidia formosana</i>	T	T	T	T	T		18	15
<i>Loxogramme salicifolia</i>	T	T	T	T	T		18	8
<i>Lysionotus pauciflorus</i>	T	T	T	T	T		16	6
<i>Microsorium brachylepis</i>	T	T	T	T	T		16	5
<i>Piper kadsura</i>	T	T	T	T	T		16	4
<i>Tetrastigma umbellatum</i>	T						13	4
<i>Davallia trichomanoides</i>	T	T	T	T			12	7
<i>Pileostegia viburnoides</i>	T	T	T	T	T		12	3
<i>Vittaria anguste-elongata</i>	T	T	T	T	T		8	3

Appendix 3. (continued) List of species used in different analyses

Species	Ordi	Phi	PCA	Ind-trait	CWM	Intra-trait	No. of plots recorded	No. of individuals measured
<i>Crepidomanes auriculatum</i>	T	T	T	T			7	5
<i>Eria corneri</i>	T	T	T	T	T		7	5
<i>Liparis nakaharae</i>	T	T	T	T	T		5	5
<i>Selaginella delicatula</i>	T	T					5	0
<i>Abrodictyum obscurum</i>	T						4	1
<i>Ophioglossum pendulum</i>	T		T	T	T		2	3
<i>Pholidota cantonensis</i>	T		T	T	T		2	3
<i>Bulbophyllum japonicum</i>	T			T			2	2
<i>Medinilla taiwaniana</i>	T			T			2	2
<i>Pyrrosia lingua</i>	T			T			2	2
<i>Asplenium cuneatifforme</i>	T			T			2	1
<i>Crepidomanes minutum</i>	T			T			2	1
<i>Liparis bootanensis</i>	T			T			2	1
<i>Carex sociata</i>	T						2	1

Appendix 3. (continued) List of species used in different analyses

Species	Ordi	Phi	PCA	Ind-trait	CWM	Intra-trait	No. of plots recorded	No. of individuals measured
<i>Elatostema platyphyllum</i>	T						2	1
<i>Actinidia callosa</i> var. <i>discolor</i>	T						2	0
Unknown (Athyriaceae)	T						2	0
<i>Liparis cordifolia</i>	T						2	0
<i>Maesa japonica</i>	T						2	0
<i>Ophiorrhiza japonica</i>	T						2	0
<i>Pilea aquarum</i> ssp. <i>brevicornuta</i>	T						2	0
<i>Asplenium antiquum</i>	T		T	T	T		1	11
<i>Asplenium nidus</i>	T		T	T	T		1	10
<i>Ficus sarmentosa</i> var. <i>nipponica</i>	T			T			1	1
<i>Hymenophyllum barbatum</i>	T			T			1	1
<i>Peperomia tetraphylla</i>	T			T			1	1
<i>Arthropteris palisotii</i>	T						1	1
<i>Elatostema lineolatum</i>	T						1	0

Appendix 3. (continued) List of species used in different analyses

Species	Ordi	Phi	PCA	Ind-trait	CWM	Intra-trait	No. of plots recorded	No. of individuals measured
<i>Phlegmariurus fordii</i>	T						1	0
Unknown (Orchidaceae)	T						1	0
<i>Trichosanthes homophylla</i>	T						1	0

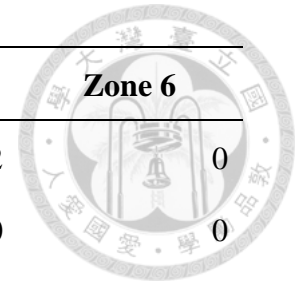
Appendix 4. Relative frequency of abundant epiphyte species in each vertical zone

For those species recorded in five or more plots, Φ coefficient and relative frequency (i.e., the proportion of plots containing the species) in each vertical zone were calculated. Species with a Φ coefficient which was significant based on Fisher's exact test and larger than 0.2 in a vertical zone were considered representative species in that zone. Values shown in the table are relative frequency (in percentage), while species in the table were sorted based on Φ coefficient. Species representative in only one vertical zone were listed first, followed by species representative in multiple zones, and then followed by species not representative in all zones. Besides, relative frequency of representative species was labeled with grey shading.

