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SECTION: BIODIVERSITY, ECOLOGY AND NATURE CONSERVATION

Diversity and leaf functional traits of vascular epiphytes along gradients of elevation and forest-use intensity.

Dissertation

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“Mere communion with nature, mere contact with the free air, exercise a soothing yet comforting and strengthening influence on the wearied mind, calm the storm of passion, and soften the heart when shaken by sorrow to its inmost depths.”

Alexander von Humboldt

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Author contributions: V.G.J, H.K and T.K conceived the main idea with input from G.Z; V.G.J collected the data; and V.G.J analysed the data with support from D.C and H.K. The manuscript was written by V.G.J, with input of A.T and M.L.M.G. All authors made substantial contributions to the interpretation of results and the editing of the manuscript.

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SUMMARY

Tropical mountains are hotspots of biodiversity and refugia for plants and animals, especially in a world of accelerating climatic change (Steinbauer et al., 2018). Biological diversity on tropical mountains is shaped by abiotic and biotic factors. Therefore, elevational gradients provide an opportunity to study effects of different ecological and evolutionary factors over relatively short geographical distances (Körner, 2007). This is a unique opportunity that inspired naturalist to use them as natural laboratories. Along elevational gradients in tropical mountains, multiple ecological questions have been explored, from diversity patterns to trait-environment relationships. Despite scientific advances in our knowledge of elevational gradients, we still lack a comprehensive understanding of numerous aspects of environmental factors and their influence on species diversity and function.

In my thesis, I provide a detailed analysis to understand patterns of tropical plant diversity, particularly vascular epiphytes, and their vulnerability to anthropogenic disturbance at different spatial scales (chapter 1), and the interplay and relative importance of broad- and small-scale environmental gradients as drivers of variation in leaf functional traits of vascular epiphytes (chapter 2). Furthermore, I assembled a publicly available database of epiphyte species diversity, community composition and leaf functional traits based on data from previous chapters, with the aim of contribute and motivate future research on tropical mountains (chapter 3).

In chapter 1, I analysed the response of epiphyte diversity to forest-use intensity from local to landscape scales along a tropical elevational gradient. I studied the effects of forest-use intensity on alpha, beta, and gamma diversity of vascular epiphyte assemblages in old-growth, degraded and secondary forests at eight study sites, yielding a total of 120 plots along the elevational gradient. I found that the interactive effects of elevation and forest-use intensity strongly impacted local-scale patterns of vascular epiphyte diversity. Alpha diversity did not differ significantly among forest-use intensity levels. However, gamma diversity was always lower in secondary forests compared to old-growth forests across the entire elevational gradient. Furthermore, beta diversity was dominated by species turnover along the forest-use intensity gradient in the lowlands, but declined with increasing elevation, where community composition became increasingly nested. The results in this study highlight a strong interaction between forest-use intensity and elevation. Further, this study offers a framework to

better understand the ecological factors that may determine diversity patterns of epiphytes in an anthropogenic world.

In chapter 2, I examined variation in morphological and chemical leaf traits of 102 vascular epiphyte species along broad- and small-scale environmental gradients, and assessed whether the variation in traits along these gradients were consistent across photosynthetic pathways (CAM and C_3). I found that broad- and small-scale environmental gradients explained more variation in chemical traits than in morphological traits. For example, carbon isotope ratio ($\delta^{13}C$) a proxy for water-use efficiency varied systematically across both environmental gradients, suggesting a decrease of water-use efficiency with increasing elevation and an increase with relative height of attachment. Contrary to our expectations, broad- and small-scale environmental gradients explained little of the variation in morphological leaf traits, suggesting that environmental conditions do not constrain morphological leaf trait values of vascular epiphytes. Our findings suggest that analysing multiple drivers of leaf trait variation and considering photosynthetic pathways is key for disentangling functional responses of vascular epiphytes to environmental conditions.

In chapter 3, I compiled a new comprehensive database (BIOVERA-Epi) that contains information on epiphyte species diversity, community composition and leaf functional traits. Moreover, I included data from 120 forest plots distributed along the studied elevational gradient which included six different forest types and three levels of forest-use intensity. In this chapter, I provided information describing two datasets in which, I assembled distribution and frequency data of 271 epiphytes species surveyed along the entire elevational gradient. Further, I measured a set of nine morphological and chemical leaf traits for 102 species surveyed along 45 plots in a section of the elevational gradient. With this chapter, I aim to contribute to future synthetic studies on the ecology, diversity, conservation, and functional plant ecology of tropical epiphyte assemblages in the Neotropics

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General introduction

Tropical forests are estimated to host over half of all global terrestrial biodiversity (Pimm & Raven, 2000), yet are being rapidly lost due to deforestation and land-use change (Gibson et al. 2011; Newbold et al. 2015). In tropical and subtropical rainforests epiphytes, plants growing non-parasitically on other plants (Zotz 2013), are a conspicuous and important component (Schimper 1888; Gentry & Dodson 1987; Benzing 1990), with more than 27,000 described species, representing ~9% of the world vascular plant diversity (Zotz 2013). However, their distribution is not restricted to low latitude regions, the northern and southern temperate forest also harbor rich epiphytic floras (Zotz 2005). The arboreal life of epiphytes allows them to reach the most light-exposed strata in the canopies, without having to invest extensively in plant structure (Benzing 1990). Nevertheless, as they are isolated from the nutrients in the ground, they exhibit a diverse array of strategies to acquire, process, and use available resources in the canopy of their host plants (Zotz 2016). In the canopy, epiphytes cope with an intermittent nutrient regime influenced by two types of inputs. External nutrient inputs stem from dry deposition and rain, but also droplets in clouds or fog (also known as “horizontal” precipitation, Reynolds & Hunter 2004), and internal inputs including leaf fall of the host tree, decomposition of leaf litter, branches and bark, leachates in stemflow and throughfall (Zotz 2016). Particularly water availability is a key factor in epiphytic habitats, as the diversity and abundance of these plants generally increases with precipitation and humidity (Gentry & Dodson 1987; Kreft et al. 2004; Ding et al. 2016).

Despite progress on our understanding of the impacts of climate change and biodiversity losses (Newbold et al. 2015; Peters et al. 2019), many aspects of epiphyte ecology are still not well studied, particularly when compared to other plant groups (Mendieta-Leiva & Zotz 2015). Moreover, our knowledge of how forest-use intensity affects tropical biodiversity along natural environmental gradients remains limited, especially with a scarce of studies in the field of trait-based ecology concerning vascular epiphytes. Developing effective conservation and management strategies depends on assessing the current status of tropical biodiversity and on improving our understanding of the role of human-modified forests for conservation of different plant groups. Additionally, expanding our knowledge on environmental-trait relationships can help us explain the distribution of vascular epiphytes and their strategies to acquire nutrients and water under different environmental conditions.

Elevational gradients: diversity and distribution of plants in the tropics

Elevational gradients are among the most powerful ‘experiments by nature’ for testing ecological and evolutionary responses of biota to environmental conditions (Körner 2007). Along elevational gradients, several factors change predictably with the increase in elevation; one of the most obvious is temperature, which decreases linearly as the elevation increases. This relation can be subject of changes depending on the latitude and size and shape of the mountain (Barry 2008), i.e. tropical mountains, due to higher temperatures at low latitudes, have warmer temperatures at the base and therefore need to be much taller to reach the extreme cold temperatures seen on temperate mountains (McCain & Grytnes, 2010). Another factor that changes variably along elevational gradients is precipitation, with a recognized pattern of increasing precipitation with increasing elevation in mountains at the temperate latitudes. In the case of tropical mountains, precipitation can display decreasing, unimodal or bimodal trends with highest precipitation at middle elevations. Other abiotic factors that can be important determinants of species richness include area, cloud cover and soil quality, among others (McCain & Grytnes, 2010).

The multiple interactions among environmental factors over a long period of time, is reflected in the biota along elevational gradients (Becker et al. 2007). This was noticed long time ago by Darwin, Wallace and von Humboldt, who provided the first detailed observations of how the natural world changes with elevation (Lomolino 2001), noticing that the type of habitat and the number of species changed predictable with increases in latitude and elevation. Since then, different climatic hypotheses have been proposed to explain elevational species diversity gradients (Lomolino 2001; Graham et al. 2014), for example, the hypothesis of species richness increasing with temperature were a monotonic decrease of species richness with elevation is expected (Rahbek 1995). However, responses to environmental variation along elevational gradients can follow similar or dissimilar patters across taxa (Lomolino 2001; Peters et al. 2016). For example, diversity patterns exhibiting a “hump-shaped” pattern in which richness peaks at mid-elevation for plants (Rahbek 1995; Kessler 2000) and animals (Rahbek 1995; Nogués-Bravo et al. 2008; McCain 2009). Nevertheless, diversity patterns along elevation can fall into four common patterns: decreasing, low plateau, low plateau with a mid-elevational peak and mid-elevation peak. Decreasing richness patterns are those in which the number of species decline monotonically with increasing elevation. Low plateau patterns have consecutively high richness across the lower portion of the gradient and thereafter decreasing species richness. Low plateau patterns with a mid-elevational peak have high richness across low elevations with a maximum diversity found more than 300 m from the base. Mid-elevation peaks have a unimodal peak in diversity at intermediate elevations with 25% or more species than at the base and top of the mountain (McCain 2009).

Most of the studies exploring diversity patterns of vascular epiphytes along elevational gradients report a hump-shaped pattern, with a peak in species diversity at mid-elevations. This pattern is thought to be driven by humidity and temperature, which are at optimal levels for vascular epiphytes at mid-elevations (Bhattarai et al. 2004; Kluge et al. 2006). In Mexico, Hietz & Hietz (1995) reported along an elevational gradient between 720-2,730 m a.s.l. highest values of epiphyte species and biomass at intermediate elevations, arguing that along the transect from warm and dry to cool and humid forests, the combination of temperature and water availability is an important factor determining the diversity and abundance of epiphytes. In another study, Wolf & Flamenco (2003) recorded for the state of Chiapas 1173 vascular epiphyte species between 500-2,000 m a.s.l., confirming the presumed presence of a belt of high diversity at mid-elevations in neotropical mountains. In Costa Rica, Cardelúz et al (2007) examined epiphyte diversity and distribution along a continuous elevational gradient between 30-2600 m a.s.l., they reported a total of 555 species with cloud forest at 1000 m representing the maximum of a pronounced mid-elevation peak in epiphyte species richness. Yet, changes in the forest due to anthropogenic disturbance might negatively affect vascular epiphyte diversity and species composition in human-modified landscapes (Barthlott et al. 2001; Köster et al. 2009; Krömer & Gradstein 2003), with some epiphytic taxa being more affected than others (Flores-Palacios & García-Franco, 2004; Hietz, et al. 2006; Larrea & Werner 2010).

Forest-use intensity and species loss

Any human-driven forest-use change affects important ecosystem services such as vegetation shifts, productivity, carbon sequestration, and water provision, as well as influence negatively species richness (Murphy & Romanuk 2014) especially along elevational gradients (Nogués-Bravo et al. 2008). Epiphytic communities may be particularly threatened as they are structurally dependent on trees and are extremely abundant in relatively warm and humid tropical climates (Mondragon et al. 2015; Zotz & Bader 2009). In the last decades, a growing interest in studying epiphyte species emerged, including the impact of anthropogenic changes on epiphyte communities in tropical forests along elevational gradients. Carvajal-Hernández & Krömer (2017), reported a list of ferns and lycophytes recorded along an elevational gradient between 20-3,500 m a.s.l., including contrasting environments with different degrees of forest disturbance. They found 140 species representing 27.5% of the pteridophytes of Veracruz state with maximum species richness at mid-elevations; but Carvajal-Hernández & Krömer (2017) also found considerable species loss in the humid montane forest caused by anthropogenic disturbance. Other studies in the tropics have reported a decrease of species richness with human disturbance. Barthlott et al. (2000) studied a montane rain forest in Venezuela, they compared the epiphyte communities of the primary, disturbed, and secondary forest. Their findings show a decline with increasing degrees of disturbance where epiphyte diversity was low in the disturbed and secondary areas compared to the adjacent primary forest. The authors argue that a less diverse phorophyte structure and less differentiated microclimate in the disturbed and secondary vegetation compared to the primary forest could drove species loss. In other study, Larrea & Werner (2010) studied the response of vascular epiphyte assemblages to different intensities of land-use in a montane wet forest in Ecuador, their findings suggest that changes in the epiphyte assemblages increase with the intensity of management, showing a rapid increase in turnover with pteridophytes being replaced by more xerotolerant taxa (Bromeliaceae and Orchidaceae) within six years after land-use change. However, this was different for species richness, which did not differ significantly between land-use types. Köster et al. (2009) studied changes in the epiphyte diversity in an Ecuadorian cloud forest to assess the effect of deforestation and the potential for epiphyte conservation in anthropogenically transformed habitats. They found that epiphyte diversity was highest in continuous primary forest, followed by forest fragments and isolated remnant trees, and lowest in young secondary forests. While there is increasing research on distribution and floristic composition of epiphytes with some studies considering the impact of human disturbance on epiphyte species diversity, to my knowledge, my dissertation is one of the first studies assessing the interactive effects of forest-use intensity and elevation on vascular epiphyte diversity patterns.

Environmental influence on leaf functional traits of vascular epiphytes

Environmental conditions, particularly temperature and precipitation, are known to determine species distributions and diversity patterns in vascular epiphytes (Gentry & Dodson 1987, Kreft et al. 2004), with species distributions potentially linked to functional traits, which are characteristics of plants influencing their growth, reproduction and survival (Violle et al. 2007). For instance, tropical montane forests may favor plants that can cope with high cloud cover, high humidity and lower temperatures. Contrary, lowland forests with dryer conditions and higher temperatures might favor species with traits associated with water retention capability and a higher water-use efficiency, allowing them to tolerate periods of water deficit. Such heterogeneity in conditions is reflected in the epiphyte assemblage by the presence of a large number of ecologically and functionally diverse species. While relationships among environmental conditions and functional leaf traits can be hypothesized, studies on environmental-trait relationships on epiphytes are still scarce.

At a smaller environmental scale, evidence suggests non-random spatial distribution of epiphytes assemblages within forests, showing a pronounced vertical stratification (Zotz 2007; Zotz & Schultz 2008). For instance, epiphytes growing in the upper canopy are exposed to more direct sunlight and greater diurnal variation in abiotic conditions (Böhnert et al., 2016), compared with species growing in the darker yet more humid lower canopy (Gotsch et al., 2015; Krömer & Kessler 2006). Few studies addressed this topic, with some studies assessing epiphytes vertical stratification using pre-defined Johansson zones within trees (Hietz & Briones 1998). Studies, such as Stuntz & Zotz (2001), reported that epiphytes located in the canopy had higher photosynthetic capacities and lower specific leaf area (SLA) compared to understory epiphytes. Petter et al. (2016) analysed shifts in trait values along a vertical gradient (i.e. height) at community and species level, and trait differences among taxonomic groups. Petter et al. (2016) found significant differences in trait values among major taxonomic groups (orchids, ferns, aroids, and bromeliads). In addition, the authors found significant trait-height relationships and positive correlations between intraspecific trait variability and the vertical range occupied by species.

At a larger environmental scale, Hietz & Wanek (1999) found a decrease in the proportion of CAM species with altitude from a pre-montane to upper-montane forest, with CAM species determining based on carbon isotopic composition in vascular epiphytes along an altitudinal gradient in Mexico. In a different study, Schellenberger-Costa et al. (2018) investigated functional trait patterns of epiphytes compared with other life forms along an elevational gradient in Tanzania. They found distinct trait patterns and their relationship with the environment between groups of epiphytes and other life forms i.e., trees and terrestrial non-trees. Epiphyte distribution and functional groups along environmental gradients have also been the subject of recent studies. In example, Agudelo et al. (2020) identify changes in the functional composition of vascular epiphytes along a tropical elevational gradient, they grouped species into seven hierarchical functional groups according to leaf traits and observed a functional response of the epiphyte communities along macro- and micro- environmental gradients.

Study outline

In my thesis, I aim to improve our understanding of diversity patterns of the epiphytes along an elevational gradient and how environmental changes at different scales are influencing epiphytes assembly based on leaf trait variation. To this end, my specific objectives are to (1) analyze the influence of interactive effects between forest-use intensity and elevation influence diversity patterns of vascular epiphytes, (2) examine variation in vascular epiphyte leaf traits along a broad- and small-scale environmental gradients and assess whether this variation is consistent between photosynthetic pathways (CAM and C_3), and (3) develop a database towards future macroecological studies of diversity and functional traits of vascular epiphytes.

In chapter 1, I investigated how vascular epiphyte diversity at local and regional scales respond to different levels of forest-use intensity. To achieve that, I analysed the effects of forest-use intensity on alpha, beta, and gamma diversity of vascular epiphyte assemblages in old-growth, degraded and secondary forests at eight study sites along the elevational gradient. Moreover, I explored the if the diversity of vascular epiphytes followed a hump-shaped pattern with a mid-elevation peak, as expected based on previous studies. Further, I assessed to what extent the interactive effect between forest-use intensity and elevation alters spatial variation in beta diversity.

In chapter 2, I addressed the relative roles of broad- and small-scale environmental gradients as drivers of variation in leaf traits of vascular epiphytes. To this end, I determined the influence of sampled elevation and minimum and maximum elevation (i.e., broad-scale environmental gradients) as well as the influence of relative height of attachment within the forest (i.e., small-scale environmental gradients) as proxies for ecological limits. Moreover, I assessed whether the influence of environmental gradients on leaf traits is consistent between C_3 and CAM species.

In chapter 3, I provide detailed information describing my database on species diversity, community composition, and leaf functional traits of vascular epiphytes. To achieve that, I assembled the data of the distribution and frequency of 271 vascular epiphytes species surveyed along 120 plots along the elevational gradient as well as leaf traits data of nine morphological and chemical traits for 102 species and 474 individuals surveyed along 45 plots in the gradient.

Research chapters

Humid montane forest in Los Capulines, Veracruz, Mexico at 1500 m a.s.l.

1. Effects of forest-use intensity on vascular epiphyte diversity along an elevational gradient

Valeria Guzmán-Jacob, Gerhard Zotz, Dylan Craven, Amanda Taylor, Thorsten Krömer, María Leticia Monge-González, Holger Kreft

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1.1. Abstract

Aim: Understanding patterns of tropical plant diversity and their vulnerability to anthropogenic disturbance at different spatial scales remains a great challenge in ecology and conservation. Here, we study how the effects of forest-use intensity on vascular epiphyte diversity vary along a tropical elevational gradient.

Location: 3500-m elevational gradient along the eastern slopes of Cofre de Perote, Mexico.

Methods: We studied the effects of forest-use intensity on alpha, beta, and gamma diversity of vascular epiphyte assemblages in old-growth, degraded, and secondary forests at eight study sites at 500 m intervals along the elevational gradient. At each elevation and in each of the three forest-use intensity levels, we established five 400 m² plots yielding a total of 120 plots.

Results: Interactive effects of elevation and forest-use intensity strongly impacted local-scale patterns of vascular epiphyte diversity. Species diversity peaked at 500 as well as 1500 m above sea-level, which deviates from the previously reported humped-shaped pattern. In most cases alpha diversity did not differ significantly among forest-use intensity levels. However, gamma diversity was always lower in secondary forests compared to old-growth forests across the entire elevational gradient. Within each elevational belt, beta diversity was dominated by species turnover along the forest-use intensity gradient in the lowlands and declined with increasing elevation, where community composition became increasingly nested. Along the elevational gradient, the spatial turnover of vascular epiphyte community composition was similar among forest-use intensity levels.

Main conclusions: Our results reveal a strong interaction between forest-use intensity and elevation, making it difficult to extrapolate findings from one elevational belt to another. Our findings highlight the value of old-growth forest for epiphyte diversity, but also show that degraded and secondary forests – depending on the elevational belt – may maintain a high species diversity, and thus play an important role in conservation planning.

Keywords: Beta diversity, bromeliads, composition, disturbance, elevation, ferns, forest-use, orchids, species richness, tropical vegetation.

1.2. Introduction

Tropical forests are estimated to host over half of all global terrestrial biodiversity (Pimm & Raven, 2000), yet are being rapidly lost due to deforestation and land-use change (Gibson et al., 2011; Newbold et al., 2015). Understanding the current status of tropical biodiversity and developing effective conservation and management strategies thus depends on improving our understanding outside of intact forest reserves (Chazdon et al., 2009a) and the role of human-modified forests for conservation. Despite recent progress (Newbold et al., 2015; Peters et al., 2019), our knowledge of how forest-use intensity affects tropical biodiversity along natural environmental gradients remains limited.

Ecological patterns are often studied along elevational gradients, which provide the opportunity to study effects of different ecological and evolutionary factors on biodiversity patterns over relatively short geographical distances (Körner, 2007). Climate (e.g., temperature and precipitation) usually plays a fundamental role in shaping diversity patterns along elevational gradients (McCain & Grytnes, 2010; Peters et al., 2019). However, different levels of forest disturbance should also play an important role in mediating microclimatic changes at local scales, which in turn may affect species diversity, especially life forms that are sensitive to air humidity and temperature, such as vascular epiphytes (Larrea & Werner, 2010; Werner & Gradstein, 2009; Zotz & Bader, 2009). Most studies investigating the distribution and diversity of vascular epiphytes along tropical elevational gradients report a hump-shaped pattern, with a peak in species diversity at mid-elevations (e.g. Acharya et al., 2011; Bhattarai et al., 2004; Cardelús et al., 2006; Ding et al., 2016; Gentry & Dodson, 1987; Hietz & Hietz-Seifert, 1995; Kluge et al., 2006; Krömer et al., 2005; Salazar et al., 2015). The shape of this pattern is thought to be driven by humidity and temperature, which are at optimal levels for vascular epiphytes at mid-elevations (Bhattarai et al., 2004; Kluge et al., 2006).

Forest use intensity and anthropogenic disturbance might negatively affect vascular epiphyte diversity in human-modified landscapes (Barthlott et al., 2001; Köster et al., 2009; Krömer & Gradstein, 2003). Depending on the degree (e.g., severity and/or frequency) of forest disturbance, species composition might also change, with some epiphytic taxa being more affected than others (Flores-Palacios & García-Franco, 2004; Hietz et al., 2006; Larrea & Werner, 2010). Effects of forest disturbance on vascular epiphyte diversity have also been attributed to isolation and time effects, due to site-specific factors that affect seed availability, dispersal, and recovery (Cascante-Marín et al., 2006). The younger age and reduced structural complexity of host trees in secondary forests may further limit the availability of different microhabitats that vascular epiphytes can colonize within a host tree (Hietz & Briones, 1998; Krömer & Gradstein, 2003; Taylor & Burns, 2015), depending on their preference for darker and more humid lower canopy or more sun exposed branches in the upper canopy (Hietz, 1998; Krömer et al., 2007). Reduced structural complexity of the canopy might further reinforce changes in the microclimate, resulting in a less pronounced vertical zonation within the tree (Böhnert et al., 2016), higher drought stress, and an overall decrease in a host tree's suitability for certain species (Krömer & Gradstein, 2003; Werner et al., 2005). Nevertheless, while some groups of vascular epiphytes in tropical cloud forests may be negatively affected by decreased humidity (e.g. orchids, filmy and grammitid ferns), more drought-resistant species (e.g. xeromorphic bromeliads) may benefit from the novel climatic conditions generated by land-use change (Barthlott et al., 2001; Krömer et al., 2014; Zotz & Bader, 2009). To date, however, the joint effects of forest-use intensity and elevation on vascular epiphyte diversity patterns have not been examined.

Assessing how diversity patterns vary across multiple spatial scales has the potential to deepen current understanding of the consequences of disturbance on species diversity and composition in human-dominated tropical landscapes. In their seminal paper, Gentry & Dodson (1987) hypothesized that the high alpha and gamma diversity of Neotropical vascular epiphytes is due to niche partitioning along environmental gradients, which implies high beta diversity (i.e. spatial variation in composition), a component of diversity that remains poorly studied in vascular epiphytes. In this regard, analysing beta diversity and its nestedness and turnover components offers a compelling framework to understand the contribution of historical and ecological factors that may determine diversity patterns (Baselga, 2010). The nestedness component of beta diversity captures to what extent the assemblage with a lower number of species is a subset of an assemblage with higher number of species (Ulrich & Gotelli, 2007). Nestedness may be the dominant component of beta diversity in disturbed ecosystems, in which increasing land-use intensity reduces the number of species that can persist. The species turnover component of beta diversity, in contrast, reflects the replacement or change in species composition across ecological gradients

(Baselga, 2010; Qian et al., 2005), where environmental filtering excludes species that do not have adaptive traits for establishing in particular parts of the gradient (Kraft et al., 2015). Therefore, the relative contribution of the nestedness and turnover components to beta diversity may reveal ecological mechanisms that determine how the composition of vascular epiphyte communities varies with elevation and forest-use intensity.