Species	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6
No. of plots	34	24	22	19	25	6
<i>Crepidomanes auriculatum</i>	21	0	0	0	0	0
<i>Microsorium brachylepis</i>	29	17	9	0	0	0
<i>Vittaria anguste-elongata</i>	3	4	0	21	8	0
<i>Goniophlebium formosanum</i>	15	58	68	79	56	83
<i>Loxogramme salicifolia</i>	0	8	23	32	20	0
<i>Pothos chinensis</i>	85	88	68	37	20	33
<i>Davallia trichomanoides</i>	0	0	0	5	28	67
<i>Hoya carnosa</i>	6	8	23	26	44	67
<i>Dischidia formosana</i>	0	0	5	32	28	67

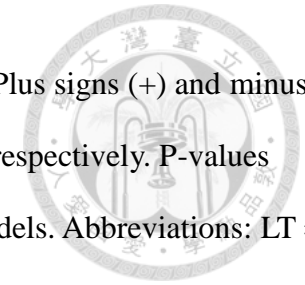
Appendix 4. (continued) Relative frequency of abundant epiphyte species in each vertical zone

Species	Zone 1	Zone 2	Zone 3	Zone 4	Zone 5	Zone 6
<i>Ficus pumila</i>	44	46	32	37	32	0
<i>Lemmaphyllum microphyllum</i>	41	58	55	11	40	0
<i>Peperomia blanda</i>	26	25	14	5	4	0
<i>Procris laevigata</i>	26	25	14	5	8	0
<i>Aeschynanthus acuminatus</i>	24	46	36	42	16	0
<i>Asplenium neolaserpitiifolium</i>	21	33	45	42	32	17
<i>Nephrolepis cordifolia</i>	21	21	9	37	28	50
<i>Lysionotus pauciflorus</i>	21	8	9	11	8	17
<i>Piper kadsura</i>	12	17	23	5	8	0
<i>Pileostegia viburnoides</i>	12	0	9	5	12	33
<i>Vittaria zosterifolia</i>	9	17	18	32	4	17
<i>Eria corneri</i>	9	8	5	5	0	0
<i>Selaginella delicatula</i>	9	8	0	0	0	0
<i>Liparis nakaharae</i>	6	8	5	0	0	0



Appendix 5. Results of individual-based functional trait analysis

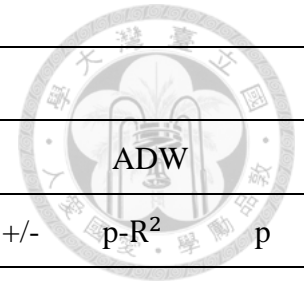
The relationships between individual-based functional trait values and positional variables were examined by linear models. Plus signs (+) and minus signs (-) in the table indicate significantly ($p < 0.05$) or marginally significantly ($p < 0.1$) positive and negative relationships respectively. P-values were calculated based on partial-F tests. No result was shown for those positional variables not included in optimal linear models. Abbreviations: LT = leaf thickness; SLA = specific leaf area; LDMC = leaf dry matter content; LWC_area = leaf water content (per unit area); Chl_area = chlorophyll content (per unit area); Chl_mass = chlorophyll content (per unit mass); ADS = angle difference for sunlight; ADW = angle difference for water; $p\text{-}R^2$ = partial R^2 .



Traits	Transformation	Positional variables											
		Height			Inclination angle			ADS			ADW		
Simple-leaved species		+/-	$p\text{-}R^2$	p	+/-	$p\text{-}R^2$	p	+/-	$p\text{-}R^2$	p	+/-	$p\text{-}R^2$	p
LT	natural log	+	0.03	0.009	-	0.01	0.098						
SLA	natural log	-	0.24	<0.001									
LDMC	natural log	+	0.01	0.082									
LWC_area	square root	+	0.03	0.012									
Chl_area	square root	+	0.02	0.045	+	0.01	0.094						
Chl_mass	square root	-	0.10	<0.001	+	0.02	0.062						

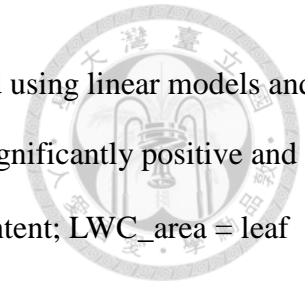
Appendix 5. (continued) Results of individual-based functional trait analysis

Traits	Transformation	Positional variables											
		Height			Inclination angle			ADS			ADW		
Compound-leaved species		+/-	p-R ²	p	+/-	p-R ²	p	+/-	p-R ²	p	+/-	p-R ²	p
LT	natural log							+	0.05	0.064	+	0.11	0.006
SLA	natural log												
LDMC	natural log	-	0.08	0.041									
LWC_area	square root	+	0.17	0.002									
Chl_area	square root				+	0.04	0.095						
Chl_mass	square root												



Appendix 6. Results of plot-based community weighted mean analysis

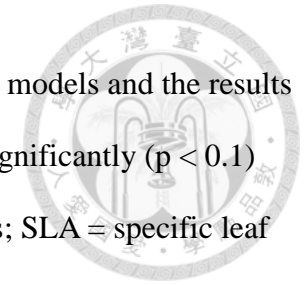
The relationships between plot-based community weighted mean (CWM) trait values and positional variables were examined using linear models and tested by p_{\max} permutation tests, and the results were summarized in this table. Plus signs (+) and minus signs (-) indicate significantly positive and negative relationships respectively. Abbreviations: LT = leaf thickness; SLA = specific leaf area; LDMC = leaf dry matter content; LWC_area = leaf water content (per unit area); Chl_area = chlorophyll content (per unit area); Chl_mass = chlorophyll content (per unit mass); ADS = angle difference for sunlight; ADW = angle difference for water. (*: $p < 0.05$; **: $p < 0.01$; ***: $p < 0.001$)



Traits	Positional variables											
	Height			Inclination angle			ADS			ADW		
	+/-	R ²	p_{\max}	+/-	R ²	p_{\max}	+/-	R ²	p_{\max}	+/-	R ²	p_{\max}
LT	+	0.28	0.019*	<0.01	0.770		<0.01	0.782		0.01	0.460	
SLA	-	0.36	0.004**	0.01	0.253		<0.01	0.888		<0.01	0.604	
LDMC		0.10	0.303	<0.01	0.959		0.01	0.412		<0.01	0.737	
LWC_area	+	0.28	0.021*	<0.01	0.746		<0.01	0.789		0.01	0.443	
Chl_area		<0.01	0.884	0.02	0.131		<0.01	0.929		<0.01	0.871	
Chl_mass	-	0.32	0.018*	<0.01	0.820		<0.01	0.837		<0.01	0.622	

Appendix 7. Results of intraspecific functional trait analysis

For four species with 20 or more measured individuals, the intraspecific trait-height relationships were examined using linear models and the results were summarized in this table. Plus signs (+) and minus signs (-) in the table indicate significantly ($p < 0.05$) or marginally significantly ($p < 0.1$) positive and negative relationships respectively. P-values were calculated based on F-tests. Abbreviations: LT = leaf thickness; SLA = specific leaf area; LDMC = leaf dry matter content; LWC_area = leaf water content (per unit area); Chl_area = chlorophyll content (per unit area); Chl_mass = chlorophyll content (per unit mass).



Traits	Species											
	<i>Lemmaphyllum microphyllum</i> (n = 35)			<i>Goniophlebium formosanum</i> (n = 31)			<i>Hoya carnosa</i> (n = 23)			<i>Aeschynanthus acuminatus</i> (n = 22)		
	+/-	R ²	p	+/-	R ²	p	+/-	R ²	p	+/-	R ²	p
LT		0.07	0.135		0.01	0.604		0.01	0.680		0.04	0.350
SLA	-	0.08	0.093		0.01	0.657		<0.01	0.798		0.02	0.522
LDMC	+	0.09	0.078		0.02	0.443		0.02	0.529		0.10	0.154
LWC_area		0.01	0.679		0.06	0.201		<0.01	0.975		0.12	0.130
Chl_area		0.02	0.372		0.02	0.460	-	0.14	0.081		<0.01	0.978
Chl_mass		0.02	0.449		0.04	0.313		0.07	0.232		0.04	0.363

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