Here, we investigate how vascular epiphyte diversity at local to landscape scales responds to different levels of forest-use intensity (FUI) along a 3500-m elevational gradient within the Mesoamerica biodiversity hotspot (Albuquerque *et al.*, 2015; Brooks et al., 2002). We were interested in determining whether effects of FUI on species diversity patterns varied along the elevational gradient, which we addressed with the following questions: 1) Does the diversity of vascular epiphytes follow a hump-shaped pattern with a mid-elevation peak? 2) How is species diversity affected by FUI, and does this vary with elevation? 3) To what extent do FUI and elevation alter spatial variation in beta diversity? We expected vascular epiphyte diversity to peak at mid-elevations (Cardelús et al., 2006; Krömer et al., 2005) and FUI to reduce species diversity (Nöske et al., 2008; Wolf, 2005) and to influence beta diversity via the nestedness component more than turnover by reducing the size of the species pool. Moreover, we anticipated that elevation would have stronger effects on the turnover component of beta diversity, reflecting environmental filtering processes (Myers et al., 2013; Socolar et al., 2016).

1.3. Methods

Sampling design

We studied vascular epiphyte diversity along an elevational gradient from sea-level to 3500 m on the eastern slopes of Cofre de Perote, a 4282 m high extinct volcano located in the central part of Veracruz State, Mexico (Fig. 1.1). In this region, the Trans-Mexican volcanic belt and the Sierra Madre Oriental converge, combining floristic elements from the Nearctic and Neotropics. The climate in the study region ranges from dry-hot in the lowlands (mean annual temperature (MAT): 25 °C; mean annual precipitation (MAP): 1222 mm), to humid-temperate at mid-elevations (MAT: 13-19 °C; MAP: 2952-1435 mm) and dry-cold at high elevations (MAT: 9 °C; MAP: 708 mm; data according to the National Meteorological Service of Mexico 1951-2010).

Along this gradient, six main vegetation types are present (Carvajal-Hernández & Krömer 2015): 1) semi-humid deciduous forest at 0-700 m, 2) tropical oak forest at 700-1300 m, 3) humid montane forest at 1300-2400 m, 4) pine-oak forest at 2400-2800 m, 5) pine forest at 2800-3500 m, and 6) fir forest at 3500-3600 m (Table 1.1).

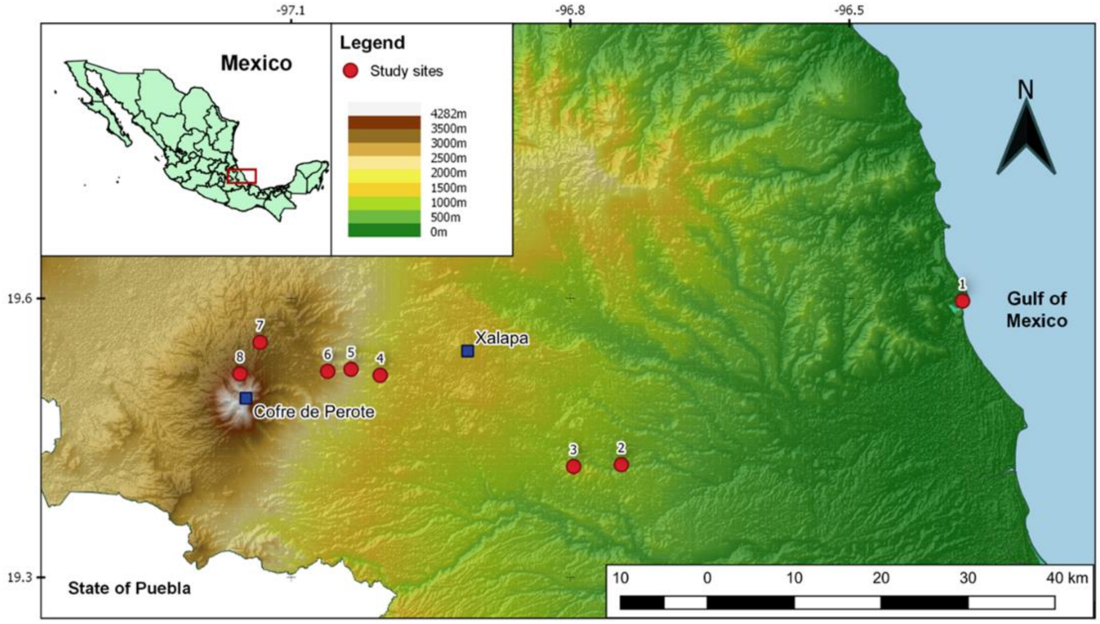

Figure 1.1 Eastern slopes of the Cofre de Perote mountain in the state of Veracruz, Mexico. Red dots indicate the eight study sites (Table 1.1). Blue squares indicate summit of the Cofre de Perote mountain and the city of Xalapa as reference points.

The current conservation status of the natural forests in this region is critical. More than 80% of the forests have been converted to pastures, plantations, and secondary forests (Ellis et al., 2011; Gómez-Díaz et al., 2018). Consequently, the remaining forests are highly fragmented, and subjected to ongoing disturbance and deforestation for agriculture, cattle ranching, and extraction of timber and non-timber forest products. We investigated three levels of forest-use intensity (FUI) that could be consistently found along the entire gradient following (Gómez-Díaz et al., 2017): 1) old-growth forests (OG) encompass mature forests with no or little signs of logging and other human impacts, classified as the lowest FUI; 2) degraded forests (DF) were defined as forests with clear signs of previous logging, sometimes with on-going cattle grazing, removal of understory, and / or harvesting of non-timber forest products, classified as intermediate FUI; 3) secondary forests (SF) were young forests at an intermediate successional stage of 15-25 years after abandonment (based on explanations by the land-owners), often with signs of continued human impacts, such as the removal of understory vegetation, non-timber forest products or partial tree cutting and occasional cattle grazing, classified as high FUI.

Table 1.1. Locations and climatic conditions of the eight study sites along the elevational gradient at the Cofre de Perote, central Veracruz, Mexico. Elevational range, vegetation type according to Carvajal-Hernández & Krömer (2015), mean annual temperature (MAT) (°C) and mean annual precipitation (MAP) (mm/a) according to the National Meteorological Service of Servicio Meteorológico Nacional (SMN, 2019). Data cover 1951-2010.

Site	Elevation range (m)	MAT (°C)	MAP (mm/a)	Canopy height (m)	N latitude	W longitude	Vegetation type
1	0-45	26	1222	~ 33	19.59	-96.38	Semi-humid deciduous forest
2	610-675	23	946	~ 34	19.41	-96.74	Semi-humid deciduous forest
3	980-1050	21	1331	~ 38	19.41	-96.79	Tropical oak forest
4	1470-1700	19	1436	~ 53	19.52	-96.98	Humid montane forest
5	2020-2200	14	2952	~ 47	19.50	-97.03	Humid montane forest
6	2470-2600	12	1104	~ 42	19.52	-97.05	Pine-oak forest
7	3070-3160	9	708	~ 30	19.55	-97.13	Pine forest
8	3480-3545	9	708	~ 32	19.51	-97.16	Fir forest

Data collection

We selected eight study sites each separated by c. 500 m along the elevational gradient with the following elevational ranges (Table 1.1): 0-45 m, 610-675 m, 980-1050 m, 1470-1700 m, 2020-2200 m, 2470-2600 m, 3070-3160 m, and 3480-3545 m (hereafter referred to as 0, 500, 1000, 1500, 2000, 2500, 3000, 3500 m). At each study site, we surveyed vascular epiphytes in five non-permanent 20 m × 20 m plots for each of the three FUI levels (Fig. 1.2), respectively, from July 2014 to May 2015. This yielded a total number of 120 plots. Vascular epiphytes were surveyed following the sampling protocol of Gradstein et al. (2003). First, ground-based surveys were conducted; each plot was divided in four quadrants to better record the presence of epiphyte assemblages in the forest understory up to a height of ~8 m (Krömer et al., 2007), using collecting poles and binoculars (Flores-Palacios & García-Franco 2001). Second, one mature host tree per plot was chosen by its size, health, and crown structure for safe canopy access. We climbed from the base to the outer portion of the tree crown using the single-rope climbing technique (Perry, 1978) and examined each of the five Johansson zones for vascular epiphytes, which are frequently used to describe the spatial distribution of vascular epiphytes in tree canopies (Johansson, 1974; Sanger & Kirkpatrick, 2017). For each plot, we recorded the frequency of each species as the sum of incidences in the four sub-plots and the host tree (max. frequency per plot = 5). We used a Garmin® GPSMAP 60Cx device (Garmin International, Inc. Kansas, USA) to record geographical coordinates and elevation of all plots.

Vascular epiphytes were first identified as morphospecies in the field and collected, if possible, in triplicates to be preserved as herbarium specimens. These specimens were identified using relevant literature (Croat & Acebey, 2015; Espejo-Serna et al., 2005; Hietz & Hietz-Seifert 1994; Mickel & Smith, 2004) and by comparison with specimens deposited at the National Herbarium (MEXU), Universidad Nacional Autónoma de México, in Mexico City, and the herbarium of the Institute of Ecology (XAL) in Xalapa, Veracruz. Some taxa were sent to specialists for identification: namely, Crassulaceae (Dr. Pablo Carrillo Reyes, Universidad de Guadalajara), Cactaceae (Dr. Miguel Cházaro Bazáñez, Universidad Veracruzana), Bromeliaceae and Orchidaceae (Dr. Adolfo Espejo-Serna and MSc. Ana Rosa López-Ferrari, Universidad Autónoma de México, Iztapalapa), Pteridophytes (Dr. Alan Smith, UC Berkeley), and *Peperomia* (Guido Mathieu, Botanic Garden Meise, Belgium). Species not identified to species level were assigned to morphospecies, using the genus or family name followed by the registered elevation and a consecutive number. The collection of protected species mentioned in Mexican law was facilitated by a plant collection permit (NOM-059-SEMARNAT-2010) issued by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT SGPA/DGVS/2405/14). All species names follow The Plant List version 1.1 (2013).

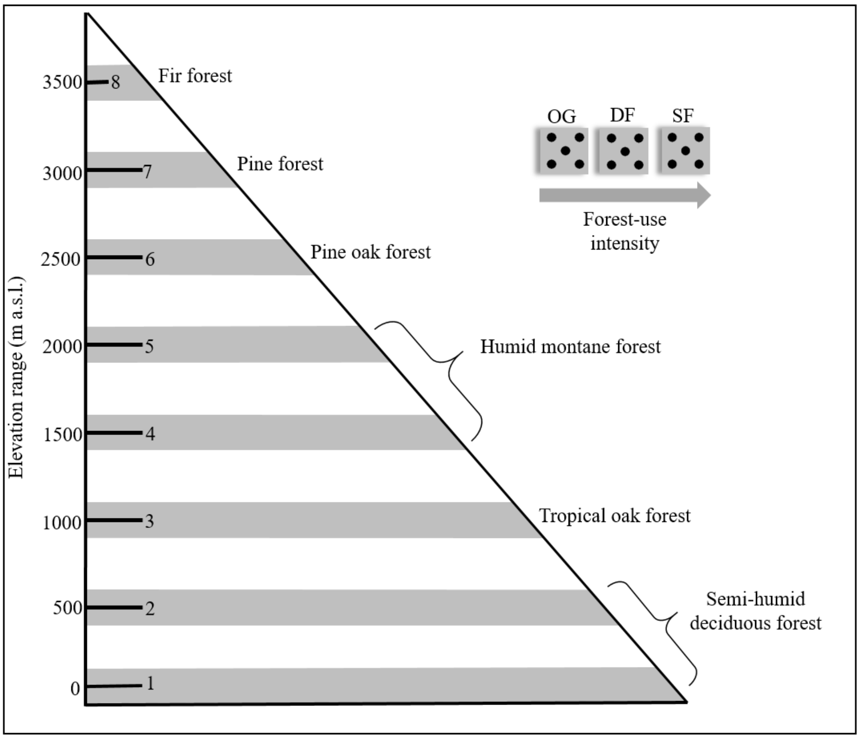

Figure 1.2. Schematic diagram illustrating the sampling design along the elevational gradient. Eight study sites were placed at every 500 m in elevation (numbered 1 to 8), and the respective vegetation type is given (following each section of the elevation). Forest-use intensity at each study site is represented with five plots each in old-growth forest (OG), degraded forest (DF), and secondary forest (SF) (total n = 120 plots).

Data analysis

Species diversity

We estimated plot-level species diversity using Hill numbers (Chao et al., 2014) in terms of the effective numbers of species to facilitate comparisons across elevations and FUI levels (Jost, 2006). As we recorded species incidences in plots and Johansson zones rather than abundances, we used incidence-based diversity estimators following

Chao et al. (2014). In this framework (Chao & Jost, 2012), q=0 (^{0}D) is species richness and gives equal weight to frequent and infrequent species; q=1(^{1}D) is Shannon diversity and gives more weight to more frequently observed species; and q=2 (^{2}D) is Simpson diversity, which can be interpreted as the effective number of dominant species (Chao et al., 2014). We calculated species richness (^{0}D) for the entire elevational gradient, although Shannon diversity (^{1}D) and Simpson diversity (^{2}D) were only analysed from 0 m to 2500 m due to the low number of species occurring at the two uppermost elevations. We calculated species accumulation curves for each FUI within each elevation using sample-size based rarefaction and extrapolation (Chao et al., 2014). We used the iNeXT package (Hsieh et al., 2016) for estimating plot-level diversity and fitting species accumulation curves.

Effect of forest-use intensity on vascular epiphyte diversity across elevation

To test how species diversity and the effects of FUI varied along the elevational gradient, we fitted separate nested analyses of variance for species richness, Shannon and Simpson diversities using the function *aov*, where elevation and FUI nested in elevation were the main factors. We then used Tukey's Honest Significant Differences post-hoc test to evaluate differences among FUI levels within each elevation with function *glht* in the R package 'multcomp' (Hothorn et al., 2008). To meet the assumption of normality, all diversity indices were natural logarithm transformed.

Effect of forest-use intensity and elevation on vascular epiphyte beta diversity

To investigate how species composition varies among FUI levels and along the elevational gradient, we calculated beta diversity using the Sørensen index (βSOR) and partitioned it into its turnover component (βSIM), which indicates that species of a specific site are replaced by other species, and its nestedness component (βSNE), which describes a species assemblage of a site as a subset of species of another site, reflecting species loss (Baselga, 2010). In this framework, βSOR = βSNE + βSIM (Baselga, 2012). We partitioned beta diversity and its components using the function *beta.sample* in the R package 'betapart' (Baselga & Orme, 2012) in two ways: i) among FUI levels at each elevation and ii) along the elevational gradient for each level of FUI using 1,000 randomly sampled subsets of 5 and 13 plots, respectively. We then calculated mean and 95% confidence intervals to compare beta diversity and its components across elevations and FUI levels. All analyses were performed using R version 3.4 (R Core

Team, 2018) with the packages ‘vegan’ (Oksanen et al., 2018), ‘car’ (Fox & Weisberg, 2019), ‘ggplot2’ (Wickham, 2016), ‘nlme’ (Pinheiro et al., 2018), ‘plyr’ (Wickham, 2011), ‘ecodist’ (Goslee & Urban, 2007), ‘MASS’ (Venables & Ripley, 2002), ‘iNeXT’ (Hsieh et al., 2016), and ‘betapart’ (Baselga & Orme, 2012).

1.4. Results

Across our 120 study plots, we recorded a total of 271 species of vascular epiphytes belonging to 92 genera and 23 families. The most species-rich families were Orchidaceae (82 species), Polypodiaceae (50), Bromeliaceae (41), Piperaceae (20), Cactaceae (14), and Araceae (12). We found the highest number of species at intermediate elevations (93 species, 1500 m). We recorded only 17 species at the lowermost elevation and only two species at the uppermost elevation. Identification to species level was possible for 72% of records, while another 26% were identified to genus level, and 1% to family level (for a complete species list, see Appendix Table A1).

Species diversity

Overall, species accumulation curves showed that the highest species richness (^{0}D) per FUI (n= 5 plots) was found in OG for sites at 0 m, 1000 m, 1500 m, and 2000 m elevation and in DF at 500 m and 2500 m, whereas SF consistently ranked lowest (Fig. 1.3). Accumulation curves revealed differences in species richness between FUI for three sites, as 95% confidence intervals were not overlapping at 500 m, 1000 m, and 1500 m between OG and SF. At the lowermost and two uppermost sites, as well as at 2000 m and 2500 m, the rarefaction and extrapolated curves indicated no differences among FUI (Fig. 1.3). Species accumulation curves approached saturation for all sites with the exception of those at 1500 m and 2000 m, suggesting that additional sampling at these locations is likely to result in finding more species. Species accumulation curves for Shannon diversity (^{1}D) (Appendix Fig. A1) and Simpson diversity (^{2}D) (Appendix Fig. A2) showed similar patterns, with higher diversity in OG at 0 m, 1000 m, 1500 m, 2000 m, and 2500 m and in DF at 500 m.

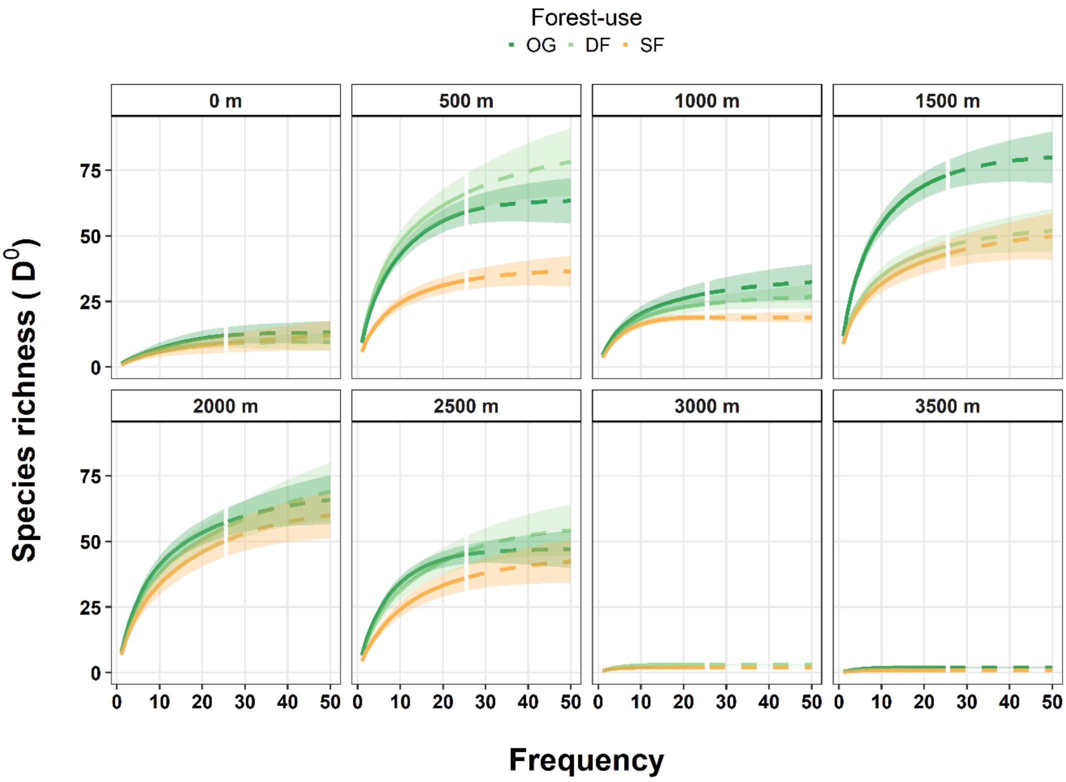

Figure 1.3. Incidence-based species accumulation curves for species richness of vascular epiphytes, showing rarefaction (solid lines) and extrapolated (dashed lines) curves for species richness Hill numbers (^{0}D), n= 5 plots per forest-use intensity across the eight study sites. Confidence intervals 95 % (shaded areas). Abbreviations: Old-growth forest (OG, dark green), degraded forest (DF, light green), and secondary forest (SF, orange). See Figs. A3.1 and A3.2 for Shannon (^{1}D) and Simpson (^{2}D) diversities.

Effect of forest-use intensity on vascular epiphyte diversity across elevation

Plot-level epiphyte species richness (^{0}D) varied significantly among elevations ($F_{7.96}$ =73.2, P-value: < 0.001) and among FUI levels along the elevational gradient ($F_{16.96}$ =2.52, P-value: < 0.001) (Fig. 1.4). Shannon and Simpson diversity also varied significantly with elevation (Appendix Table A2). Multiple comparisons among FUI and elevation revealed significant differences between OG and SF at 500 m, 1000 m, 1500 m, and 2500 m, between OG and DF at 1500 m (P-value <0.01), between DF and SF at 500 m (P-value <0.1), and between DF and SF at 2500 m (P-value<0.10, Appendix Table A3). Forest-use intensity levels showed similar results, with epiphyte species richness being almost consistent with a mid-elevation peak. Similar patterns were observed for Shannon and Simpson diversity (Appendix Fig. A3 and A4). Species richness was lowest in SF across all study sites. However, at 0 m, 2000 m, 3000 m, and 3500 m we observed no significant differences in species richness within FUI. Similarly, we found no differences in Shannon and Simpson diversities at 0 m and 2000 m within FUI.

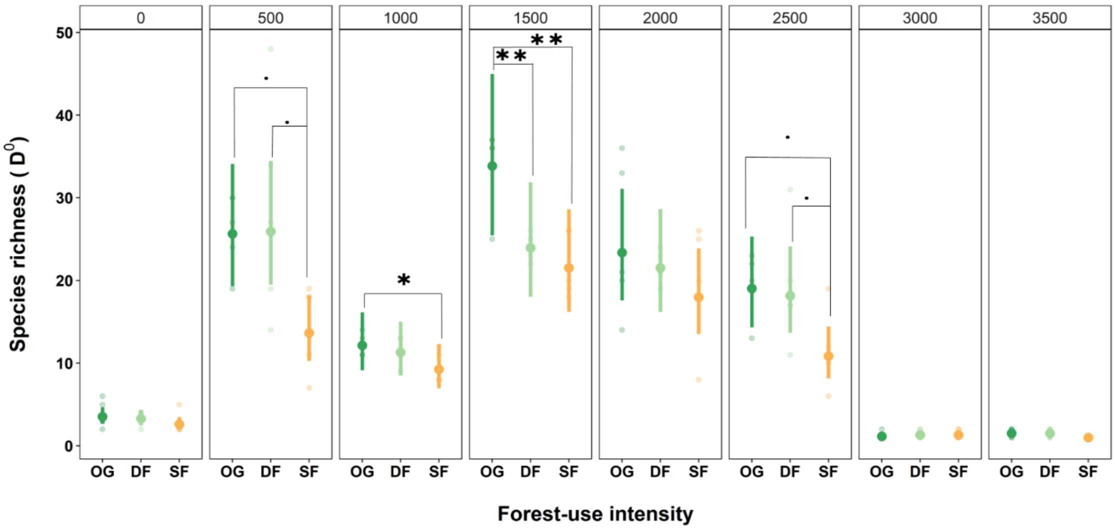

Figure 1.4. Variation in species richness (^{0}D) of vascular epiphytes across different levels of forest-use intensity along an elevational gradient. 95% Confidence intervals shown with colour bars. We tested multiple comparisons among forest-use intensity types (n= 5 plots per forest-use intensity across the eight study sites), which revealed significant differences between OG and SF at 500 m, (P-value <0.1, indicated as '.'), at 1000 m (P-value <0.05, indicated as '*'), at 1500 m (P-value <0.01, indicated as '**'), and 2500 m (P-value <0.1, '.'), between OG and DF at 1500 m (P-value <0.01,'**'), and between DF and SF at 500 m (P-value <0.1, '.'), and at 2500 m (P-value <0.1, '.', Appendix Table A3).

Effect of forest-use intensity and elevation on vascular epiphyte beta diversity

Across all elevations, beta diversity (βSOR) was dominated by turnover (βSIM) along the forest-use intensity gradient, while nestedness (βSNE) played only a minor role (Fig. 1.5). In general, we found a decrease in βSOR with increasing elevation. βSIM was significantly greater than βSNE across FUI levels, except at 3500 m where βSNE was higher. Nevertheless, our results show that βSOR (i.e. spatial variation among FUI levels) did not vary with elevation, except for the uppermost elevation (3500 m, Fig. 1.5). Within each FUI level, we found that beta diversity along the elevational gradient was similar, i.e. 95% confidence intervals did overlap (Fig. 1.6). Similarly, beta diversity was dominated by the turnover component (BSIM) along the elevational gradient for each FUI.

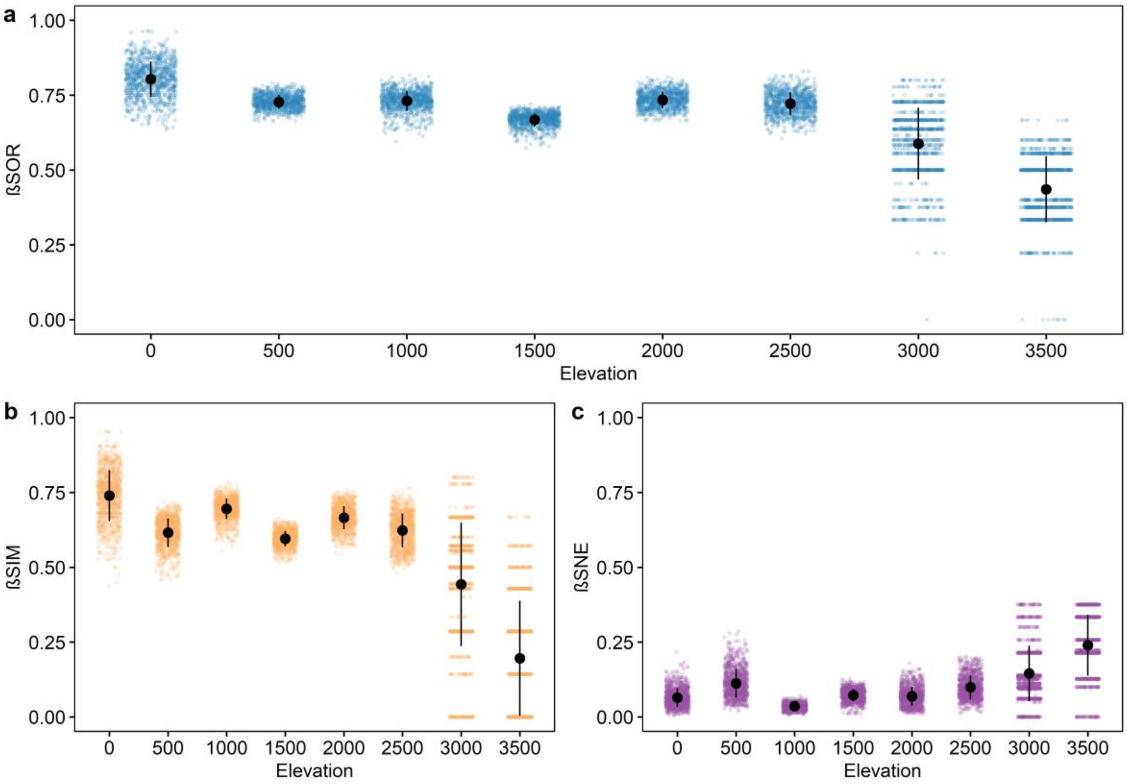

Figure 1.5. Beta diversity across the forest-use intensity gradient within each elevational belt. Beta diversity is based on the Sørensen index (a; βSOR), and partitioned into both its turnover component (b; βSIM) reflecting species replacement, and nestedness component (c; βSNE) reflecting species loss of vascular epiphytes. Each black point represents average beta diversity, which was derived from 1000 randomly sampled subsets of 5 plots within each elevation belt across forest-use intensity gradient. Bars are 95% confidence intervals.

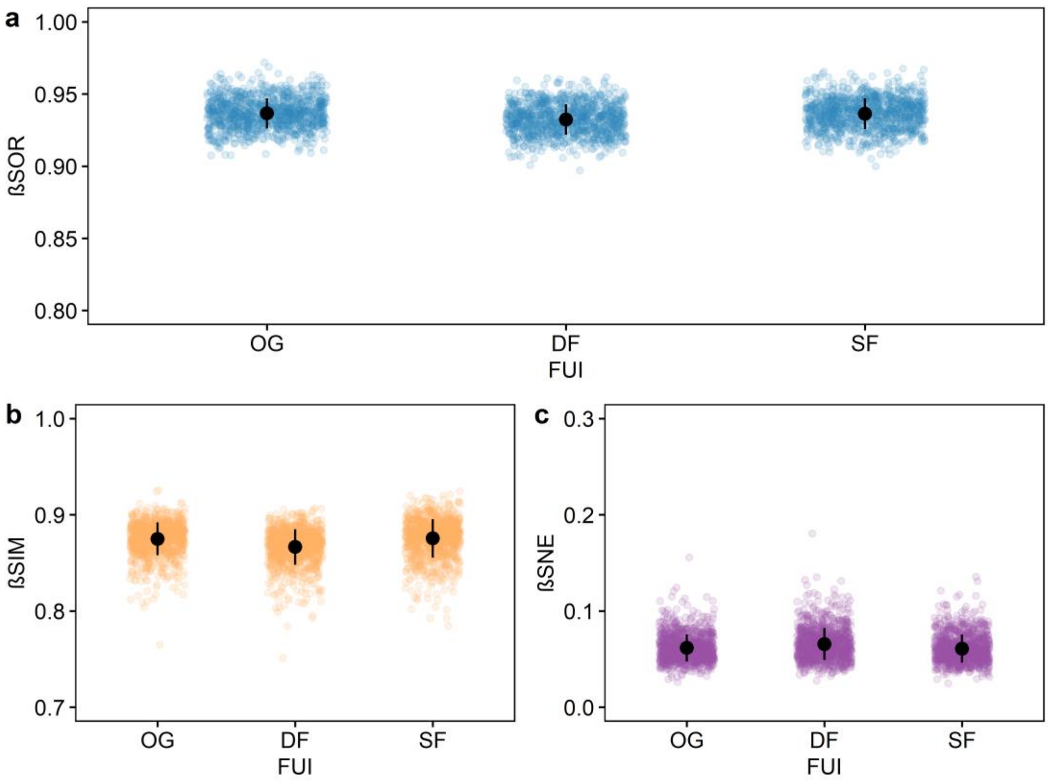

Figure 1.6. Beta diversity across elevations within each forest-use intensity type. Beta diversity is based on the Sørensen index (a; βSOR) and partitioned into its turnover component (b; βSIM) reflecting species replacement, and nestedness component (c; βSNE) reflecting species loss of vascular epiphytes. Each black point represents average beta diversity based on 1000 randomly sampled subsets of 13 plots within each forest-use intensity across the elevational gradient. Bars are 95% confidence intervals.

1.5. Discussion

This is the first study to investigate the effect of forest-use intensity on vascular epiphyte diversity and composition along a 3500-m elevational gradient. We found that the interactive effects of elevation and forest-use intensity strongly impacted local-scale patterns of vascular epiphyte diversity. In parallel, the spatial turnover in species composition among forest-use intensity levels was similar at most elevational belts and – with the exception of the highest elevations – were dominated by the turnover component of beta diversity.

Elevational patterns in vascular epiphyte diversity

In line with our first hypothesis, we found that species richness of vascular epiphytes along the Cofre de Perote transect peaked in humid montane forests at mid-elevations, and monotonically decreased from 1500 m towards the upper limit of the elevational gradient. This observation is consistent with previous studies on elevational patterns in epiphytes (Cardelús et al., 2006; Kessler et al., 2011; Kluge et al., 2006; Krömer et al., 2005; Wolf & Flamenco, 2003). Unexpectedly, species richness showed a bimodal pattern with a second peak of species richness occurring in tropical oak forests at 500 m. It is unclear whether this deviation from the expected hump-shaped pattern (McCain & Grytnes, 2010) is due to an unusually high diversity found at 500 m, which was on average comparable to diversity at 1500 m, or an unusually low diversity of vascular epiphytes at the 1000 m site. Interestingly, the low gamma richness of epiphyte communities at 1000 m (40 species) compared to 500 m (89) mirrors results of previous studies on terrestrial herbaceous angiosperms (Gómez-Díaz et al., 2017) and ferns and lycophytes (Carvajal-Hernández & Krömer, 2015) in the same study area. The lower species richness at 1000 m might also be not related to lower rainfall at this elevation (Carvajal-Hernandez & Krömer, 2015). Few species occurred at the lowest end of the elevational gradient, which we attribute to the pronounced dry seasons, deciduous host trees, high mean annual temperatures, and low mean annual precipitation (Gentry & Dodson, 1987; Kreft et al., 2004). Furthermore, this site is located close to the Gulf of Mexico, where the studied forests grow on sandy soils and are exposed to strong winds and high salinity (García-Franco, 1996).

Above 2000 m, epiphyte diversity declined with elevation in all forest-use intensities, most likely reflecting changing climatic conditions. A potential explanation for declines of epiphyte diversity at higher elevations are low temperatures and frequent frost events above 3000 m (-3°C absolute minimum temperature; Carvajal-Hernández, unpublished data; Bhattarai et al., 2004; Krömer et al., 2005). Additionally, it is important to note that the only three species found at both uppermost elevations were ferns of the Polypodiaceae family. Interestingly, Polypodiaceae species were also reported as the highest-growing epiphytes above 4000 m in the Peruvian Andes (Sylvester et al., 2014) and *Polypodium vulgare* is also the epiphyte species with the northernmost and highest occurrences in Europe, where it is able to survive prolonged periods of frost (Zotz, 2005). Because all these regions are comparatively humid, we tentatively suggest that frost is a main constraining factor at upper elevations. Besides the effect of harsh climatic condition, an alternative factor might be that conifers of the genera *Pinus* and *Abies* are poor epiphyte hosts. Whereas there is no information about the quality of *Abies* as hosts, pines have been considered as poor epiphyte hosts, not only because of phenolic and resinous substances (Hietz & Hietz, 1995; Wolf, 2005), but also because of low water-holding capacities of their bark (Callaway et al., 2002). Additionally, the monopodial growth and lack of large horizontal branches of some conifers might be a constraining factor limiting epiphyte abundance and diversity.

Effect of forest-use intensity on vascular epiphyte diversity across elevation

Contrary to our second hypothesis, we did not observe a consistent decrease in species richness with increasing forest-use intensity. We expected that vascular epiphytes would be particularly affected by the conversion of intact forest into other land-use types, mainly because of the loss of suitable host trees that provide a complex mosaic of microhabitats (Benzing, 1995; Hietz-Seifert et al., 1996). This has been shown previously in studies demonstrating that epiphyte diversity decreases with increasing levels of disturbance in montane areas (Barthlott et al., 2001; Köster et al., 2009; Krömer & Gradstein, 2003; Nöske et al., 2008; Wolf, 2005).

We present evidence that this pattern does not always hold. Species diversity may even be slightly higher in more disturbed areas, such as DF occurring at 500 m, a pattern which also has been reported from Indonesia (Böhnert et al., 2016). However, species richness was consistently lowest in SF across all elevations and differed significantly from OG at half of the sites (Fig. 1.4). The largest differences in species diversity between OG, DF and SF were observed at 1500 m (Fig. 1.4). Our results are in line with Carvajal-Hernández et al. (2017), who found a significant reduction in fern species richness in disturbed and secondary forests compared to the intact forest, which the authors related to changes in forest structure and microclimate. Moreover, Krömer et al. (2014) found that a disturbed forest at this elevation had reduced species richness of epiphytes due to harvesting activities of epiphytes (mainly orchids) that are sold as ornamental plants in local markets (Flores-Palacios & Valencia-Díaz, 2007; Toledo-Aceves et al., 2014).

At the two uppermost elevations, we did not find differences in species diversity among FUI levels. This likely reflects the low local species richness where the few fern species present are physiologically preadapted to tolerate environmental conditions at high elevations (Hietz, 2010; Stuart, 1968), which might also be an advantage in degraded and secondary forests. At the lowest elevation, we did not observe differences in species diversity among FUI levels either, again reflecting the low overall species richness, which may be attributable to the physiological and morphological preadaptations of drought-tolerant species to cope with changes in forest structure (Barthlott et al., 2001). While OG forests had the highest species richness in most of our study sites (except 500 m and 2500 m), DF and SF also showed comparable levels of species richness at most elevations (Fig. 1.4), highlighting the potential of degraded and secondary forests to maintain, to some extent, the epiphyte diversity in tropical forests (Chazdon et al., 2009b; Böhnert et al., 2016). However, species with specific habitat requirements, such as shade- and humidity-adapted understory orchids and ferns, might not be able to persist in highly disturbed forests (Krömer et al., 2014) and can only be protected in old-growth forests. Furthermore, other forest- or land-use types that maintain isolated trees or live fences where epiphytes can persist should be taken into account when developing conservation strategies (Einzmann & Zotz, 2016; Köster et al., 2009).

Effect of forest-use intensity and elevation on vascular epiphyte beta diversity

Our results show that the magnitude of spatial turnover of vascular epiphyte community composition across FUI levels was similar within most elevations and that it was usually dominated by the turnover component of beta diversity. This suggests that similar ecological mechanisms, such as niche partitioning, operate along the entire elevational gradient and likely determine shifts in community composition (Soinen et al., 2018). Our results agree with those of previous studies, which have reported changes in the composition of vascular epiphytes across land-use or habitat types, e.g. preserved forests and forest fragments or isolated trees in pastures (Barthlott et al., 2001; Benavides et al., 2006; Flores-Palacios & García-Franco, 2008; Hietz-Seifert et al., 1996; Larrea & Werner, 2010; Werner et al., 2005; Wolf, 2005).

Along the elevational gradient, we found no difference in beta diversity among forest-use intensity levels (Fig. 1.6). This suggests that even when controlling for differences in forest-use intensity, species composition in vascular epiphyte communities is strongly regulated by the changes in environmental conditions that occur along the elevational gradient. Moreover, the high relative importance of the turnover component illustrates the high degree of habitat specialization of epiphytes within each forest-use intensity level. Thus, our analysis reveals that similar ecological processes, e.g. niche partitioning, likely operate along both forest-use intensity (Fig. 1.5) and elevational gradients (Fig. 1.6) via their influence on microclimate.

1.6. Conclusions

We found that interactive effects of elevation and forest-use intensity strongly influence the spatial patterns of vascular epiphyte diversity in this tropical mountainous region. Our results also show that the impact of forest-use intensity on epiphyte diversity is not consistently negative, suggesting that tropical landscapes with degraded and secondary forests can maintain high levels of epiphyte diversity. Degraded and - to a lesser extent - secondary forests may host a considerable level of epiphytic biodiversity and therefore may act as reservoirs for conservation and restoration. The differences between forest-use intensity levels only emerged at the scale of gamma diversity, calling for a landscape-level perspective to understand the effects of land-use change on tropical biodiversity. Consequently, conservation and restoration initiatives should integrate such a perspective by conserving heterogeneity within landscapes, rather than relying uniquely on the protection of old-growth forest fragments.

Acknowledgements

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Humid montane forest in El Zapotal, Veracruz, Mexico at 2000 m a.s.l.

2. Leaf trait variation in vascular epiphytes along broad- and small-scale environmental gradients

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2.1. Abstract

1 Variation in leaf functional traits along environmental gradients can reveal how vascular epiphytes respond to broad- and small-scale environmental gradients. Along elevational gradients, both temperature and precipitation likely play an important role as drivers of leaf trait variation, but these traits may also respond to small-scale changes in light, temperature, and humidity along the vertical environmental gradient within forest canopies. However, the interplay and relative importance of broad- and small-scale environmental gradients as drivers of variation in leaf functional traits of vascular epiphytes is poorly understood.

2 Here, we examined variation in morphological and chemical leaf traits of 102 vascular epiphyte species along two environmental gradients: *i*) a broad-scale environmental gradient approximated by sampled elevation, as well as by species' minimum and maximum elevational distributions, and *ii*) small-scale environmental gradients represented by the relative height of attachment of an epiphyte on a host tree. We also assessed whether variation in morphological and chemical leaf traits along these gradients were consistent across photosynthetic pathways (CAM and C_3).

3 Broad- and small-scale environmental gradients explained more variation in chemical traits (marginal R^2: 12-90%) than in morphological traits (marginal R^2: 1-23%). For example, carbon isotope ratio ($\delta^{13}C$) a proxy for water-use efficiency varied systematically across both environmental gradients, suggesting a decrease of water-use efficiency with increasing minimum and maximum elevational distributions and an increase with relative height of attachment. The influence of minimum and maximum elevational distributions on trait variation differed between photosynthetic pathways, except for leaf dry

matter content and leaf nitrogen-to-phosphorus ratio. Contrary to our expectations, broad- and small-scale environmental gradients explained little of the variation in morphological leaf traits, suggesting that environmental conditions do not constrain morphological leaf trait values of vascular epiphytes.

4 Our findings suggest that analysing multiple drivers of leaf trait variation and considering photosynthetic pathways is key for disentangling the mechanisms underlying responses of vascular epiphytes to environmental conditions.

Keywords: chemical and morphological traits, trait-environment relationships, elevational gradients, tropical forests, vascular epiphytes, Mexico

2.2. Introduction

Vascular epiphytes differ from other life forms by growing non-parasitically on other plants. They lack direct contact with the soil and therefore exhibit a diverse array of highly specialized strategies to acquire, process, and use available resources in the canopy of their hosts (Zotz, 2016). While functional traits and associated ecological strategies of vascular epiphytes may vary in response to broad-scale climatic conditions along environmental gradients, similar to other plant life forms (Schellenberger-Costa et al., 2018), they may also vary along vertical small-scale microclimatic gradients within their host trees (Petter et al., 2016). For example, leaves of vascular epiphytes range from soft and hygrophilous to xeromorphic and/or succulent, and vary in relation to changes in water and nutrient availability along elevational (Hietz & Briones, 1998; Schellenberger-Costa et al., 2018) and vertical gradients (Petter et al., 2016; Agudelo et al., 2019). While broad- and small-scale climatic gradients likely influence ecological strategies of vascular epiphytes jointly, their relative importance is unresolved.

Epiphytism has evolved independently in many plant groups, with orchids accounting for 68% of all epiphyte species, other prominent taxa being ferns and bromeliads (Zotz, 2013). Different lineages have evolved distinct morphological and physiological traits to cope with the many environmental constraints of the epiphytic habitat (Zotz, 2016). Consequently, the ecological strategies of vascular epiphytes are likely phylogenetically conserved (Dubuisson et al., 2008). A universal trait relationship for all plants is reflected in the leaf economics spectrum, representing a fundamental trade-off between two contrasting ecological strategies, i.e. rapid resource acquisition for fast growth versus resource conservation for high survival (Wright et al. 2004; Reich, 2014). In general, vascular epiphytes are considered slow growing plants that exhibit traits associated with “slow” species, because of their low foliar nutrient concentrations and long leaf lifespan (Zotz, 1998).

Vascular epiphytes use two kinds of photosynthetic pathways: C_3-photosynthesis (C_3) and Crassulacean acid metabolism (CAM) (Zotz, 2016). Variation in the photosynthetic pathway is reflected in the carbon isotope ratio ($\delta^{13}C$; Silvera et al., 2010), which captures variation in water-use efficiency (Ehleringer, 1993a). On the one hand, C_3 plants are typically better adapted to cooler climates and have a wide range of optimum temperatures for photosynthesis (Yamori et al., 2014). On the other hand, CAM species absorb CO_2 during night-time, resulting in higher water-use efficiency (Cernusak et al., 2013), which provides an advantage in drier environments (Van de Water et al., 2002; Torres-Morales et al., 2020). In addition, CAM epiphytes generally have thicker leaves and often grow in the upper canopy (Winter et al., 1983; Smith et al., 1986). We therefore expect C_3 and CAM plants to respond differently along gradients in water availability.

Environmental conditions, particularly temperature and precipitation, are known to determine species distributions and diversity patterns in vascular epiphytes (Gentry & Dodson, 1987, Kreft et al., 2004), which may influence leaf trait variation. For instance, environmental conditions in tropical montane forests may favor plants that can tolerate high cloud cover, high humidity, and lower temperatures. Adaptations to these environmental conditions may be reflected in plant traits, such as in lower leaf dry matter content (LDMC) and C_3 photosynthesis (Hietz, et al., 1999). In contrast, vascular epiphyte species with CAM photosynthesis dominate in seasonally dry tropical forests, where thicker leaves and other water storage organs allow them to tolerate extended periods of water deficit. Therefore, changes in water availability along a broad-scale environmental gradient may determine dominant ecological strategies of vascular epiphytes through environmental filtering (Hietz et al., 1999; Petter et al., 2016).

Marked vertical environmental gradients also exist within the canopy, and this may also influence the distribution of species and leaf traits in vascular epiphytes. For example, vascular epiphytes growing in the upper canopy are exposed to more direct sunlight, hotter temperatures and greater diurnal variation in abiotic conditions (Krömer et al., 2007; Böhnert et al., 2016). Thus, vascular epiphytes growing in the upper canopy are expected to have higher LDMC, higher $\delta^{13}C$ values (i.e. less negative $\delta^{13}C$ values and higher water-use efficiency), lower leaf area, and lower specific leaf area (SLA) compared to epiphytes growing in the darker yet more humid lower canopy (Gotsch et al., 2015; Hietz & Briones, 1998; Petter et al., 2016; Wagner et al., 2013).

In addition to light and water availability, nutrient availability within forest canopies may also affect the distribution of vascular epiphytes (Wania et al., 2002). The nutrient regime in the canopy is mostly influenced by two types of inputs: *i*) external nutrient inputs from dry deposition, rain, and droplets in clouds or fog (also known as “occult” or “horizontal” precipitation; Reynolds and Hunter, 2004), and *ii*) internal inputs including leaf fall of the host tree, decomposing leaf litter, branches and bark, and host tree leachates in stemflow and throughfall (Zotz, 2016). Together, these inputs produce a heterogeneous mosaic of nutrient availability within the canopy, where epiphytes in the upper canopy almost completely depend upon atmospheric sources, while nutrient uptake by plants in the lower canopy is largely from leachates and run-off of dry deposited aerosols and gaseous materials from leaves and branches (Zotz, 2016). The N:P relationship is of particular interest as nitrogen and phosphorus are important elements that regulate plant growth, with both elements being critical in regulating ecosystem functions and dynamics (Güsewell, 2004; Vitousek et al., 2010). Studies on stable isotopes have provided evidence of differences in nutrient acquisition strategies among canopy positions by tracking the source of nitrogen through stable nitrogen isotopes ($\delta^{15}N$) (Stewart et al., 1995; Hietz et al., 2002; Wania et al., 2002). While some epiphytes with strong ^{15}N depletion appear to obtain nitrogen mainly from direct atmospheric deposition, others have access to nitrogen through intercepted water and decomposition of organic matter on the branches or in tanks (i.e. phytotelmata; Zotz, 2016). Thus, we expect that canopy position, i.e. the relative height of attachment, may lead to consistent effects on leaf $\delta^{15}N$ of vascular epiphytes.

In this study, we assessed the relative importance of broad- and small-scale environmental gradients in determining variation in leaf traits of 102 vascular epiphyte species. We further assessed whether the influence of environmental gradients on leaf traits is consistent among C_3 and CAM plants. We expected trait values of epiphyte species growing under conditions with lower water supply and higher temperatures, i.e. at the lowest elevations or in the upper canopy, should shift towards trait values associated with greater drought tolerance and nutrient retention, in contrast with epiphyte species occurring at higher elevations or lower in the canopy, with a more stable water and nutrient supply and lower temperatures.

2.3. Methods

Study area

Data were collected at three different elevations on the eastern slopes of the Cofre de Perote mountain in the central part of Veracruz State, Mexico. In this region, the Trans-Mexican volcanic belt and the Sierra Madre Oriental converge, combining floristic elements from the Nearctic and Neotropics. We sampled at three different elevations (0, 500, and 1500 m). The climate changes from tropical dry at 0 m a. s. l. with mean annual temperature (MAT) of 26 °C and mean annual precipitation (MAP) of 1222 mm, to intermediate (MAT: 23 °C; MAP: 946 mm) at 500 m a. s. l., and humid-temperate at 1500 m a. s. l. (MAT: 19 °C, MAP: 1436 mm; data from the National Meteorological Service of Mexico, 1951–2010). The vegetation of the first two sampled elevations is dominated by semi-humid deciduous forest and at the highest sampled elevation by humid montane forest (Carvajal-Hernández et al., 2020).

Data collection

Sampling took place within 45 non-permanent plots of 20 m × 20 m distributed across the three sampled elevations (15 plots per elevation; details about the diversity and composition of vascular epiphyte species along the entire elevational gradient in Guzmán-Jacob et al., 2020). At each plot, vascular epiphytes were sampled up to a height of 20 m on one or more trees using the single-rope climbing technique (Krömer & Gradstein, 2016). Vascular epiphytes below 6 m were sampled from the ground using a collecting pole. Traits were assessed for all species classified as holoepiphytes (epiphytes in the strict sense, i.e. species that complete their whole life cycle as epiphytes), excluding nomadic vines, and hemiepiphytes because of their imminent contact with the ground (Zotz, 2013). Additionally, we excluded species of the family Cactaceae because the main photosynthetic organs in cacti are stems.

Leaf trait measurements

We collected between one and three leaves per adult individual to obtain, if possible, a maximum of 10 leaves per species. We only sampled fully expanded leaves without visible signs of herbivory or disease. Collected leaves were rehydrated in a sealed plastic bag and kept cool in a refrigerator at 7°C for a minimum of 8 h before taking additional measurements. Leaf area was measured with a portable laser area meter (CI-202, CID Bio Science Inc. U.S.A.). Leaf thickness was measured with an electronic calliper (precision: 0.05 mm). Leaves were weighed to obtain fresh weight (balance: A&D GR-202; A&D Company, Tokyo, Japan; precision: 0.1 mg), oven dried at 70°C for 48 h or until obtaining a constant dry weight, and reweighed to obtain dry weight. For each individual leaf sample, we determined the following morphological traits following the protocols described by Pérez-Harguindeguy et al. (2013) and Kitajima et al. (2010): specific leaf area (SLA = leaf area/dry weight; mm^2 mg^{-1}), leaf dry matter content (LDMC = dry weight/fresh weight; g g^{-1}), leaf density (SLA/leaf thickness; g cm^{-3}), and leaf area (mm^2).

We determined the following chemical leaf traits: leaf nitrogen content (leaf nitrogen; %), nitrogen isotope ratio ($\delta^{15}N$; ‰), carbon isotope ratio ($\delta^{13}C$; ‰), leaf phosphorus content (leaf phosphorus; %), and nitrogen-to-phosphorus ratio (N:P; mass-based). Dried leaf samples were homogenized using a ball mill. To quantify nitrogen content, $\delta^{15}N$ and $\delta^{13}C$, we used an elemental analyser-isotope ratio mass spectrometer (Carlo Erba 1110 EA coupled via a Conflo III to a Delta^{PLUS}; Thermo Electron, Bremen, Germany). As international standards, atmospheric air (AIR) was used for $\delta^{15}N$ and the Vienna Pee Dee Belemnite (V-PDB) for $\delta^{13}C$.

The carbon isotope ratio was calculated as:

$$\delta^{13}C\ (‰) = [(^{13}C/^{12}C\ \text{sample})/\ (^{13}C/^{12}C\ \text{standard})-1] \times 1000$$

The nitrogen isotope ratio was calculated as:

$$\delta^{15}N\ (‰) = [(^{15}N/^{14}N\ \text{sample})/\ (^{15}N/^{14}N\ \text{standard})-1] \times 1000$$

We categorized species as either CAM or C_3 based on carbon isotope ratios as a proxy (Silvera et al., 2010), using the widely accepted threshold of $\delta^{13}C$ values of > -20 ‰ for strong CAM species and < -20 ‰ for C_3 species (Hietz et al., 1999; Winter, 2019).

To determine leaf phosphorus, aliquots (5 mg) of leaf samples were digested in 200 µl concentrated HNO_3 and 30 µl 30% H_2O_2 (Huang & Schulte, 1985). Leaf phosphorus concentrations were determined colorimetrically (Murphy & Riley, 1958). After the digestion, 770 µl distilled water was added and the absorption by the molybdenum-phosphorous complex was measured at 710 nm using a UV-VIS spectrophotometer (Specord 50, Analytik Jena, Jena, Germany). Chemical analyses of samples were performed at the University of Oldenburg for leaf phosphorus and at the University of Vienna, Department of Microbiology and Ecosystem Science for leaf nitrogen, $\delta^{15}N$ and $\delta^{13}C$.

Broad-scale environmental gradients

Sampled elevation corresponds to the elevation where each sample was collected, i.e. either 0 m, 500 m, or 1500 m. As proxies for ecological limits, e.g. climate, we determined minimum and maximum elevational distributions of each species based on reported species occurrences in the study region (Veracruz state) from the literature

(Hietz & Hietz-Seifert, 1994; Krömer et al., 2013a, b; Acebey et al., 2015; Carvajal & Krömer, 2015; Vergara-Rodríguez et al., 2017) and herbarium specimens deposited at the herbarium XAL of the Instituto de Ecología, A. C. in Xalapa, Mexico. Minimum and maximum elevational distributions likely relate to the ecological limits of each species, i.e. the minimum and maximum temperatures at which a species can survive and reproduce.

Small-scale environmental gradients

For all individuals we measured the point of attachment, which we defined as the height above ground at which an epiphyte is attached to the trunk or tree branch using a laser distance meter (DISTO™ X310, Leica Geosystems AG, Switzerland). Relative height of attachment was then calculated as the ratio of the observed height of attachment of the epiphyte and the mean height of the five tallest trees with a diameter at breast height ≥ 5 cm in each plot (King et al., 2006) based on data from the same study region by Monge-González et al. (2020). Using height above ground instead of the pre-defined Johansson zones might be better to approximate the environmental gradient within the forest (Zotz, 2007).

Data analysis

Trait variation among species was visualized using principal component analysis (PCA; R package ‘vegan’; Oksanen et al., 2013), for which all leaf traits were scaled and centred.

We used linear mixed-effect models to analyse variation in morphological and chemical leaf traits along broad- and small-scale environmental gradients and to assess if trait variation along environmental gradients is consistent among photosynthetic pathways. We used the same fixed effects across all models. For fixed effects, we included sampled elevation and photosynthetic pathway (CAM, C_3) as categorical variables, minimum and maximum elevational distributions and relative height of attachment as continuous variables, and two-way interactions between each variable associated with environmental gradients and photosynthetic pathway. The random effect structure differed between models for morphological and chemical traits due to differences in sampling resolution. Morphological traits included within-individual variation, while chemical traits did not. For morphological traits, we therefore included individuals nested in species nested in families (family/species/individual) as a random intercept.

For chemical traits, we included species nested in families (family/species) as a random intercept. As ecological strategies of vascular epiphytes may be conserved within families (Dubuisson et al., 2008), we included family as a random effect. For model convergence, we used the ‘Nelder-Mead’ optimizer in the R package ‘lme4’ (Bates et al., 2015). Model assumptions were checked by visually inspecting residuals for homogeneity of variance and Pearson residuals for normality. To evaluate model variation explained by fixed and random effects, marginal and conditional R^2 were calculated using the ‘performance’ package (Lüdecke et al., 2019). Marginal R^2 values represent model variation explained by fixed effects and conditional R^2 values represent model variation jointly explained by random and fixed effects. We extracted the results of the linear mixed-effect models using the ‘Anova’ function with type III sum of squares and Wald F-test in the R package ‘car’ (Fox & Weisberg, 2019). Variance partitioning of the random effects was assessed using the ‘VarCorr’ function in the ‘lme4’ R package (Bates et al., 2015). Differences in trait variation among families and between pathways were tested using a permutational multivariate analysis of variance (PERMANOVA, adonis from ‘vegan’ R package; Anderson 2001). To meet the assumption of normality, all non-normally distributed response variables were natural logarithm-transformed prior to analysis. For all model predictions, we calculated 95% confidence intervals with the ‘ggeffects’ package (Lüdecke, 2018). Model estimates were plotted using the R package ‘dotwhisker’ (Solt & Hu, 2018). All analyses were performed in R 3.6.0 (R Development Core Team, 2018).

2.4. Results

Overall, we collected and measured 1595 leaves from 474 individuals belonging to 102 species of vascular epiphytes in 10 families. Most species were orchids (42.7%), followed by ferns (28.1%) and bromeliads (20.4%) (Table 1). We recorded three families at the lowermost elevation, five at 500 m, and all ten families at 1500 m (Appendix Fig. B1). The proportion of CAM species sharply dropped from 77.7% at 0 m, to 33.3% at 500 m and 5.4 % at 1500 m (Appendix Fig. B2).

Vascular epiphyte species varied markedly in their leaf traits (Fig. 2.1), with the first two axes of the principal component analysis (PCA) explaining 35% and 26% of variation. The first principal component (PC1) was largely determined by leaf phosphorus, leaf nitrogen, and SLA. The second principal component (PC2) was associated principally with leaf density, LDMC and leaf N:P. $\delta^{13}C$ and $\delta^{15}N$ contributed to both axes. Trait variation along both axes of the PCA among families was similar, as ellipses of most families overlapped (Fig. 2.1a). However, trait variation along both axes of the PCA among photosynthetic pathways showed a moderate degree of overlap among photosynthetic pathways (Fig. 2.1b). The PERMANOVA indicated significant differences among the five most diverse families (R^2: 35%, F-value 12.8, P-value < 0.001) and between photosynthetic pathways (R^2: 21%, F-value 28.5, P-value < 0.001).

Table 2.1. Leaf trait values per taxonomic group of vascular epiphytes. Proportions of species are given in parentheses. Data are: means, SD in brackets. Leaf area, specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen, leaf phosphorus, leaf nitrogen-to-phosphorus ratio (N:P), nitrogen isotope ratio (δ^{15}N), and carbon isotope ratio (δ^{13}C). Because only one species was observed for Hymenophyllaceae, SD values do not apply for leaf chemical traits for this family.

	Araceae	**Aspleniaceae**	**Bromeliaceae**	**Dryopteridaceae**	**Hymenophyllaceae**	**Lycopodiaceae**	**Orchidaceae**	**Piperaceae**	**Polypodiaceae**	**Pteridaceae**
Individuals	14	7	175	13	3	2	128	29	100	3
Measurements	51	23	521	48	6	11	485	124	315	11
Species	2 (1.9%)	2 (1.9%)	21 (20.3%)	4 (3.8%)	1 (0.9%)	2 (1.9%)	44 (42.7%)	7 (6.7%)	19 (18.4%)	1 (0.9%)
Leaf area$_{\mathrm{mm}^2}$	3012 ± 5362	58124 ± 3630	6647 ± 12024	6645 ± 5613	136 ± 51	15 ± 4	4383 ± 4514	837 ± 81	11268 ± 15930	136.6 ± 61.4
Leaf density $_{\mathrm{g\ cm}^3}$	0.26 ± 0.94	0.46 ± 0.16	0.21 ± 0.18	0.50 ± 0.23	0.88 ± 0.42	0.26 ± 0.12	0.17 ± 0.09	0.07 ± 0.03	0.36 ± 0.24	0.24 ± 0.13
SLA$_{\mathrm{mm}^2\mathrm{mg}}$	12.8 ± 3.2	20.99 ± 5.28	10.03 ± 6.02	11.2 ± 5.2	13.7 ± 3.5	17.6 ± 6.7	11.8 ± 7.03	24.08 ± 13.3	16.6 ± 9.6	7.5 ± 3.1
LDMC $_{\mathrm{mg\ g}}$	184.04 ± 31.6	305.3 ± 56.6	148.1 ± 53.9	277.9 ± 56.9	677.3 ± 107.5	205. 3 ± 82.7	159.9 ± 79.7	77.1 ± 31.6	254.01 ± 97.7	154.4 ± 53.09
Leaf nitrogen $_{\%}$	1.2 ± .24	2.1 ± 0.1	0.76 ± 0.36	1.4 ± 0.4	1.4	1.8 ± 0.5	1.2 ± 0.69	2.05 ± 0.80	1.5 ± 0.6	1.8 ± 0.5
Leaf phosphorus $_{\%}$	0.24 ± 0.06	0.33 ± 0.03	0.12 ± 0.07	0.21 ± 0.02	0.29	0.28 ± 0.13	0.26.9 ± 0.11	0.4 ± 0.1	0.34 ± 0.15	0.3 ± 0.20
N:P	5.3 ± 1.3	6.2 ± 0.62	6.6 ± 3	6.9 ± 2.7	5.08	6.8 ± 1.5	4.6 ± 1.37	5.1 ± 1.9	5.2 ± 2.3	5.7 ± 1.8
δ^{15}N $_{(‰)}$	-3.32 ± 2.9	-5.10 ± 0.1	-6.7 ± 2.6	-7.14 ± 1.1	-7	-4.23 ± 0.2	-3.9 ± 2.1	-4.7 ± 1.4	-4.62 ± 1.3	- 4.86 ± 1.3
δ^{13}C $_{(‰)}$	-28.8 ± 1.3	-31.9 ± 1.11	-19.6 ± 5.9	-31.2 ± 1.01	-29.9	-30.6 ± 1.4	-25.5 ± 6.02	-29.7 ± 4.9	-29.5 ± 1.5	-32.7 ± 0.6

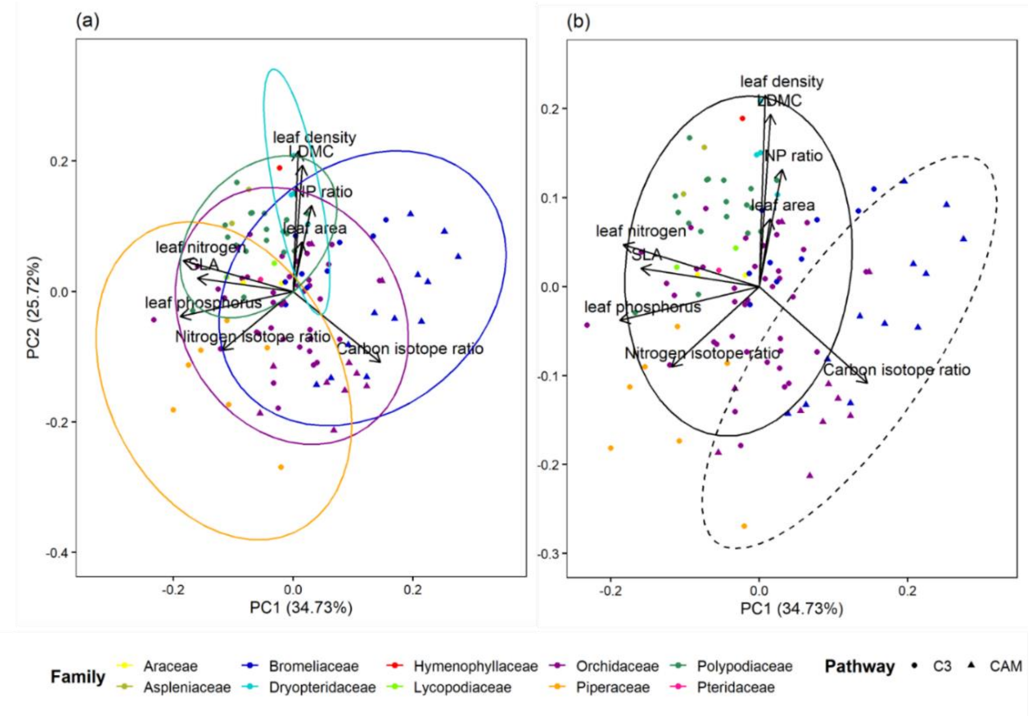


Figure 2.1. Principal component analysis (PCA) of morphological and chemical leaf traits of 102 vascular epiphyte species**.** Trait variation among (**a**) families and (**b**) photosynthetic pathways. Solid arrows indicate direction and weighting of vectors representing the nine morphological and chemical leaf traits considered in this study. Only the five most diverse families are shown with ellipses in **a)**. Trait variation differed significantly among the five most diverse families (R^2: 35%, F-value 12.8, P-value < 0.001) and between photosynthetic pathways (R^2: 21%, F-value 28.5, P-value < 0.001) Points and triangles in different colours are measurements aggregated at the species level for each family. C_3 photosynthetic pathway is indicated by circles and CAM by triangles. Dashed line groups CAM species in panel **b**).

Trait variation along broad- and small-scale environmental gradients

For morphological leaf traits, our models explained between 87% and 99% of their variation (conditional R^2; Table 2). Yet most of the explained variation was associated with the random effects, while explained variation associated with fixed effects, i.e. broad- and small-scale environmental gradients, photosynthetic pathway, and their interactions, explained between 1% and 23% of trait variation. Our models also explained a large amount of variation in chemical leaf traits. In contrast to morphological traits, fixed effects explained up to 90% of variation in chemical leaf traits (Table 3).

Morphological trait variation along broad- and small-scale environmental gradients

We found significant interactions between sampled elevation and photosynthetic pathway for leaf area (F = 4.03, P = 0.01), leaf density (F = 3.64, P = 0.02) and SLA (F = 5.44, P = 0.004; Table 2.2, Fig. 2.2). Specifically, CAM species tended to have smaller leaf areas than C_3 species at 1500 m. For leaf density, at 0 m and 1500 m CAM and C_3 species tended to have similar leaf density values, but not at 500 m where CAM species had lower values than C_3 species. For SLA, CAM species had lower SLA than C_3 species across all sampled elevations, yet differences in SLA values between CAM and C_3 species were stronger at 0 m (Figs. 2.2 and 2.3). Trait variation for leaf density (F = 4.18, P = 0.04) and LDMC (F = 6.16, P = 0.01) was significantly explained by relative height of attachment, with leaf density and LDMC decreasing with increasing relative height of attachment (Fig. 2.4). Minimum and maximum elevational distributions did not significantly predict variation in any morphological leaf trait.

Table 2.2. Summary of linear mixed-effects models evaluating variation in morphological leaf traits of vascular epiphytes. Marginal and conditional R^2 represent the model variation explained by fixed effects and the combination of fixed and random effects, respectively. Values in bold are statistically significant at $\alpha = 0.05$.

Morphological trait	**Leaf area**			**Leaf density**			**SLA**			**LDMC**		
Fixed effect	***Df, df.res***	***F-value***	***P-value***	***Df, df.res***	***F-value***	***P-value***	***Df, df.res***	***F-value***	***P-value***	***Df, df.res***	***F-value***	***P-value***
Sampled elevation	2, 402.2	2.75	0.06	2, 333.1	3.90	0.14	2, 365.1	8.16	<**0.001**	2, 361.8	1.95	0.14
Minimum elevational distribution	1, 106.8	0.0005	0.98	1, 114	0.04	0.84	1, 110.4	0.26	0.61	1, 114.1	0.23	0.63
Maximum elevational distribution	1, 96.4	0.08	0.76	1, 97.6	0.16	0.68	1, 102.5	0.01	0.91	1, 98	0.40	0.52
Relative height	1, 381.6	1.26	0.26	1, 429.2	4.18	**0.04**	1, 423.5	0.001	0.96	1, 417.5	6.16	**0.01**
Photosynthetic pathway	1, 414.1	0.18	0.66	1, 354.3	0.003	0.95	1, 372.7	24.80	<**0.001**	1, 361.2	0.50	0.47
Sampled elevation × Photosynthetic pathway	2, 392.7	4.03	**0.01**	2, 412.2	3.64	**0.02**	2, 415.7	5.44	**0.004**	2, 413.8	0.96	0.38
Minimum elevational distribution × Photosynthetic pathway	1, 392.6	0.66	0.41	1, 200.1	0.16	0.68	1, 238.6	0.001	0.96	1, 229.2	1.74	0.18
Maximum elevational distribution × Photosynthetic pathway	1, 128.1	1.01	0.31	1, 110.1	3.66	0.058	1, 118.8	0.05	0.81	1,116.3	0.96	0.32
Relative height × Photosynthetic pathway	1, 396.5	0.83	0.36	1, 423	0.78	0.37	1, 414.3	2.11	0.14	1, 412.5	2.95	0.08
Marginal R^2 (%)		0.01			0.11			0.23			0.02	
Conditional R^2 (%)		0.99			0.91			0.87			0.92	

Table 2.3. Summary of linear mixed-effects models evaluating variation in chemical leaf traits of vascular epiphytes. Marginal and conditional R^2 represent the model variation explained by fixed effects and the combination of fixed and random effects, respectively. Values in bold are statistically significant at $\alpha = 0.05$.

Chemical trait	**Leaf nitrogen**			**Leaf phosphorus**			**N:P ratio**			**δ^{15}N**			**δ^{13}C**		
Fixed effect	***Df, df.res***	***F-value***	***P-value***	***Df, df.res***	***F-value***	***P-value***	***Df, df.res***	***F-value***	***P-value***	***Df, df.res***	***F-value***	***P-value***	***Df, df.res***	***F-value***	***P-value***
Sampled elevation	2, 155.7	4.24	**0.016**	2, 152.6	8.01	**<0.001**	2, 145.9	1.24	0.28	1, 135.4	1.06	0.30	1, 162.2	23.40	**<0.001**
Minimum elevational distribution	1, 109.4	0.18	0.67	1, 108.4	5.42	**0.02**	1, 102.3	6.66	**0.01**	1, 106.4	0.27	0.60	1, 98.4	6.58	**0.011**
Maximum elevational distribution	1, 95.8	1.17	0.28	1, 92	3.22	0.07	1, 92.7	9.34	**0.002**	1, 97.4	0.12	0.72	1, 99.9	4.06	**0.039**
Relative height	1, 174	0.16	0.68	1, 172.1	0.94	0.33	1, 175.8	0.10	0.75	1, 178.8	2.07	0.15	1, 157.8	13.37	**<0.001**
Photosynthetic pathway	1, 165.3	13.03	**<0.001**	1, 164.4	12.50	**<0.001**	1, 170.8	0.003	0.95	1, 96	30.54	**<0.001**	1, 124.1	350.54	**<0.001**
Sampled elevation × Photosynthetic pathway	2, 164.6	4.59	**0.01**	2, 164.1	4.03	**0.019**	2, 155.1	1.81	0.16	2, 165.7	7.02	**0.001**	2, 144.7	7.61	**<0.001**
Minimum elevational distribution × Photosynthetic pathway	1, 124.7	0.85	0.35	1, 119.3	6.58	**0.011**	1, 71.2	2.32	0.13	1, 118.7	0.34	0.55	1, 161.9	0.84	0.35
Maximum elevational distribution × Photosynthetic pathway	1, 98.2	0.007	0.93	1, 96.1	0.004	0.94	1, 86.9	0.07	0.77	1, 107.3	17.49	**<0.001**	1, 117.4	0.11	0.73
Relative height × Photosynthetic pathway	1, 144.2	0.03	0.84	1, 144.8	0.003	0.95	1, 170.7	0.04	0.83	1, 154.5	1.88	0.17	1, 116.7	1.94	0.16
Marginal R^2 (%)		0.26			0.12			0.24			0.30			0.90	
Conditional R^2 (%)		0.66			0.72			0.46			0.64			0.96	

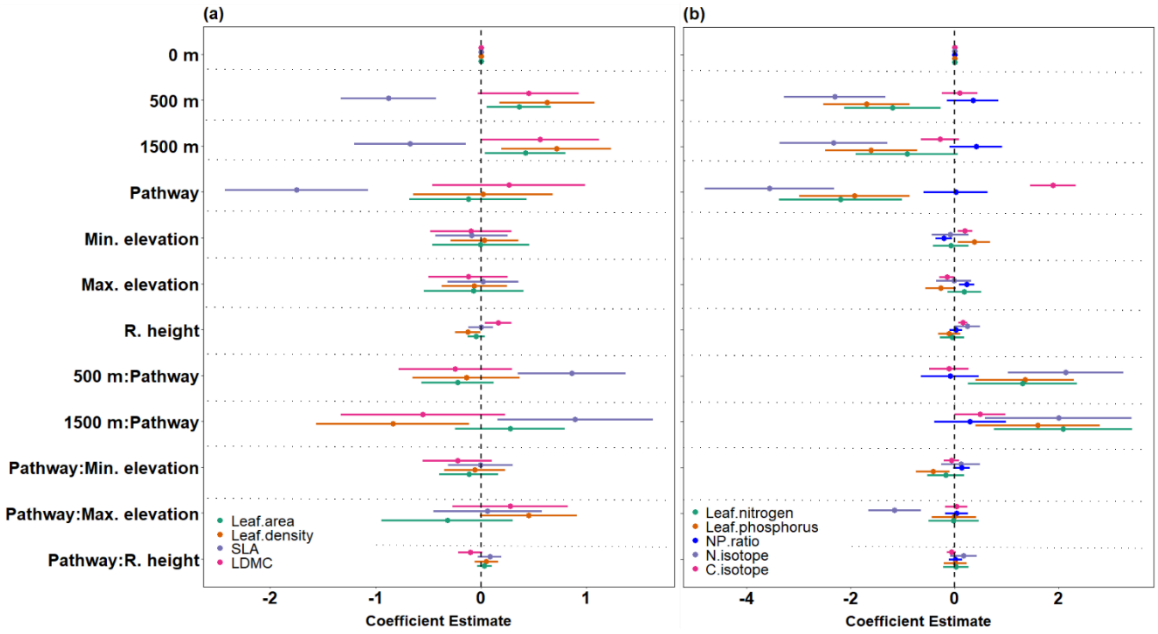


Figure 2.2. Coefficient estimates (dots) and 95% confidence intervals (bars) for linear mixed-effect models of (**a**) morphological and (**b**) chemical leaf traits for vascular epiphytes. Broad- and small-scale factors included as fixed effects are given along the y-axis. Factors tested include sampled elevations (0 m, 500 m, 1500 m), photosynthetic pathway (Pathway), relative height of attachment (R. height), minimum elevational distribution (Min. elevation) and maximum elevational distribution (Max. elevation). A model was fitted for each morphological and chemical leaf trait indicated by different colours. Significant effects are given when coefficient estimates do not include zero. Coefficient estimates were scaled for direct comparison.

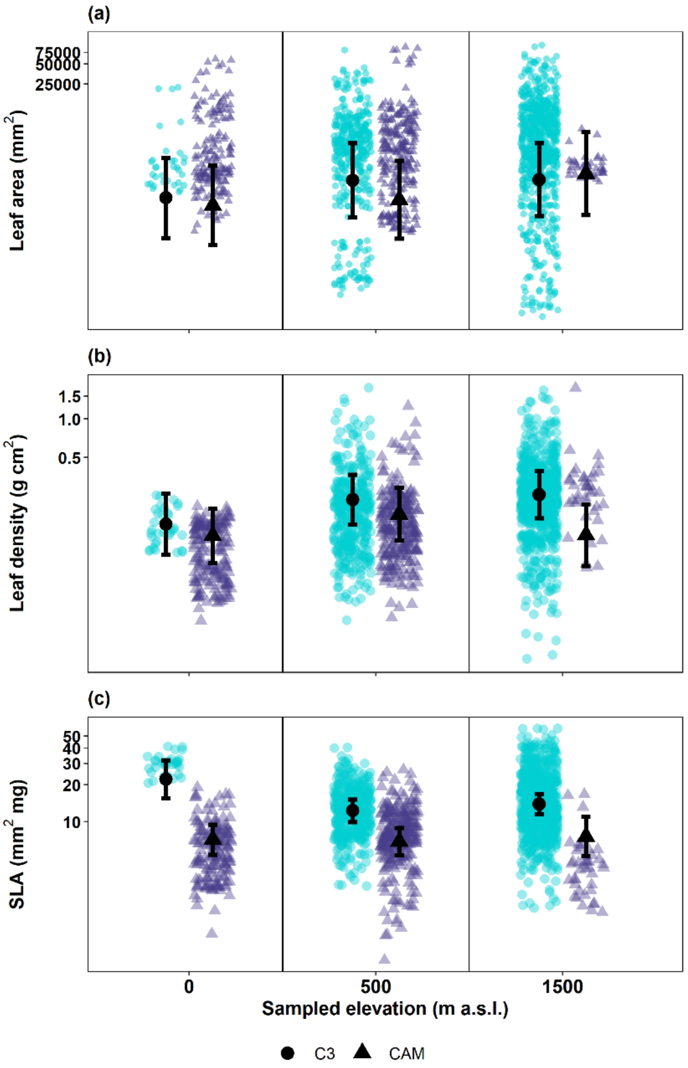


Figure 2.3. Linear mixed effect model fits for morphological leaf traits showing interactive effects of sampled elevation and photosynthetic pathway (mean and 95% CI) on (**a**) leaf area, (**b**) leaf density, and (**c**) specific leaf area (SLA) for vascular epiphytes. Black symbols represent model predictions, with circles indicating C_3 pathway and triangles indicating CAM species. Y axes are in logarithmic scale.

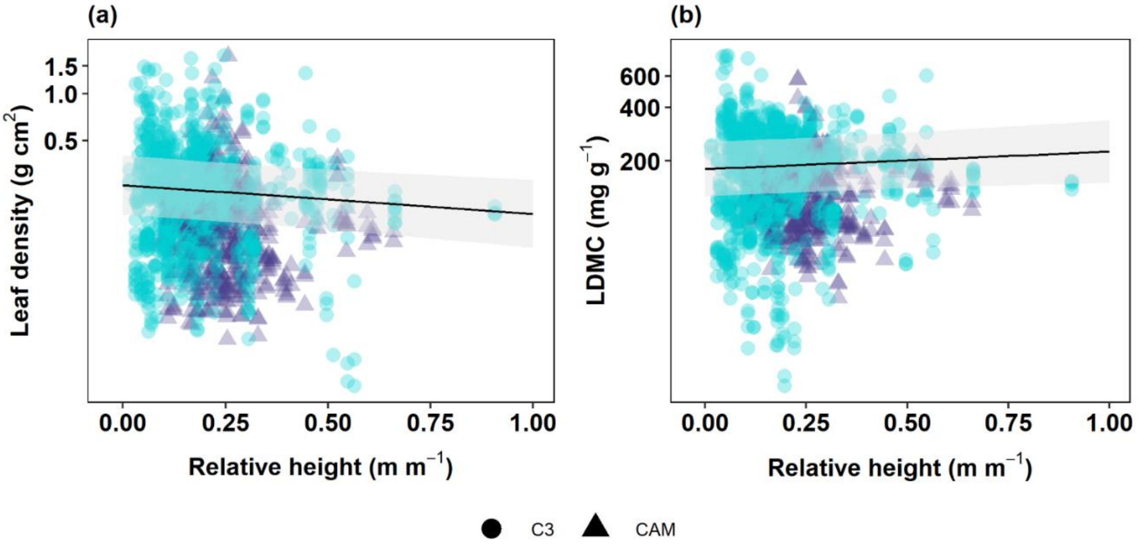


Figure 2.4. Estimated relationships of leaf density and leaf dry matter content with relative height of attachment. (**a**) leaf density and (**b**) leaf dry matter content (LMDC). C_3 photosynthetic pathway is indicated with circles and CAM with triangles. Model predictions are indicated by black lines, and shaded areas are 95% confidence intervals.

Chemical trait variation along broad- and small-scale environmental gradients

The interaction between sampled elevation and photosynthetic pathway significantly influenced leaf nitrogen (F = 4.59, P = 0.01), leaf phosphorus (F = 4.03, P = 0.01), δ^{15}N (F = 7.02, P = 0.001), and δ^{13}C (F = 7.61, P = 0.001; Table 3). Specifically, while CAM species tended to have lower leaf nitrogen, leaf phosphorus, and δ^{15}N values than C_3 species across sampled elevations, these differences were more pronounced at the lowest elevation. CAM species had higher δ^{13}C than C_3 across sampled elevations (Fig. 2.5). However, while CAM species did not differ strongly in terms of δ^{13}C, C_3 species had lower δ^{13}C with increasing elevation. Additionally, there was a significant interaction between maximum elevational distribution and photosynthetic pathway for leaf δ^{15}N (F = 17.49, P = 0.01), with values of leaf δ^{15}N decreasing with increasing maximum elevational distribution for CAM and C_3 species. However, this decrease was stronger for CAM species. Variation in leaf phosphorus was explained by a significant interaction between minimum elevational distribution with photosynthetic pathway (F = 6.58, P = 0.01), with leaf phosphorus decreasing for CAM species and increasing for C_3 species with increasing minimum elevational distribution (Fig. 2.6). Moreover, δ^{13}C varied significantly with maximum (F = 4.06, P = 0.04) and minimum elevational distribution (F = 6.58, P = 0.01), showing more negative values with increasing maximum and minimum elevational distribution (Figs. 2.2 and 2.7).

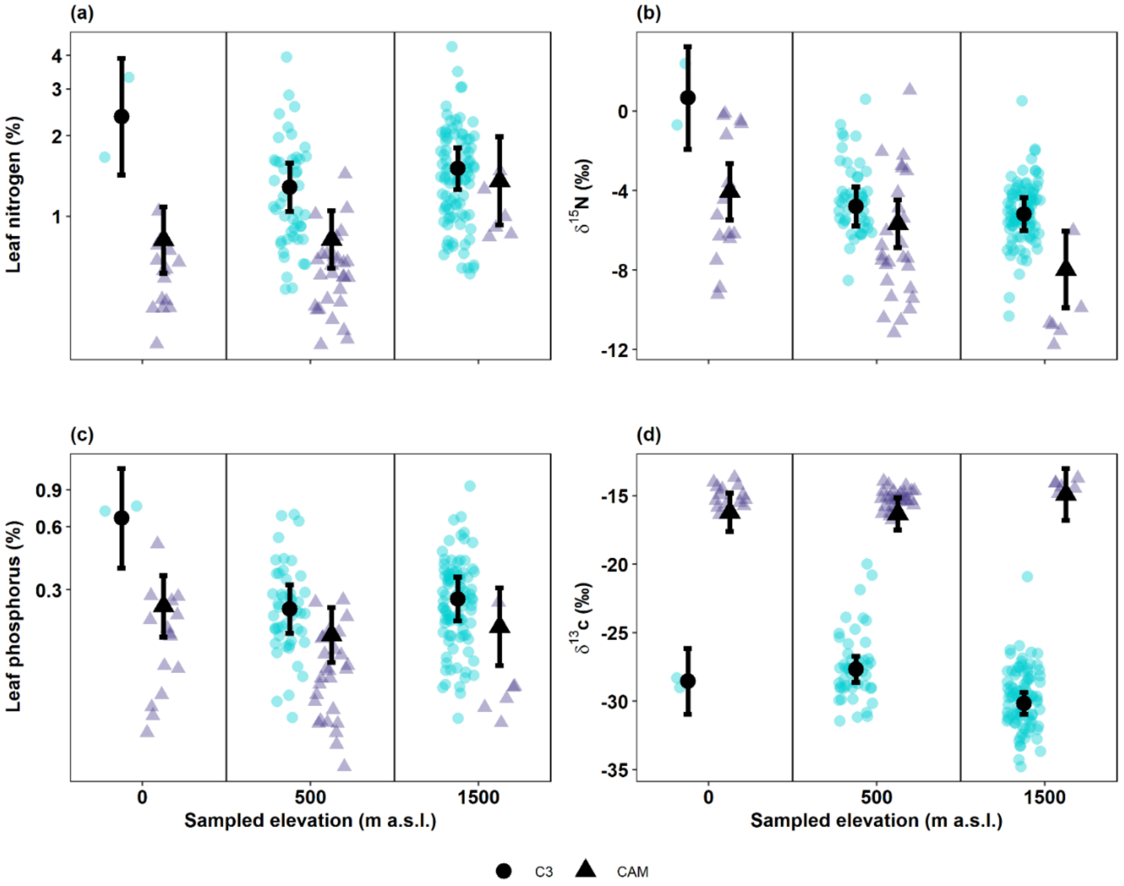


Figure 2.5. Linear mixed-effect model fits for chemical leaf traits showing the interactive effects of sampled elevation and photosynthetic pathway (mean and 95% CI) on (**a**) leaf nitrogen, (**b**) leaf nitrogen isotope ratio ($\delta^{15}N$), (**c**) leaf phosphorus, and (**d**) leaf carbon isotope ratio ($\delta^{13}C$) of vascular epiphyte species. There was a significant effect of the interaction between sampled elevation and photosynthetic pathway for leaf nitrogen ($F_{2,164.68}$ = 4.59, P-value = 0.01), leaf nitrogen isotope ratio ($\delta^{15}N$; $F_{2,165.7}$ = 0.05, P-value = 0.001), leaf phosphorus ($F_{2,164.12}$ =4.03, P-value = 0.019) and leaf carbon isotope ratio ($\delta^{13}C$; $F_{2,144.77}$ = 7.61, P-value = 0.0007). Black symbols represent model predictions, with circles indicating C_3 pathway and triangles indicating CAM species. Note the log scale of the y-axes of (**a**) leaf nitrogen and (**c**) leaf phosphorus.

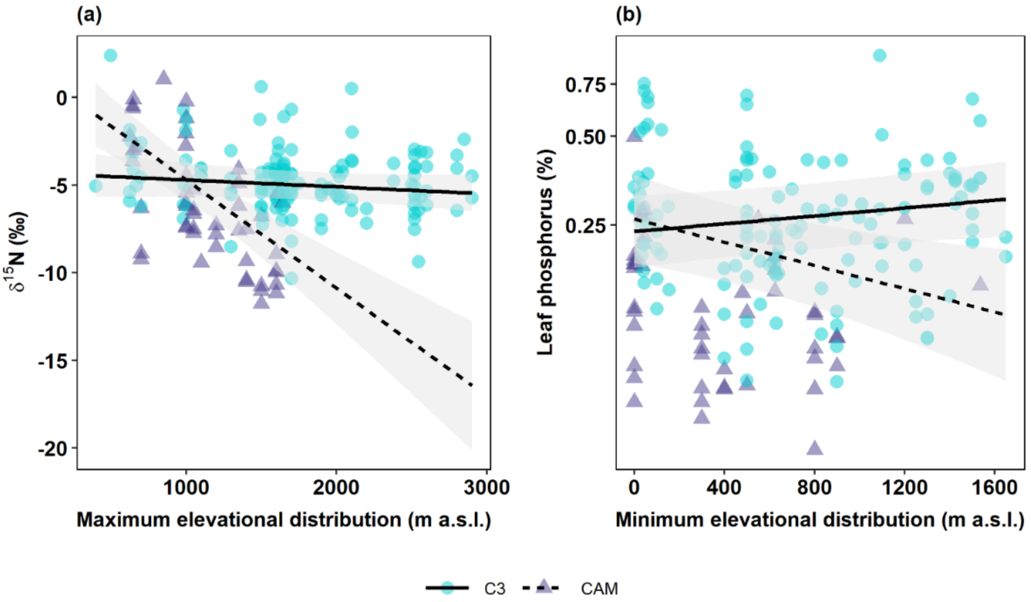


Figure 2.6. Linear mixed effects model fits for leaf nitrogen and leaf phosphorus (mean and 95 % CI) showing the interactive effects of maximum elevational distribution and photosynthetic pathway on (**a**) leaf nitrogen isotope ratio (δ^{15}N), and of minimum elevational distribution and photosynthetic pathway on (**b**) leaf phosphorus content. There was a significant effect of the interaction between minimum elevational distribution and photosynthetic pathway for leaf phosphorus content ($F_{1,119.33} = 6.58$, P-value = 0.01) and between maximum elevational distribution and photosynthetic pathway for leaf δ^{15}N ($F_{1,107.31}$ = 17.49, P-value = 0.0001). Full lines represent model predictions for C_3 and dashed lines for CAM species. Circles indicate C_3 pathway and triangles indicate CAM species. Y axes in panel (**b**) are on a logarithmic scale.

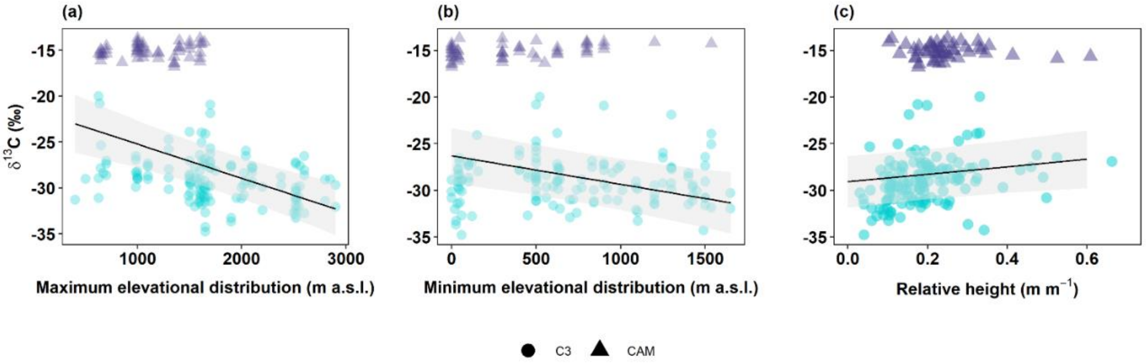


Figure 2.7. Relationships between leaf carbon isotope ratio (δ13C) with (**a**) maximum elevational distribution, (**b**) minimum elevational distribution, and (**c**) relative height of attachment of vascular epiphyte species. C_3 photosynthetic pathway is indicated by circles and CAM by triangles. Model predictions are indicated in black colour lines, shaded areas indicate 95% confidence intervals.

2.5. Discussion

We explored variation in leaf traits of vascular epiphytes, jointly considering broad- and small-scale environmental gradients, as well as photosynthetic pathway. Broad- and small-scale environmental gradients did not emerge as strong drivers of variation in morphological leaf traits, suggesting that trait-environment relationships are highly variable and that-trait values vary more among families or species to a greater extent than they are mediated by environmental conditions. In contrast, broad- and small-scale environmental gradients played a stronger role in driving trait variation of chemical leaf traits. For morphological and chemical traits, we found consistent differences in trait variation to sampled elevation among photosynthetic pathways.

Vascular epiphytes are usually considered slow-growing plants, with low nutrient concentrations and long leaf live spans (Zotz, 1998). However, there is a wide spectrum of ecological strategies among vascular epiphytes, reflecting how they partition niche space and adjust to the gradual changes along broad- and small-scale environmental gradients of light, temperature, and resource availability. Our PCA analyses showed a clear separation between species performing CAM or C_3 photosynthesis, reflecting traits associated with water relations and water-use efficiency (i.e. $\delta^{13}C$), which is consistent with previous studies on vascular epiphytes in the Neotropics (Petter et al., 2016; Schellenberger-Costa et al., 2018). In this study, two important families performed different photosynthetic pathways, i.e. Bromeliaceae and Orchidaceae which, apart from being taxonomically diverse, represented the entire CAM species. Our PCA analysis also revealed consistent differences in leaf traits among photosynthetic pathways, where CAM species were associated with water-use efficiency and C_3 species were associated with traits associated with light and nutrient acquisition. In line with Hietz et al. (1999) we found a higher proportion of CAM species at lower sampled elevations, where water availability is a stronger limiting factor for C_3 species. While C_3 species occurred at all elevations, they were much more frequent at higher sampled elevations that are characterised by higher precipitation and milder temperatures. We also found that traits of CAM and C_3 species responded differently to sampled environments. Specifically, we found that most morphological and chemical leaf traits, apart from of LDMC and leaf N:P, showed a significant interaction between sampled elevation and photosynthetic pathway. This suggests that CAM and C_3 species exhibit coordinated, yet contrasting responses to elevation (Jager et al., 2014; Rosas et al., 2019), i.e. adaptations to water availability are not limited to physiological processes, but also extend to leaf-level morphological adaptations. Our analysis therefore reveals the importance of combining both functional groups and single traits to understand the distributions of vascular epiphytes along environmental gradients.

Variation of morphological leaf traits along broad- and small-scale environmental gradients

Leaf morphological traits varied to a greater extent along small-scale environmental gradients than along broad-scale environmental gradients. Among the morphological traits, we found that only SLA was influenced by broad-scale environmental gradients (i.e. sampled elevation). Rather, our results pointed to a stronger influence of small-scale environmental gradients on leaf density and LDMC, which both decreased slightly with increasing relative height of attachment. These results are not fully consistent with the findings of Petter et al. (2016), who found a negative correlation of height of attachment with SLA and LDMC, which was attributed to heterogeneous light conditions along the vertical environmental gradient within the canopy.

We found generally weak or variable trait-environment relationships for morphological leaf traits, meaning that a wide range in trait values are possible under similar environmental conditions. This result was unexpected, as Guzman-Jacob et al., (2020) found high spatial turnover in vascular epiphyte species composition along the same elevational gradient. Variation in morphological leaf traits across different spatial and ecological scales is notoriously difficult to disentangle (Messier et al., 2010), in part because “soft” (i.e. easily measured) traits are proxies for mechanistic links to plant performance (Wright et al., 2010). Nevertheless, other factors can be more important in determining trait variation, such as phylogenetic trait conservatism. Our results showed that variation among families contributed between 52% and 56% of variation in leaf area, leaf density, and LDMC. For SLA, 55% of variation was among species (Appendix Table B1). Another possible explanation for the weak trait-environment relationships of morphological leaf traits in this study is the extent of the environmental gradient studied; increasing the length of the gradient in sampled elevation to the treeline, where environmental conditions are more stressful, may reveal stronger impacts of broad-scale environmental gradients on the variation of morphological leaf traits.

Variation of chemical lead traits along broad- and small-scale environmental gradients

Chemical leaf traits varied along broad- and small-scale environmental gradients, with environment explaining a larger fraction of variation in chemical leaf traits than in morphological leaf traits. For instance, leaf nitrogen, leaf phosphorus, and $\delta^{15}N$ of CAM species was lower than in C_3 species across sampled elevations. We found that minimum elevational distribution differentially affected leaf phosphorus, with that of C_3 species exhibiting a moderate increase with increasing minimum elevational distribution, while that of CAM species decreased sharply with increasing minimum elevational distribution. Our results showed that leaf N:P increased in relation to minimum and maximum elevational distributions, possibly indicating that elevation mediates nitrogen or phosphorus limitation of vascular epiphyte communities (Verhoeven et al., 1996; Bedford et al., 1999; Matson et al., 1999).

We observed a significant negative interaction between maximum elevation and photosynthetic pathway on leaf nitrogen and $\delta^{15}N$, both of which decreased with elevation. Nevertheless, for C_3 plants the change was not as pronounced as for CAM plants. Differences between CAM and C_3 species in leaf nitrogen, leaf phosphorus, and $\delta^{15}N$ at 0 m in relation to maximum elevation might be the result of the higher proportion of CAM species compared to C_3 species at this elevation, but may also be related to changes in the availability of these nutrients at the different sampled elevations. Previous studies have shown that foliar nutrient concentrations, e.g. leaf phosphorus and leaf nitrogen, decline with elevation (Vitousek et al., 1992; Kitayama & Aiba, 2002; Soethe et al., 2008). Yet the acquisition of nitrogen and phosphorus by vascular plants is influenced by several factors, including climate (Reich & Oleksyn, 2004), soil conditions (Chen et al., 2011), phylogeny (Stock & Verboom, 2012), and physiological growth strategies (Kerkhoff et al., 2006). At a global scale, phosphorus in tropical leaves has lower concentrations than leaf nitrogen (Kerkhoff et al., 2005; but see Wright 2019), which is usually attributed to the low availability of this nutrient in old, weathered, tropical soils (Sanchez, 1979). Our results also show that CAM species have higher water-use efficiency than C_3 species, with pronounced differences at the lowest elevation. $\delta^{13}C$ was the only chemical leaf trait influenced by relative height of attachment, showing that species higher in the canopy were more water-use efficient (Fig. 2.6). Thus, our results are consistent with the idea that species in the outer canopy require adaptations such as CAM photosynthesis or increased water-use efficiency to withstand drought and greater vapour pressure deficits (Zotz, 2004).

Our results also showed lower variation in chemical leaf traits among families than what we observed for morphological leaf traits (see Table S2). Leaf phosphorus content was the only trait where variation among families contributed as much as 50%, which could suggest that certain plant families, e.g. bromeliads (Winkler & Zotz, 2009), follow conservative acquisition strategies for limiting nutrients, such as phosphorus. Variation among species accounted for 59% of the variation between families for $\delta^{13}C$, likely reflecting differences between photosynthetic pathways (Appendix Table B2). The amount of interspecific trait variation in this study is consistent with global analyses of other plant growth forms (Kattge et al., 2020).

2.6. Conclusions

We show that trait variability plays an important role in explaining the distribution of vascular epiphytes along broad- and small-scale gradients in light, nutrient, and water availability. Our findings indicate that broad-scale environmental gradients have less impact on the variation in morphological leaf traits than on chemical leaf traits, the latter of which also responded strongly to small-scale environmental gradients. The high degree of trait variation associated with either families or species suggests that broad-scale analyses of trait-environment relationships of vascular epiphytes should account for evolutionary history, as the phylogenetic signal likely varies across traits. In conclusion, vascular epiphytes exhibit a wide range of ecological strategies to acquire resources across environmental gradients that likely shape epiphyte species distributions in tropical mountains.

Fir forest in Los Conejos, Veracruz, Mexico at 3500 m a.s.l.

3. BIOVERA-Epi: A new database on species diversity, community composition, and leaf functional traits of vascular epiphytes along an elevational gradient in Mexico

Valeria Guzmán-Jacob, Patrick Weigelt, Dylan Craven, Gerhard Zotz, Thorsten Krömer, Holger Kreft

3.1. Abstract

Background

This data paper describes a new, comprehensive database (BIOVERA-Epi) on species distributions and leaf functional traits of vascular epiphytes, a poorly studied plant group, along gradients of elevation and forest-use intensity in the central part of Veracruz State, Mexico. The distribution data includes frequencies of 271 vascular epiphyte species belonging to 92 genera and 23 families across 120 20 m x 20 m forest plots at eight study sites along an elevational gradient from sea level to 3500 m a. s. l. In addition, BIOVERA-Epi provides information on 1595 measurements of nine morphological and chemical leaf traits from 474 individuals and 102 species. For morphological leaf traits, we provide data of each sampled leaf. For chemical leaf traits, we provide data at the species level per site and land-use type. We also provide complementary information for each of the sampled plots and host trees. BIOVERA-Epi contributes to an emerging body of synthetic epiphytes studies combining functional traits and community composition.

New information

BIOVERA-Epi includes data on species frequency and leaf traits from 120 forest plots distributed along an elevational gradient including six different forest types and three levels of forest-use intensity. It will expand the breadth of studies on epiphyte diversity, conservation, and functional plant ecology in the Neotropics and will contribute to future synthetic studies on the ecology and diversity of tropical epiphyte assemblages.

Keywords: elevational gradient, vascular epiphytes, functional traits, forest-use intensity, carbon isotope ratio, nitrogen isotope ratio.

3.2. Introduction

Elevational gradients provide a wide range of opportunities for studying the effects of different ecological and evolutionary factors on biodiversity patterns. Steep elevational gradients in temperature, precipitation, and other climatic variables usually play a fundamental role in shaping plant diversity (McCain and Grytnes 2010; Peters et al. 2019), and also contribute to linkages between plant traits and environmental conditions (Bruelheide et al. 2018; Keddy 1992). They are also used as proxies for understanding diversity patterns across latitudinal gradients (McCain and Grytnes 2010), while controlling for species pools and biogeographic history (Ricklefs 2004). Additionally, anthropogenic forest disturbance may modify climatic conditions at local and regional scales, which in turn may affect the response of species, especially for canopy-dwelling life forms such as vascular epiphytes that are sensitive to changes in air humidity and temperature (Larrea and Werner 2010; Werner and Gradstein 2009; Zotz and Bader 2009).

Functional traits are measurable characteristics of individual plants impacting their growth, reproduction and survival (Violle et al. 2007) and reflect how species interact with their environment (Vesk 2013). Functional traits are widely used to elucidate mechanisms that underpin many ecological processes along vertical and horizontal environmental gradients (e.g. Petter et al. 2016, Bruelheide et al. 2018) but also evolutionary patterns associated with variation in plant form and function, such as geographic distributions of woody and non-woody species (Díaz et al. 2016). Despite recent progress (e.g. Agudelo et al. 2019, Petter et al. 2016), studies in the field of functional traits of vascular epiphytes are rare, suggesting that our knowledge of the factors that determine the distribution of vascular epiphytes along environmental gradients is similarly limited.

Deforestation and forest fragmentation represent major threats to biodiversity, as well as to ecosystem integrity and functioning (Tapia-Armijos et al. 2015; Scholes et al. 2018). Furthermore, increasing temperatures and changing precipitation patterns may negatively affect mountain biodiversity, causing upward shifts in the treeline (Cazzolla Gatti et al. 2019), and shifting the distribution of plants and animals (McCain et al. 2016). While a growing number of studies shows that climate change affects a wide range of species and ecosystems (Peters et al. 2019; Root et al. 2003; Trisos et al. 2020; Walther et al. 2002), the effects of deforestation and fragmentation on tropical mountain ecosystems are still poorly understood (Payne et al. 2017). Due to their dependence of trees, vascular epiphytes are particularly vulnerable to these changes (Barthlott et al. 2001; Krömer and Gradstein 2003; Köster et al. 2009).

Mexico is a country with high floristic diversity and endemism. Almost 50% of its 23,114 native species of vascular plants are endemic. Thus, Mexico ranks fourth in species richness globally, after Brazil, China, and Colombia, and is second in terms of endemism (Villaseñor, 2016). However, Mexico has lost approximately half of its forest cover in the past 50 years (Barsimantov and Kendall 2012). Although deforestation rates have been declining in recent years, the country lost 155,000 ha/year^{-1} between 2000 and 2005 (Barsimantov and Kendall 2012; FAO 2010; Velázquez et al. 2002). The Mexican state of Veracruz, has one of the highest rates of deforestation with more than 80% of primary vegetation having been converted to pastures, plantations, and secondary vegetation (Ellis et al. 2011; Gómez-Díaz et al. 2018; Williams-Linera et al. 2002). Given its species richness and endemism (c. 30% of 8500 vascular plant species are endemic to Mexico; Villaseñor 2016), Veracruz also plays an important role in biodiversity conservation (Gómez-Pompa, et al. 2010; Sarukhán et al. 2014). It has been estimated that about 7.8% of the Mexican vascular flora are epiphytes, 750 of which (569 angiosperms and 181 pteridophytes) are native to Veracruz (Krömer et al. in press). Vascular epiphytes usually reach their highest diversity in humid tropical forests at mid elevations (Guzmán-Jacob et al. 2020; Küper et al. 2014; Krömer et al. 2005; Cardelús et al. 2006). Moreover, they contribute significantly to ecosystem functioning through biotic interactions and by providing microhabitats for other organisms (Nadkarni 1984; Veneklaas et al. 1990; Zotz 2016). Our study sites in the central part of Veracruz host a wide variety of different ecosystems including tropical semi-humid deciduous forest and humid montane and pine-oak forests (Williams-Linera et al. 2007; Carvajal-Hernández et al. 2020) and have a diverse epiphyte flora (Krömer et al. 2020).

General description

BIOVERA-Epi includes plot data from an elevational gradient located in the central part of the State of Veracruz, Mexico. Specifically, it contains two distinct but related datasets: the first dataset includes distribution and frequency information for 271 vascular epiphyte species, sampled in 120 20 m x 20 m plots along the elevational gradient, ranging from 0 to 3500 m a.s.l. The second dataset includes measurements of nine morphological and chemical leaf traits for 102 species, 474 individuals and a total of 1595 leaves, which were sampled in 45 plots at three sites along the same elevational gradient. The leaf traits studied were: leaf area, leaf density, specific leaf area (SLA), leaf dry matter content (LDMC), leaf nitrogen content, leaf phosphorus content, leaf carbon content, nitrogen isotope ratio ($\delta^{15}N$), and carbon isotope ratio ($\delta^{13}C$). For each plot, we also provide geographical coordinates, forest-use intensity (old-growth, degraded, secondary), and elevation. For the surveyed host trees, we report diameter at breast height (DBH), total height (H), and species identity (see data collection).

3.3. Methods

Sampling design

The elevational gradient spanned from sea level to 3500 m on the eastern slopes of Cofre de Perote, a 4282 m extinct volcano located in the central part of Veracruz State, Mexico (Fig. 3.1). In this region, the Trans-Mexican volcanic belt and the Sierra Madre Oriental converge, creating complex geological conditions and combining floristic elements from the Nearctic and Neotropics. The climate in the study region ranges from dry and hot in the lowlands (mean annual temperature (MAT): 25 °C; mean annual precipitation (MAP): 1222 mm yr^{-1}) to humid and temperate at mid-elevations (MAT: 13-19 °C; MAP: 2952-1435 mm yr^{-1}) and dry and cold at high elevations (MAT: 9 °C; MAP: 708 mm yr^{-1}; data according to the National Meteorological Service of Mexico 1951-2010). Along the elevational gradient, six main vegetation types are commonly found (Carvajal-Hernández and Krömer 2015): (1) semi-humid deciduous forest at 0-700 m, (2) tropical oak forest at 700-1300 m, (3) humid montane forest at 1300-2400 m, (4) pine-oak forest at 2400-2800 m, (5) pine forest at 2800-3500 m and (6) fir forest at 3500-3600 m.

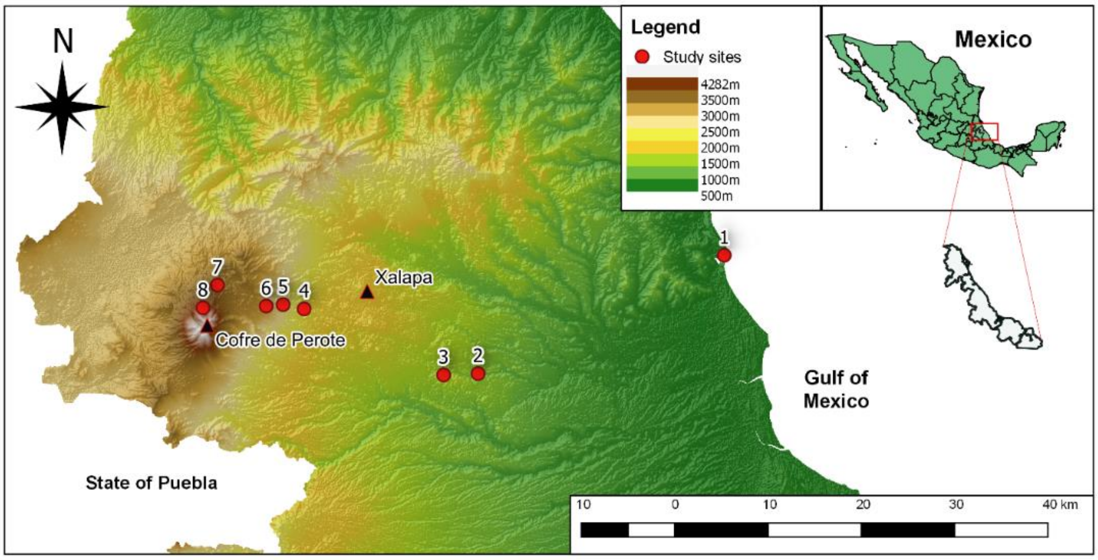


Figure 3.1. Map of the study sites along the Eastern slopes of the Cofre de Perote mountain in the state of Veracruz, Mexico. Red dots indicate the location of the eight study sites. Black triangles indicate the summit of the Cofre de Perote mountain, and the city of Xalapa as reference points.

We investigated three levels of forest-use intensity (FUI) that could consistently be found along the entire gradient (following Gómez-Díaz et al. 2017): (1) old-growth forests (OG) encompass mature forests with no or only few signs of logging and other human impacts, and are classified as the lowest FUI; (2) degraded forests (DF) are forests with clear signs of past logging, sometimes with ongoing cattle grazing, removal of understory and/or harvesting of non-timber forest products, and are classified as intermediate FUI; and (3) secondary forests (SF) represent forests at an intermediate successional stage 15-25 years after abandonment (based on interviews with local landowners), often with signs of continued human impacts, such as the removal of understory vegetation, non-timber forest products or partial tree cutting and occasional cattle grazing, and are classified as high FUI.

Data collection: species distribution

We selected eight study sites each separated by c. 500 m in altitude along the elevational gradient representing the following elevational ranges: 0-45 m, 610-675 m, 980-1050 m, 1470-1700 m, 2020-2200 m, 2470-2600 m, 3070-3160 m, and 3480-3545 m. At each study site, we surveyed vascular epiphytes in five non-permanent 20 m × 20 m plots for each of the three FUI levels respectively yielding a total of 120 plots (Table1). We used a Garmin® GPSMAP 60Cx device (Garmin International, Inc. Kansas, USA) to record geographical coordinates and elevation of all plots.

Vascular epiphytes were surveyed between July 2014 and May 2015 following the sampling protocol of Gradstein et al. (2003). First, ground-based surveys were conducted in four 10 m x 10 m subplots nested within each plot, to represent epiphyte assemblages in the forest understory up to a height of ~8 m (Krömer et al. 2007; Krömer and Gradstein 2016) using collecting poles and binoculars (Flores-Palacios and García-Franco, 2001). We selected one mature host tree per plot based on size, vigor, and crown structure for safe canopy access (Table 2). We climbed from the base to the outer portion of the tree crown using the single-rope climbing technique (Perry, 1978) and recorded the presence of vascular epiphyte species in each of the five vertical tree zones according to Johansson (1974). Johansson zones are a frequently used scheme to record and describe the spatial distribution of vascular epiphytes within tree trunks and canopies (Gradstein et al. 2003; Sanger and Kirkpatrick 2017 (Fig. 3.2). We recorded DBH and total height for each climbed tree. We recorded the frequency of each species as the sum of incidences in the four nested subplots and the central host tree (maximum frequency per plot = 5).

Data collection leaf trait dataset

In a separate sampling campaign from June to September 2016, leaf trait sampling took place at three of our studied elevational sites (0, 500, and 1500 m a. s. l.). In this field campaign, we aimed to resample as many vascular epiphyte species from the first survey as possible. At each elevation, epiphytes were sampled up to a height of 20 m on one or more trees using the single-rope climbing technique. Epiphytes below 6 m were sampled from the ground using a collecting pole. Functional traits were collected for all vascular epiphyte species classified as holoepiphytes (epiphytes in the strict sense, i.e. living their whole life cycle as epiphytes). In this dataset, we excluded nomadic vines because of their contact to the ground (Zotz 2013). Additionally, we excluded species of the family Cactaceae from trait measurements because stems are their main photosynthetic organs. This dataset differs in the sampling resolution between morphological and chemical traits; morphological traits include leaf measurements per individual at each study site and chemical traits include one measurement (from pooled samples) per species from each study site.

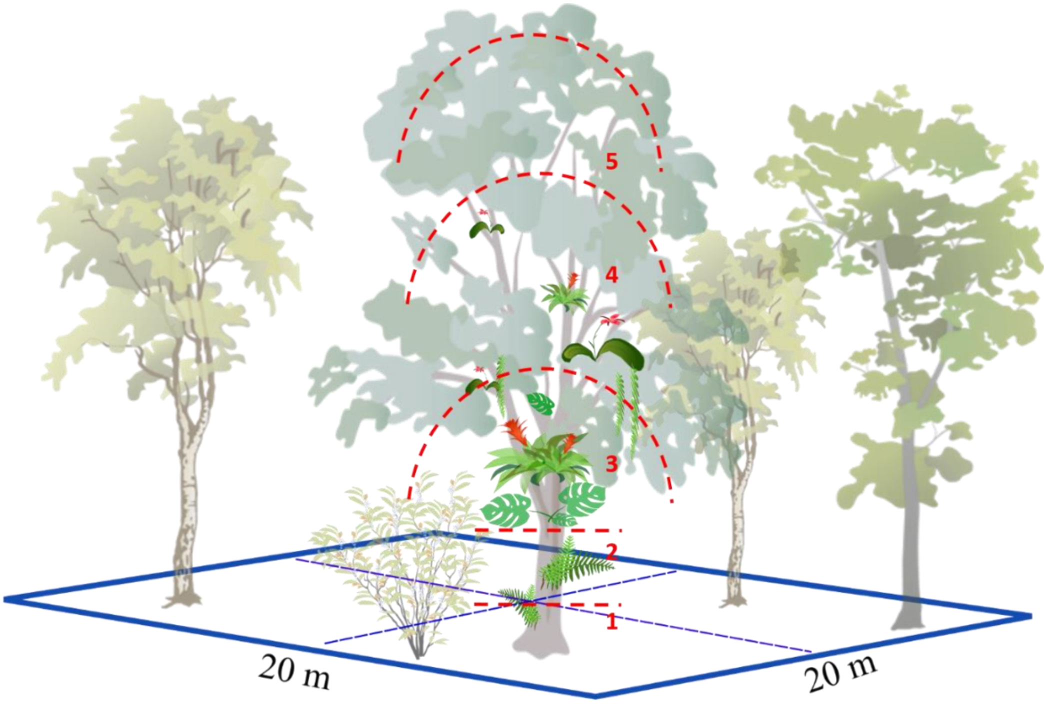


Figure 3.2. Design of the 20 x 20 m plot for sampling vascular epiphytes. The four subplots are indicated by dashed blue lines. The central tree shows the five Johansson zones indicated with red lines.

Leaf trait measurements

We collected between one and three leaves per adult individual from three individuals to obtain, if possible, a maximum of 10 leaves per species. We sampled fully expanded leaves without visible signs of herbivory or disease. Collected leaves were rehydrated in a sealed plastic bag and kept cool in a refrigerator at 7 °C for a minimum of 8 hours before taking measurements. Leaf area was measured with a portable laser area meter (CI-202, CID Bio Science Inc. U.S.A.). Leaf thickness was measured with an electronic calliper (precision: 0.05 mm). Leaves were weighed to obtain fresh weight (balance: A and D GR-202; A and D Company, Tokyo, Japan; precision: 0.1 mg), then oven dried at 70 °C for 48 h or until obtaining a constant dry weight, and reweighed to obtain dry weight. For each leaf, we determined the following morphological traits following Pérez-Harguindeguy et al. (2013) and Kitajima and Poorter (2010): i) leaf area (LA = mm^2), ii) specific leaf area (SLA = leaf area/dry weight; mm^2 mg^{-1}), iii) leaf density

(LD = SLA/leaf thickness; g cm^3), and iv) leaf dry matter content (LDMC = dry weight/fresh weight; g g^{-1}) (Fig. 3.3). We measured the following leaf chemical traits: i) leaf nitrogen content (leaf nitrogen; %), ii) leaf carbon content (leaf carbon; %), iii) leaf phosphorus content (leaf phosphorus; %), iv) nitrogen isotope ratio ($\delta^{15}N$; ‰), and v) carbon isotope ratio ($\delta^{13}C$; ‰) (Fig. 3.4). Dried leaf samples were ground and homogenized using a ball mill. To quantify leaf nitrogen content, leaf carbon content, $\delta^{15}N$, and $\delta^{13}C$, we used an elemental analyser-isotope ratio mass spectrometer (Carlo Erba 1110 EA coupled via a Conflo III to a Delta^{PLUS}; Thermo Electron, Bremen, Germany). Atmospheric air (AIR) was used for $\delta^{15}N$ and the Vienna Pee Dee Belemnite (V-PDB) for $\delta^{13}C$ as standards.

$$\delta^{13}C\ (‰) = [(^{13}C/^{12}C\ \text{sample})/\ (^{13}C/^{12}C\ \text{standard})-1] \times 1000$$

$$\delta^{15}N\ (‰) = [(^{15}N/^{14}N\ \text{sample})/\ (^{15}N/^{14}N\ \text{standard})-1] \times 1000$$

To determine leaf phosphorus, 5 mg of the sample were digested in 200 µl concentrate HNO_3 and 30 µl 30% H_2O_2 (Huang and Schulte 1985). Leaf phosphorus concentrations were determined colorimetrically (Murphy and Riley 1962). After digestion, 770 µl distilled water was added and the absorption by the molybdenum-phosphorous complex was measured at 710 nm using a UV-VIS spectrophotometer (Specord 50, Analytik Jena, Jena, Germany). Chemical analyses of samples were performed at the University of Oldenburg for phosphorus and at the University of Vienna, Department of Microbiology and Ecosystem Science for nitrogen, $\delta^{15}N$, and $\delta^{13}C$.

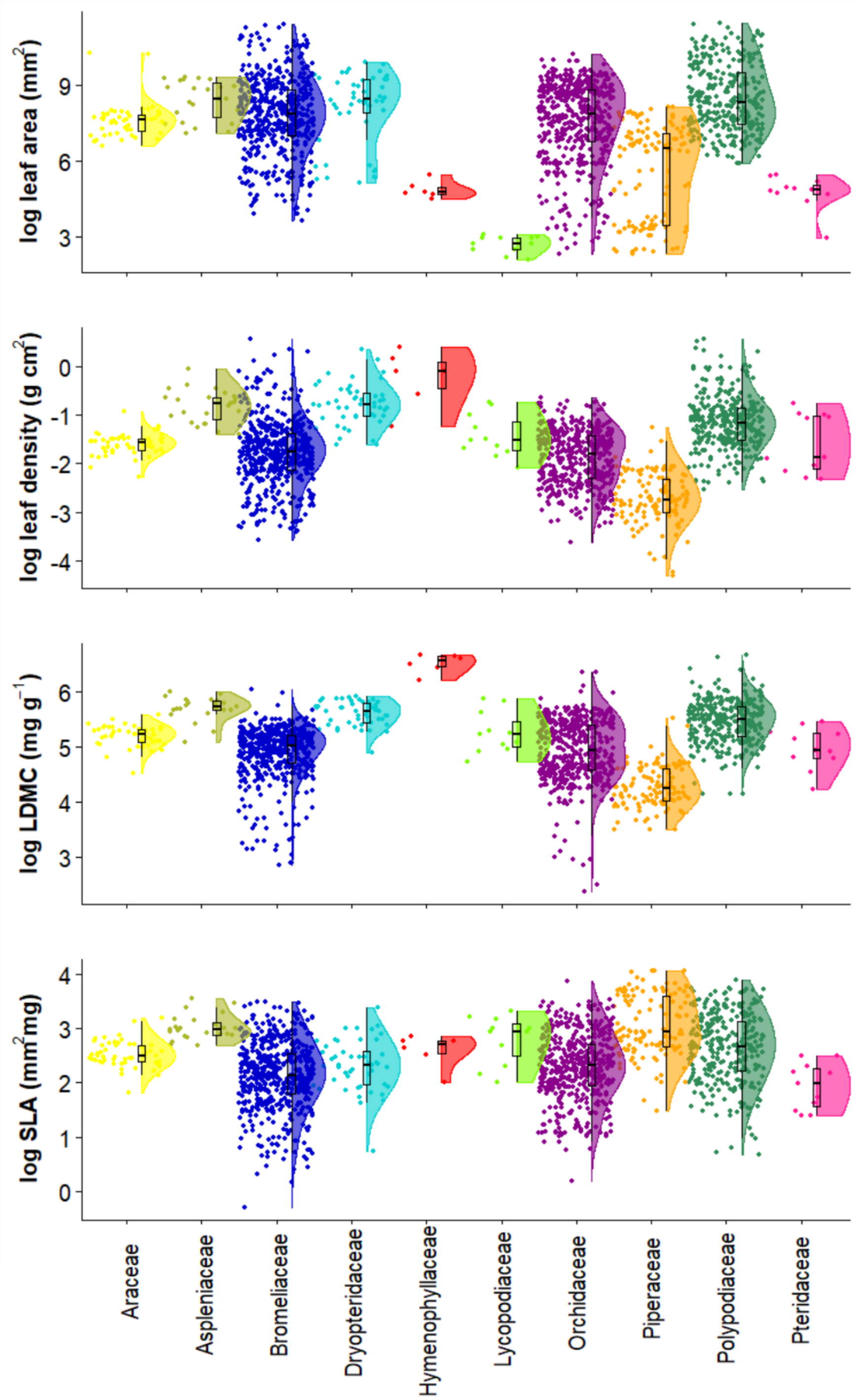


Figure 3.3. Morphological leaf traits per family. Distribution of trait measurements across the 102 species and 10 families at 500, 1500, and 2500 m. Each point represents a leaf measurement (n=1595).

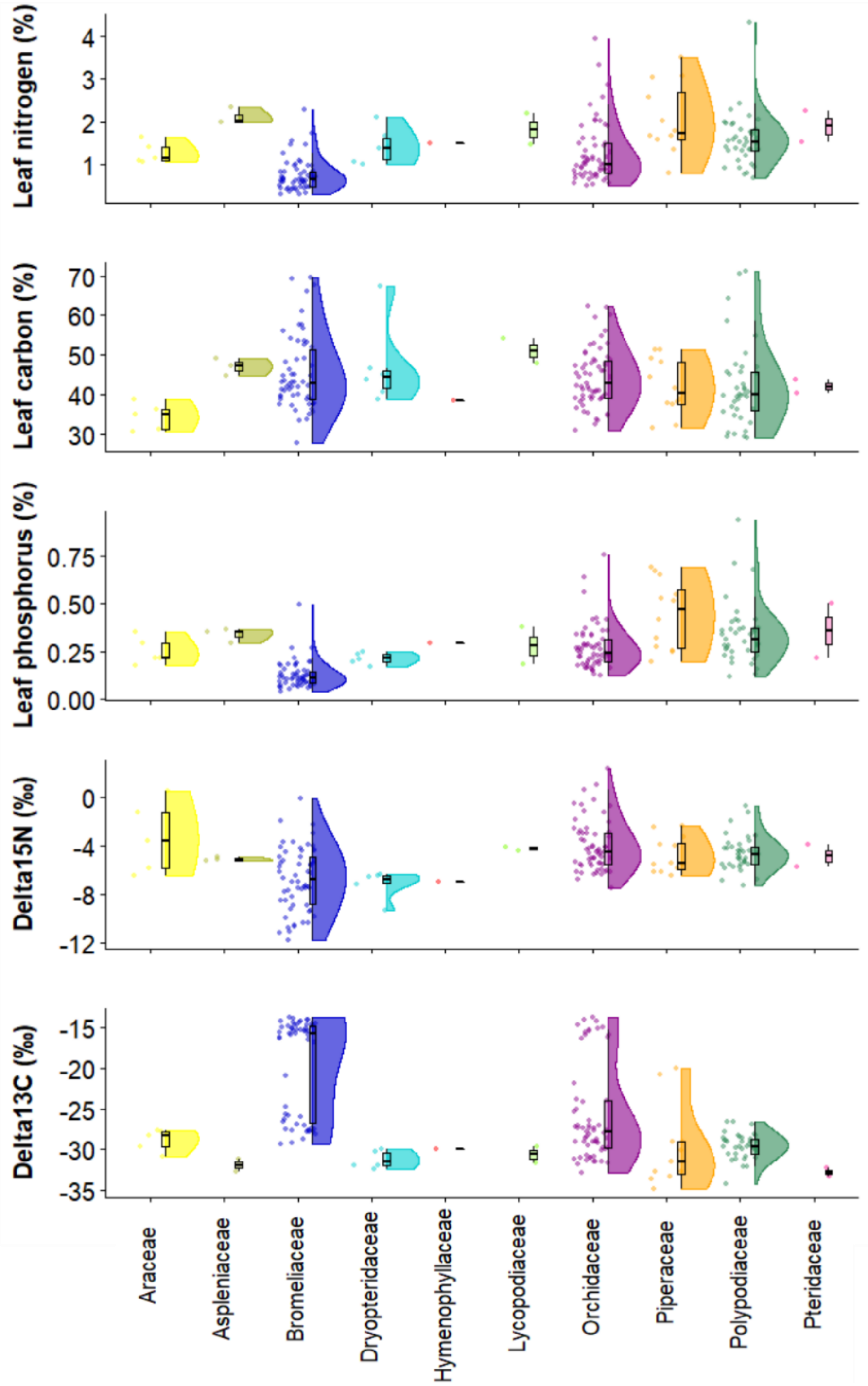


Figure 3.4. Chemical leaf traits per family. Distribution of trait measurements across the 102 species and 10 families at 500, 1500, and 2500 m. Each point represents a species measurement (n=189).

Species identification

Vouchers from the first field campaign were collected, if possible, in triplicate for preservation as herbarium specimens. These specimens were identified using relevant literature (Croat and Acebey 2015; Espejo-Serna et al. 2005; Hietz and Hietz-Seifert 1994; Mickel and Smith 2004) and by comparison with specimens deposited at the National Herbarium (MEXU) and Universidad Nacional Autónoma de México in Mexico City and the herbarium of the Institute of Ecology (XAL) in Xalapa. Some taxa were sent to the following specialists for identification: Crassulaceae (Dr. Pablo Carrillo-Reyes, Universidad de Guadalajara), Cactaceae (Dr. Miguel Cházaro-Bazáñez, Universidad Veracruzana), Bromeliaceae and Orchidaceae (Dr. Adolfo Espejo-Serna and MSc. Ana Rosa López-Ferrari, Universidad Autónoma de México, Iztapalapa), Pteridophytes (Dr. Alan Smith, UC Berkeley, USA), and *Peperomia* (Guido Mathieu, Botanic Garden Meise, Belgium). Species not identified to species level were assigned to morphospecies, using the genus or family name followed by the registered elevation and a consecutive number (Table 5). The collection of species protected by Mexican law was facilitated by a plant collection permit (NOM-059-SEMARNAT-2010) issued by the Secretaría de Medio Ambiente y Recursos Naturales (SEMARNAT SGPA/DGVS/2405/14). All scientific names follow The Plant List version 1.1 (2013).

Geographic coverage

Description:

Data was collected at eight different sites distributed across an elevational gradient along the eastern slopes of Cofre de Perote mountain, Veracruz State, Mexico.

Coordinates:

19.59 Latitude, -96.38 Longitude (study site at the lowermost elevation)

19.51 Latitude, -96.15 Longitude (study site at the uppermost elevation)

Taxonomic coverage

1) Epiphytes: The species distribution data set covers 271 epiphyte species belonging to 92 genera and 23 families. The most species-rich families are Orchidaceae (82 species), Polypodiaceae (50), Bromeliaceae (41), Piperaceae (20), Cactaceae (14), and Araceae (12), (Fig. 3.5 and 3.6). 72.2% of the sampled epiphyte individuals could be identified to species level, while another 26.1% were identified to genus level, and 1.7% to family level. The trait data set includes measurements for 1595 leaves from 474 individuals belonging to 102 species in 10 families. In total, most species were orchids (42.7%), followed by ferns (28.1%), and bromeliads (20.4%).
2) Phorophytes: The 120 climbed host trees belong to 32 tree species distributed in 25 genera and 21 families. Tree identification to the species level was possible in 53% of the cases, while another 44 % were identified to genus level and 3% to family level.

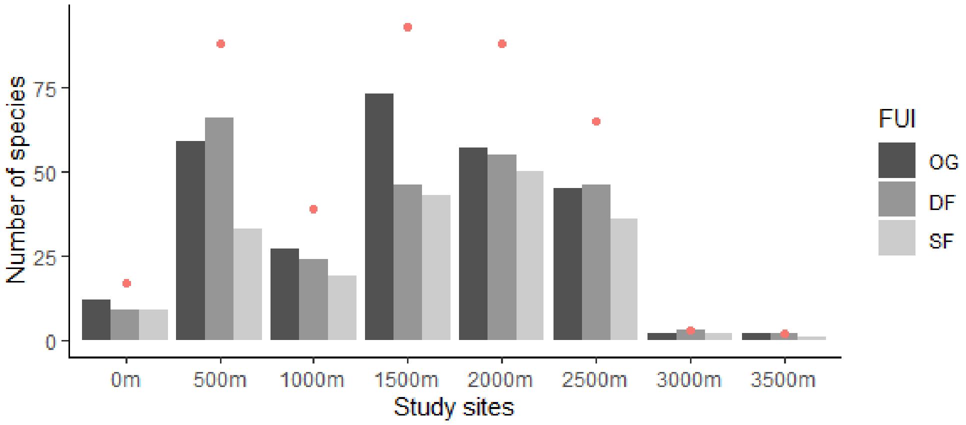


Figure 3.5 Total species number per elevation and forest-use intensity. Number of species of vascular epiphytes recorded at the different levels of forest-use intensity (FUI: OG; Old-growth forest, DF; degraded forest, and SF; secondary forest) at each of the study sites (0 m, 500 m, 1000 m, 1500 m, 2000 m, 2500 m, 3000 m, and 3500 m). At each elevational site, five plots were sampled per FUI. Red points indicate the total number of species per study site.

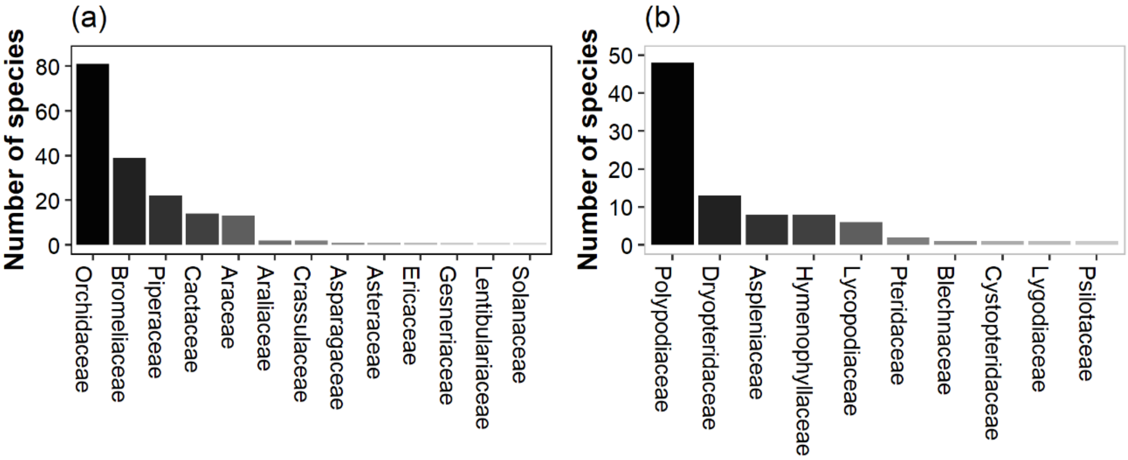


Figure 3.6. Total number of species per family recorded in the 120 plots: a) Angiosperms, (b) Pteridophytes. Note the different scales of the y-axes.

3.4. Data resources

Data package title: BIOVERA-Epi, a new database on species diversity, community composition, and leaf functional traits of vascular epiphytes along an elevational gradient in Mexico:

Dataset 1: Plot table.

Description: Location of the 120 forest plots along the elevational gradient at the eastern slopes of Cofre de Perote mountain, Veracruz, Mexico.

Dataset 2: Distribution table.

Description: Distribution data of 271 vascular epiphyte species at each plot along the elevational gradient and three levels of forest-use intensity (n= 5 plots per forest-use intensity within each elevation)

Dataset 3. Morphological leaf traits.

Description: Single leaf trait measurements (leaf area, leaf density, specific leaf area and leaf dry matter content) per 474 individuals of 102 species and a total of 1595 leaves.

Dataset 4. Chemical leaf traits.

Description: Chemical leaf trait measurements (leaf nitrogen content, leaf phosphorus content, leaf carbon content, nitrogen isotope ratio, and carbon isotope ratio) per 102 species.

Dataset 5. Species names.

Description: Species scientific name and its corresponding family and species code.

Dataset 6. Metadata.

Description: Description of the content and structure of each of the previous tables with the source of standardization for each term used according to Darwin Core glossary and the Thesaurus of Plant characteristics.

Quality control

Taxonomic names were resolved and harmonized with The Plant List v. 1.1 (The Plant List 2013).

Data availability statement:

Data underpinning the analyses will be available once accepted via Dryad Digital Repository

3.5. Metadata

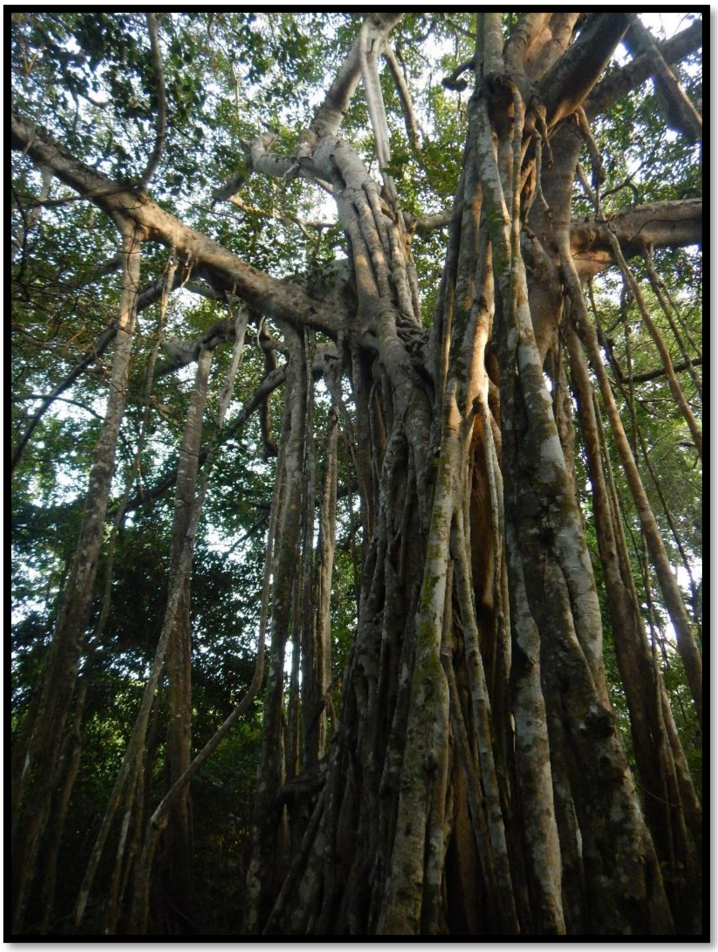
Data documentation with information that describes the content and structure of each of the previous tables. The source of standardization for each term used is provided in the *Standardized according to* column based on the Darwin Core glossary and the Thesaurus of Plant characteristics (TOP). The name of the standardized term in the *Standardized Term* column. The term used in the preset study in the *Term in this study* column. A definition is provided in the *Definition* column (following the Darwin Core, Thesaurus of Plant characteristics or the given reference.) and, if applicable, the unit of measurement in the *Unit* column.

Standardized according to	Standardized Term	Term in this study	Definition	Unit
Darwin Core	Family	Family	The full scientific name of the family in which the taxon is classified.	
Darwin Core	Habitat	Vegetation	A category or description of the habitat in which the Event occurred.	
Darwin Core	locationID	Plot_ID	An identifier for the set of location information (data associated with dcterms: Location). May be a global unique identifier or an identifier specific to the data set.	
Darwin Core	Locality	Site	The specific description of the place. Less specific geographic information can be provided in other geographic terms (higherGeography, continent, country, stateProvince, county, municipality, waterBody, island, islandGroup). This term may contain information modified from the original to correct perceived errors or standardize the description.	
Darwin Core	organismID	Sp.code	An identifier for the Organism instance (as opposed to a particular digital record of the Organism). May be a globally unique identifier or an identifier specific to the data set.	
Darwin Core	organismQuantityType	Frequency.SP Frequency.JZ	The type of quantification system used for the quantity of organisms.	

Darwin Core	scientificName	Species name / Tree name	The full scientific name, with authorship and date information if known. When forming part of an Identification, this should be the name in lowest level taxonomic rank that can be determined. This term should not contain identification qualifications, which should instead be supplied in the IdentificationQualifier term.	
Darwin Core	verbatimElevation	Elevation	The original description of the elevation (altitude, usually above sea level) of the Location.	meters above sea level (m a.s.l.)
Darwin Core	DecimalLatitude	Latitude	The geographic latitude (in decimal degrees, using the spatial reference system given in geodeticDatum) of the geographic center of a Location. Positive values are north of the Equator; negative values are south of it. Legal values lie between -90 and 90, inclusive.	
Darwin Core	DecimalLongitude	Longitude	The geographic longitude (in decimal degrees, using the spatial reference system given in geodeticDatum) of the geographic center of a Location. Positive values are east of the Greenwich Meridian; negative values are west of it. Legal values lie between -180 and 180, inclusive.	
Functional Diversity thesaurus	Plant height trait	Height	the height (PATO:height) of a whole plant (PO:whole plant)	m

Functional Diversity thesaurus	Leaf density	Lamina density (LD)	leaf dry mass per leaf volume	g cm^3
Functional Diversity thesaurus	Leaf area	Leaf area (LA)	the area (PATO:area) of a leaf (PO:leaf) in the one sided projection	mm^2
Functional Diversity thesaurus	Leaf dry matter content	Leaf dry matter content (LDMC)	the ratio of the dry mass of a leaf (TOP:leaf dry mass) to its water saturated fresh mass	g g^{-1}
Functional Diversity thesaurus	Specific leaf area	Specific Leaf Area (SLA)	the ratio of the area of a leaf (TOP:leaf area) to its dry mass (TOP:leaf dry mass)	mm^2 mg^{-1}
Functional Diversity thesaurus	Leaf nitrogen content per leaf dry mass	Leaf nitrogen content	The ratio of the quantity of nitrogen of a leaf per unit dry mass.	%
Functional Diversity thesaurus	Leaf carbon content per leaf dry mass	Leaf carbon content	The ratio of the quantity of carbon of a leaf per unit dry mass.	%
Functional Diversity thesaurus	Leaf phosphorus content per leaf dry mass	Leaf phosphorus content	The ratio of the quantity of phosphorus of a leaf per unit dry mass.	%
Craine et al. (2009)	Nitrogen isotope ratio (δ^{15}N;‰)	Nitrogen isotope ratio (δ^{15}N;‰)	The ratio of ^{15}N to^{14}N of a leaf.	‰
Dawson et al. (2002)	Carbon isotope ratio (δ^{13}C;‰)	Carbon isotope ratio (δ^{13}C;‰)	The ratio of ^{13}C to ^{12}C of a leaf.	‰
This study		Forest-use intensity. (OG - old-growth forest, DF - degraded forest, SF -	A level of forest fragmentation, subjected to ongoing disturbance and/or deforestation.	

		secondary forest)		
This study		DBH	Diameter at the breast height	cm



Semi-humid deciduous forest in La Mancha, Veracruz, Mexico at 0 m a.s.l.

4. SYNOPSIS

Old-growth forests are becoming increasingly affected by forest-use intensity and forest fragmentation. To investigate the effects of these pressures on vascular epiphytes, different vegetation types along an elevational gradient and forest-use intensity gradient in central Veracruz (Mexico) were studied. The central aim of my thesis was to explore the underlying factors driving epiphyte diversity patterns along gradients of elevation, and the processes underpinning leaf trait variation across environmental gradients at different scales. In chapter 1, I analysed species distribution data of epiphytes in 120 forest plots along a 3500 m elevational gradient to expand the ecological knowledge of patterns of epiphyte species diversity. In chapter 2, I investigated the influence of broad- and small-scale environmental gradients on leaf trait variation of epiphytes. In chapter 3, I present a detailed database on species diversity, community composition, and leaf functional traits of epiphytes that also provides complementary information of field records of the two previous chapters. In the following sections, I discuss the main results of my thesis and point towards future perspectives for epiphytes research.

Diversity and distribution of plants in the tropics

In chapter 1, I analysed the effects of forest-use intensity on alpha, beta, and gamma diversity of epiphyte assemblages in old-growth, degraded and secondary forests at eight study sites along an elevational gradient. This study addresses for the first time the interactive effect of elevation and forest-use intensity on the diversity of epiphytes. As hypothesized, I observed that the above interaction strongly impacted local-scale patterns of epiphyte diversity. Furthermore, I found that some types of vegetation at certain elevations resulted more affected in terms of alpha diversity by forest-use than others. These results highlight the value of old-growth forests for epiphyte diversity, but also show that degraded and secondary forests may maintain a high species diversity, and thus play an important role in conservation planning. Nevertheless, long term studies on epiphyte communities in secondary and degraded forests in this region could reveal if epiphyte communities are stable and viable in the long term, contributing to the complexity of human disturbed systems making them more valuable for conservation. In parallel, I observed that spatial turnover in species composition among forest-use intensity levels was similar at most elevational belts (Fig. 1.6), suggesting that environmental conditions along the elevational gradient strongly regulate the composition of epiphytes. As postulated by Gentry and Dodson (1987), these results could be related to niche partitioning along environmental gradients in the neotropics, which also implies a high beta diversity (i.e. spatial variation in composition). The spatial turnover observed in this research is comparable with the previous study of Larrea & Werner (2010), that showed a rapid increase in the turnover of epiphytes with increasing forest-use intensity.

Lastly, I observed a peak in species richness at mid-elevations, which monotonically decreased from 1,500 m towards the upper limit of the elevational gradient. This was consistent, to some extent, with previous studies on elevational patterns in epiphytes (Cardelús et al., 2006; Kessler, Kluge, Hemp, & Ohlemüller, 2011; Kluge et al., 2006; Krömer et al., 2005; Wolf & Flamenco, 2003) but slightly differed in that species richness showed a second peak in tropical oak forests at 500 m**.** It is unclear whether this deviation from the expected hump-shaped pattern is related to a high variation of environmental factors that can change substantially in small regions, causing differences in the form of distributional patterns (Rahbek 1995). Nevertheless, it could also be due to an unusually high diversity found at 500 m, which was on average comparable to diversity at 1,500 m, or an unusually low diversity of epiphytes at the 1,000-m site. The results in this chapter offer a framework to better understand the ecological factors that may determine diversity patterns of epiphytes, but also contributes to the understanding of beta diversity, a component that remains poorly studied.

Environmental influence on functional traits

In chapter 2, I analysed the interplay and relative importance of broad- and small-scale environmental gradients as drivers of variation in leaf functional traits of epiphytes based on samples of 474 individuals belonging to 102 species. I observed differences in leaf traits among five main taxonomic groups represented in this study, belonging to orchids, ferns, and bromeliads. Orchid leaf traits, for instance, were associated with lower leaf density and LDMC, bromeliads were associated with lower leaf nitrogen, leaf phosphorus and SLA, and Polypodiaceae was associated with higher leaf nitrogen, leaf phosphorus and SLA. These results are in line with previous studies (Hietz et al. 1999; Petter, et al., 2016). However, even when the multidimensional trait space, occupied by the ten families overlapped considerably (Fig. 1.1a), I observed significant differences among the five most diverse families (Bromeliaceae, Orchidaceae, Polypodiaceae, Dryopteridaceae and Piperaceae). These results suggest that unique tendencies within some taxonomic groups could indicate that some leaf traits are taxonomically conserved. In addition, the PCA analyses showed a clear separation between species performing CAM or C_3 photosynthesis (Fig. 1.1b), reflecting traits associated with water relations, where C_3 species were more associated with light and nutrient acquisition traits. As also noticed by Hietz et al. (1999), I found a higher proportion of CAM species at lower sampling elevations, where water availability is a stronger limiting factor for C_3 species. These two groups of plants responded differently to sampling elevations. I observed a significant interaction between sampling elevation and photosynthetic pathway for most morphological and chemical leaf traits, suggesting a coordinated, yet contrasting response to elevation (Jager et al., 2014; Rosas et al., 2019), which would suggest that i.e. adaptations to water availability are not limited to physiological processes, but are extended to leaf-level morphological adaptations. This reveals the importance of combining both CAM and C_3 plant functional groups and single traits in order to understand the distributions of epiphytes along environmental gradients.

At the small-scale environmental gradient, I found a greater variation of morphological traits than chemical traits, where leaf density and LDMC slightly decreased with increasing relative height of attachment. These results are not fully consistent with the findings of Petter et al. (2016) but show that trait-environment relationships for morphological traits are not always strong, suggesting that a wide range in trait values are possible under similar environmental conditions. However, phylogenetic trait conservatism could be playing a more important role in determining trait variation, since we showed that families contributed between 52% and 56% of trait variation in morphological traits, with exception of SLA where 55% of the variation was found among species. Another possible explanation for the weak trait-environment relationship showed in this research for morphological traits, could be the length of the broad-scale environmental gradient, which does not include elevations beyond 1500 m. This excludes more stressful environmental conditions that might reveal stronger impacts of broad-scale environmental gradients on the variation of morphological leaf traits.

Moreover, chemical traits varied along both broad- and small-scale environmental gradients, with the environment explaining a large fraction of leaf trait variation. I found differences between CAM and C_3 species in leaf nitrogen, leaf phosphorus, and $\delta^{15}N$ at 0 m in relation to maximum elevation, this might be the result of the higher proportion of CAM species compared to C_3 species at this elevation, which has been previously reported by Hietz et al. (1999), who showed that the proportion of epiphyte species performing CAM photosynthesis decreased with increasing elevation and precipitation from 58 to 6%. Nevertheless, it could also be related to changes in the availability of nutrients at different elevations, as it has been shown in previous studies on foliar nutrient concentrations, e.g. leaf phosphorus and leaf nitrogen, declining with elevation (Vitousek et al., 1992; Kitayama & Aiba, 2002; Soethe et al., 2008). In this regard, I observed a significant negative interaction between maximum elevation and photosynthetic pathway on leaf nitrogen and $\delta^{15}N$, both of which decreased with elevation. Nevertheless, this interaction was not as pronounced in C_3 as for CAM plants.

The CAM photosynthetic pathway is common in several families of tropical and subtropical epiphytes especially Bromeliaceae and Orchidaceae. In this study, we categorized CAM species based on carbon isotope ratios using the widely accepted threshold of $\delta^{13}C$ values > -20 ‰ for strong CAM species and < -20 ‰ for C_3 species (Hietz et al., 1999; Winter, 2019). Interestingly, carbon isotope ratio was the only chemical leaf trait influenced by relative height of attachment, where species higher in the outer canopy were more water-use efficient. This indicates that adaptations, such as CAM photosynthesis, help species in the outer canopy or in the lower elevations to withstand drought and greater vapour pressure deficits. Nevertheless, in the present study the threshold used to categorize CAM species could be discriminating weak CAM species, making difficult to consider other families different than Bromeliaceae and Orchidaceae, which might show higher water-use efficiencies as well. The results in this chapter bring new insights into plant leaf adaptations to better understand the distribution of epiphytes along environmental gradients in light, nutrient, and water availability at different scales.

The importance of field data contributions

In chapter 3, I provide a new database “BIOVERA-Epi” on species diversity, community composition and leaf functional traits of epiphytes. I presented detailed information describing two datasets which on one hand, assembled distribution and frequency data of 271 epiphytes species surveyed in 120 plots along the elevational gradient, and on the other provides a wide set of nine morphological and chemical leaf traits for 102 species surveyed along 45 plots in the same gradient. Even when epiphytes represent about 9% of all vascular plant species, they are strongly underrepresented in global traits datasets. Given that, with BIOVERA-Epi I aim at contributing to the percentage of epiphyte species represented in global datasets.

In summary, the findings of my research improved our understanding of how elevation and forest-use intensity influenced the spatial patterns of epiphyte diversity in a tropical mountainous region. Moreover, my thesis constitutes a comprehensive study on the leaf trait variability of epiphytes and the important role of broad- and small-scale gradients in light, nutrient, and water availability explaining their distribution. Furthermore, this thesis opens new avenues for future macroecological studies on the diversity of epiphytes and their functional traits. The assemblage of local information in global databases covering species occurrences and functional traits can help to validate ecological theories at larger scales. In particular, the inclusion of an increasing number of studies on functional ecology can foster new frameworks and theories to better understand how biodiversity responds to an increasingly fragmented natural world.

Challenges and future perspectives for epiphyte research

From the local to global scale we are losing biological diversity and ecosystem structure at unparalleled rates of decline (Peters et al. 2019). By now, all ecosystems are affected by anthropogenic disturbance, because even the best protected and remote sites experience atmospheric land-use and climatic changes, which are by far the most important processes altering biological diversity. In ecological research, epiphytes form an important entity. Nevertheless, forest canopies have long evaded scientists because of logistical difficulties in reaching tree crowns and the subsequent challenges of sampling ones one gets up there. Luckily throughout the last years, field biologists began extensive explorations of this unknown world of plants, insects, birds, mammals, and their interactions. These logistic advances are attributed to the development of several innovative and creative techniques that facilitate ascent into the crowns. Epiphytes have been called particularly' vulnerable to global climate change (Benzing 1998), because in habitats such as tropical cloud forests, characterized by continuously high moisture input, epiphytes may indeed be more susceptible than other life forms to changes in precipitation or humidity patterns, but also to the habitat loss rates that these habitats undergo. Therefore, I believe that understanding the canopy as part of whole-ecosystem processes is vital for forest conservation and is an obvious priority if we are to responsibly manage and conserve forests in the future. Developing new strategies in epiphyte conservation and deepening our ecological understanding of community assembly in tropical forests should therefore be of preeminent importance in future epiphyte research. Moreover, it should include multidisciplinary approaches to better understand ecological adaptations of epiphyte communities, comprising community architecture, species composition, nutrient cycling, energy transfer, plant-animal interactions, functional traits, and conservation issues from the ground to the community-atmosphere interface for all plant assemblages. Functional traits have proved to be useful surrogates to describe species ecology and ecosystem functioning (Díaz and Cabido 2001, Violle et al. 2007). Therefore, I see great potential to further studies implementing experimental designs to test for consistent ecological patterns among functional groups of epiphytes. In this human-dominated planet, we should protect “functional systems”, in which epiphytes and associated flora and fauna can then thrive as one component of biological diversity, rather than focus on individual species or isolated environmental factors.

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6. APPENDIX

A Supplementary information to Chapter 1

Table A1. List of species**.** Species of vascular epiphytes recorded along gradients of elevation and forest-use intensity in central Veracruz, Mexico. Collector: Valeria Guzmán-Jacob (VGJ); Herbaria: UC= University and Jepson Herbaria, Berkeley; MEXU= Instituto de Biología, Universidad Nacional Autónoma de México; BR= Herbarium Generale, Botanic Garden Meise, Blegium; IBUG= Universidad de Guadalajara; UAMIZ= Herbário Universidad Autónoma Metropolitana, Iztapalapa; CITRO= Centro de Investigaciones Tropicales. FUI: Forest-use intensity category (OG: old-growth forest, DF: degraded forest and SF: secondary forest), Number of observations recorded in all 120 plots (Total Obs.). Nomenclature follows The International Plant Names Index <www.ipni.org> (accessed on 01 May 2019).

Family/Species (voucher, herbarium)	**Elevation (m. a. s. l.)**	**FUI**	**Total Obs.**
Subclass Magnoliidae (‘angiosperms’)			
Araceae			
Anthurium andicola Liebm. VGJ 733 UAMIZ	2000	OG, DF, SF	7
Anthurium podophyllum (Cham. & Schltdl.) Kunth. VGJ 206 CITRO, VGJ 436 UAMIZ	500	OG, DF, SF	10
Anthurium scandens (Aubl.) Engl. VGJ 87 CITRO	500,1500,2000	OG, DF, SF	5
Anthurium schlechtendalii Kunth. VGJ 241 UAMIZ, CITRO	500,1000	OG, DF, SF	19
Monstera acuminata K. Koch. VGJ 242 CITRO	500	OG	6
Philodendron advena Schott. VGJ 24 CITRO	1500	OG, DF	5
Philodendron hederaceum (Jacq.) Schott. VGJ 324 UAMIZ, CITRO	500	DF	3
Philodendron jacquinii Schott. VGJ 319 UAMIZ, CITRO	500	DF	1
Philodendron radiatum Schott. VGJ 396 CITRO	500	OG	13
Philodendron sagittifolium Liebm. VGJ 297 CITRO	1000	OG,DF	10
Syngonium neglectum Schott. VGJ 336 CITRO	5000, 1000	OG, DF, SF	26
Syngonium 1500 sp1. VGJ 113 CITRO	1500	OG, DF, SF	8
Araliaceae			

Dendropanax arboreus (L.) Decne. & Planch. VGJ 499 UAMIZ	2000,2500	OG, DF, SF	22
Oreopanax capitatus (Jacq.) Decne. & Planch. VGJ 349 UAMIZ	2000,2500	DF, SF	7
Asparagaceae			
Maianthemum paniculatum (M. Martens & Galeotti) LaFrankie VGJ 368 UAMIZ	2000,2500	OG, DF	12
Asteraceae			
Nelsonianthus tapianus (B.L.Turner) C.Jeffrey. VGJ 371 UAMIZ	2000, 2500	OG, DF,SF	10
Bromeliaceae			
Aechmea bracteata (Sw.) Griseb. VGJ 326 CITRO	0, 500	OG, DF, SF	19
Aechmea nudicaulis (L.) Griseb. VGJ 311 UAMIZ	500	DF,SF	2
Catopsis morreniana Mez. VGJ 407 CITRO	500	DF	9
Catopsis nitida (Hook.) Griseb. VGJ 53 CITRO	1500	OG, SF	11
Catopsis paniculata E. Morren. VGJ 874 CITRO	2000, 2500	SF	11
Catopsis sessiliflora (Ruiz & Pavon) Mez. VGJ 63 CITRO	500, 1500, 2000	OG,DF,SF	62
Catopsis 2000 sp1. VGJ 717 CITRO	2000	DF	1
Tillandsia ghiesbreghtii Baker. VGJ 753 UAMIZ	1500	OG,DF	1
Tillandsia 1000 sp1. VGJ 859 CITRO	1000	DF, SF	10
Tillandsia 2000 sp1. VGJ 752 CITRO	2000	OG,DF,SF	24
Tillandsia 2500 sp1. VGJ 378 CITRO	2500	DF, SF	3
Tillandsia 2500 sp2. VGJ 673 CITRO	2500	OG	1
Tillandsia botterii E. Morren ex Baker. VGJ 467 UAMIZ	500, 1000	DF, SF	6
Tillandsia brachycaulos Schltdl. VGJ 237 UAMIZ	500	OG;DF	21
Tillandsia butzii Mez. VGJ 104 CITRO	1500	OG,DF, SF	36
Tillandsia circinnata Schltdl. VGJ 587 CITRO	0	OG,DF,SF	25
Tillandsia concolor L. B. Sm. VGJ 592 CITRO	0	OG,DF	7
Tillandsia filifolia Schltdl. & Cham. VGJ 217 CITRO	500, 1000	OG,DF,SF	12
Tillandsia foliosa M. Martens & Galeotti. VGJ 323 CITRO	500	DF,SF	9
Tillandsia gymnobotrya Baker. VGJ 41 CITRO	1500,2000,2500	OG,DF,SF	40
Tillandsia 0 sp1. VGJ 597 CITRO	0	DF	3
Tillandsia imperialis E. Morren ex Roezl. VGJ 366 CITRO	2000, 2500	OG,DF,SF	31

Tillandsia ionantha Planch. VGJ 398 CITRO	0,500,1000	OG, DF, SF	63
Tillandsia juncea (Ruiz & Pav.) Poir. VGJ 137 CITRO	500,1000,1500	OG,SF,SF	47
Tillandsia kirchhoffiana Wittm. VGJ 900 CITRO	1500	OG,DF,SF	43
Tillandsia limbata Schltdl. VGJ 292 CITRO	500, 1000	OG,DF, SF	29
Tillandsia lucida E. Morren ex Baker. VGJ 141 CITRO	1500,2000	OG,SF	3
Tillandsia macropetala Wawra. VGJ 152 CITRO	1500,2000	OG,SF	19
Tillandsia multicaulis Steud. VGJ 89 CITRO	1500,200	OG,DF, SF	64
Tillandsia paucifolia Baker. VGJ 587 UAMIZ	0	SF	1
Tillandsia polystachia (L.) L. VGJ 597 UAMIZ	500,1000	OG,DF,SF	35
Tillandsia punctulata Schltdl. & Cham. VGJ 101 CITRO	500,1500,2000	OG,DF,SF	29
Tillandsia recurvata (L.) L. VGJ 158 CITRO	500,1500	OG,SF	24
Tillandsia schiedeana Steud. VGJ 209 CITRO	500,1000	OG,DF,SF	62
Tillandsia streptophylla Scheidw. & C. Morren. VGJ 218 CITRO	500	OG,DF,SF	18
Tillandsia tricolor Schltdl. & Cham. VGJ 293 UAMIZ	500	SF	5
Tillandsia usneoides (L.) L. VGJ 443 CITRO	500	DF	2
Tillandsia utriculata L. VGJ 317 CITRO	0,500,1000	DF,SF	7
Tillandsia violacea Baker. VGJ 365 CITRO	2000,2500	OG,DF,SF	16
Tillandsia viridiflora (Beer) Baker. VGJ 79 CITRO	1500,2000	OG,DF	17
Werauhia vanhyningii (L. B. Sm.) J. R. Grant. VGJ 739 CITRO	2000	OG,SF	4
Cactaceae			
Disocactus flagelliformis (L.) Barthlott. VGJ 515 UAMIZ	2000,2500	OG,DF,SF	8
Disocactus martianus (Zucc. ex Pfeiff.) Barthlott. VGJ 830 UAMIZ	2000	DF	1
Disocactus phyllanthoides (DC.) Barthlott. VGJ 708 UAMIZ	2000	OG,SF	5
Epiphyllum 2000 sp1. VGJ 636 CITRO	2000	DF	1
Epiphyllum 2500 sp1. VGJ 532 CITRO	2500	OG	2
Epiphyllum phyllanthus (L.) Haw. VGJ 863 CITRO	500,1000	OG,DF,SF	21
Hylocereus 2500 sp1. VGJ 375 CITRO	2500	DF	1

Hylocereus 2000 sp1. VGJ 829 CITRO	2000	DF	1
Hylocereus undatus (Haw.) Britton & Rose. VGJ 282 CITRO	0,500	OG,DF,SF	13
Rhipsalis baccifera (J.S.Muell.) Stearn. VGJ 449 UAMIZ	500,1000,1500	OG,DF,SF	27
Selenicereus 500 sp1. VGJ 456 CITRO	500	DF	1
Selenicereus 500 sp2. VGJ 226 CITRO	500	DF	2
Selenicereus grandiflorus (L.) Britton & Rose. VGJ 591 CITRO	0,500	OG,DF,SF	18
Selenicereus testudo (Karw. ex Zucc.) Buxb. VGJ 283 CITRO	0,500	OG,SF	5
Crassulaceae			
Echeveria rosea Lindl. VGJ 364 IBUG	2500	OG	2
Sedum botterii Hemsl.VGJ 629 IBUG	2000,2500	OG,DF,SF	17
Sedum guatemalense Hemsl.VGJ 508 IBUG	2500	OG	2
Ericaceae			
Ericaceae 2500 sp1. VGJ 507 UAMIZ	2000,2500	OG,DF,SF	24
Gesneriaceae			
Columnea 2000 sp1. VGJ 773 CITRO	2000	OG	1
Lentibulariaceae			
Pinguicula moranensis Kunth. VGJ 343 UAMIZ	2000,2500	OG,DF,SF	6
Orchidaceae			
Acineta barkeri (Bateman) Lindl. VGJ 901 CITRO	1500	OG	1
Brassavola cucullata (L.) R. Br. VGJ 442 UAMIZ	500	OG,DF,SF	4
Brassavola nodosa (L.) Lindl. VGJ 601 UAMIZ	0,500	OG,SF	8
Brassia verrucosa Bateman ex Lindl. VGJ 425 UAMIZ	1000	OG,DF	19
Camaridium densum (Lindl.) M.A.Blanco. VGJ 401 UAMIZ	500	DF	3
Campylocentrum 1500 sp1. VGJ 165 UAMIZ	1500	DF	4
Catasetum integerrimum Hook. VGJ 853 CITRO	1000	DF,SF	8
Catasetum 500 sp1. VGJ 308 CITRO	500	DF	5
Cattleya 500 sp1. VGJ 445 CITRO	500	SF	1
Comparettia falcata Poepp. & Endl. VGJ 166 CITRO	1500	SF	2
Dichaea glauca (Sw.) Lindl. VGJ 183 UAMIZ	1500	OG,DF	5
Dichaea muricatoides Hamer & Garay. VGJ 75 CITRO	1500	OG,SF	3
Dichaea 1500 sp1. VGJ 69 UAMIZ	1500	OG	3

Dichaea 1500 sp2. VGJ 96 UAMIZ	1500	SF	2
Dinema polybulbon (Sw.) Lindl. VGJ 415 UAMIZ	1000	OG,DF	7
Elleanthus cynarocephalus (Reichb. f.) Reichb. f. VGJ 70 CITRO	1500	OG	3
Elleanthus 500 sp1. VGJ 2001 CITRO	500	OG	2
Encyclia 1500 sp1. VGJ 187 CITRO	1500	DF	4
Epidendrum 1500 sp1. VGJ 66 CITRO	1500	OG	2
Epidendrum 1500 sp2. VGJ 186 CITRO	1500	DF	2
Epidendrum nocturnum Jacq. VGJ 608 UAMIZ	500	DF	1
Epidendrum raniferum Lindl. VGJ 574 UAMIZ	500	DF	2
Epidendrum 500 sp1. VGJ 439 UAMIZ	500	SF	4
Isochilus 1000 sp1. VGJ 848 CITRO	1000	OG	1
Isochilus 1500 sp1. VGJ 31 CITRO	1500	OG	5
Isochilus 500 sp1. VGJ 299 CITRO	500	DF	2
Isochilus unilateralis B. L. Rob. VGJ 296 UAMIZ	2000,2500	OG	12
Jacquiniella teretifolia (Sw.) Britton & P. Wilson. VGJ 61 CITRO	1500	OG,DF	3
Laelia anceps Lindl. VGJ 301 CITRO	500,1000	OG,DF,SF	12
Lephanthes 2000 sp1. VGJ 694 UAMIZ	2000	OG	8
Lycaste 500 sp1. VGJ 322 CITRO	500	DF	4
Maxilaria 2000 sp1. VGJ 726 CITRO	2000	OG,DF	3
Maxillaria 500 sp1. VGJ 400 UAMIZ	500	DF	4
Maxillaria tenuifolia Lindl. VGJ 312 CITRO	500	DF	2
Myrmecophila tibicinis (Bateman ex Lindl.) Rolfe. VGJ 813 CITRO	0	OG	3
Oncidium 1500 sp1. VGJ 65 CITRO	1500	SF	2
Oncidium 15 sp1. VGJ 817 CITRO	0	OG	1
Oncidium 500 sp1. VGJ 404 CITRO	500	DF	2
Oncidium incurvum (Lindley) Baker VGJ 638 UAMIZ	2000	OG,DF,SF	5
Oncidium sphacelatum Lindl. VGJ 452 UAMIZ	500	DF,SF	9
Orchidaceae 1500 sp1. VGJ 35 CITRO	1500	OG	7
Orchidaceae 1500 sp2. VGJ 64 CITRO	1500	OG	8
Orchidaceae 1500 sp3. VGJ 168 CITRO	1500	DF	1
Ornithocephalus inflexus Lindl. VGJ 325 UAMIZ	5000,1000	OG,SF	8
Phloeophila peperomioides (Ames) Garay VGJ 278 UAMIZ	500	OG	2
Pleurothallis 1500 sp1. VGJ 103 CITRO	1500	SF	2
Pleurothallis 2000 sp1. VGJ 696 CITRO	2000	OG	9

Pleurothallis 2000 sp2. VGJ 751 UAMIZ	2000	OG	2
Pleurothallis 500 sp1. VGJ 646 CITRO	500	SF	1
Pleurothallis pachyglossa Lindl. VGJ 207 CITRO	1500	OG	2
Prosthechea cochleata (L.) W.E.Higgins. VGJ 216 UAMIZ	500,1000,2500	OG,DF,SF	9
Prosthechea livida (Lindl.) W.E.Higgins VGJ 586 UAMIZ	500	OG	1
Prosthechea radiata (Lindl.) W.E.Higgins. VGJ 320 UAMIZ	500	DF	4
Prosthechea 1500 sp1. VGJ 232 UAMIZ	1500	OG,SF	7
Prosthechea varicosa (Bateman ex Lindl.) W.E.Higgins. VGJ 483 UAMIZ	2000,2500	OG,DF	5
Prosthechea vitellina (Lindl.) W.E.Higgins. VGJ 476 UAMIZ	1500,2000,2500	OG,DF,SF	31
Restrepiella ophiocephala (Lindl.) Garay & Dunst. VGJ 315 CITRO	500	DF,SF	7
Rhyncholaelia glauca (Lindl.) Schltr. VGJ 399 UAMIZ	500	DF	5
Rhynchostele cordata (Lindl.) Soto Arenas & Salazar.VGJ 727 UAMIZ	2000	DF	2
Rhynchostele ehrenbergii (Link, Klotzsch & Otto) Soto Arenas & Salazar.VGJ 528 CITRO	500,2000,2500	OG,DF,SF	12
Rhynchostele rossii (Lindl.) Soto Arenas & Salazar VGJ 372 UAMIZ	2000	DF	1
Rinchostele 2500 sp1. VGJ 634 CITRO	2500	OG,DF	5
Scaphyglottis 1000 sp1. VGJ 236 UAMIZ	1000	OG,DF	19
Scaphyglottis 500 sp1. VGJ 579 UAMIZ	500	DF	1
Scaphyglottis livida (Lindl.) Schltr. VGJ 457 UAMIZ	500	OG	3
Specklinia 2000 sp1. VGJ 737 UAMIZ	2000	OG,SF	2
Specklinia 500 sp1. VGJ 1610 CITRO	500	OG	2
Specklinia digitale (Luer) Pridgeon & M.W.Chase VGJ 230 UAMIZ	500	OG	3
Specklinia grobyi (Bateman ex Lindl.) F.Barros. VGJ 580 CITRO	500	DF	3
Specklinia tribuloides (Sw.) Pridgeon & M.W.Chase. VGJ 572 UAMIZ	500	DF	1
Stelis 1000 sp1. VGJ 418 UAMIZ	1000	DF	1
Stelis 1500 sp1. VGJ 205 UAMIZ	1500	SF	2
Stelis 500 sp1. VGJ 309 UAMIZ	500	OG	3
Stelis emarginata (Lindl.) Soto Arenas & Solano. VGJ 328 UAMIZ	500	OG,DF	4
Stelis oaxacana R. Solano. VGJ 778 UAMIZ	2500	SF	6

Stelis pachyglossa (Lindl.) Pridgeon & M.W.Chase. VGJ 300 UAMIZ	1000	OG	1
Trichocentrum 1000 sp1. VGJ 434 UAMIZ	1000	DF,SF	3
Trichocentrum 500 sp1. VGJ 402 CITRO	500	OG,SF	6
Trichocentrum 0 sp1. VGJ 600 CITRO	0	SF	2
Trichocentrum stramineum (Bateman ex Lindl.) M.W.Chase & N.H.Williams. VGJ 235 CITRO	500,1000	OG,DF	18
Trichosalpinx 2500 sp1. VGJ 492 UAMIZ	2500	OG,DF	4
Vanilla 200 sp1. VGJ 1460 CITRO	500	DF	1
Piperaceae			
Peperomia 1500 sp1. VGJ 3 CITRO	1500	OG,SF	4
Peperomia 1500 sp2. VGJ 9 CITRO	1500	OG	4
Peperomia 2000 sp1. VGJ 630 CITRO	2000	DF	1
Peperomia 2000 sp2. VGJ 560 CITRO	2000	OG,DF	2
Peperomia 2500 sp1. VGJ 482 CITRO	2500	OG,DF	6
Peperomia 2500 sp2. VGJ 511 BR	2500	OG	2
Peperomia 500 sp1. VGJ 448 CITRO	500	DF	1
Peperomia 500 sp2. VGJ 575 CITRO	500	DF	1
Peperomia 500 sp3. VGJ 233 CITRO	500	OG	1
Peperomia arboricola C. DC. VGJ 201 BR	1500,2000	OG,DF,SF	28
Peperomia asarifolia Schltdl. VGJ 281 BR	500	OG	1
Peperomia berlandieri Miq. VGJ 194, BR	500	OG,DF,SF	29
Peperomia cobana C. DC. VGJ 695 BR	2000	OG,DF	5
Peperomia glabella (Sw.) A. Dietr. VGJ 198 CITRO	1500	DF	1
Peperomia leptophylla Miq. VGJ 385 BR	2000	OG,DF,SF	15
Peperomia obtusifolia (L.) A. Dietr. VGJ 275 BR	500,1500	OG,DF	23
Peperomia quadrifolia (L.) Kunth. VGJ 199 BR	500,1500,2000	OG,DF,SF	44
Peperomia sanjoseana C. DC. VGJ 74, 130 BR	1500,2000	OG,DF,SF	6
Peperomia tenerrima Schltdl. & Cham. VGJ 33 BR	1500,2000,2500	OG,DF,SF	44
Peperomia tetraphylla (G. Forst.) Hook. & Arn. VGJ 429 CITRO	1000	OG	6
Solanaceae			
Solanum 2500 sp1. VGJ 516 CITRO	2500	DF,SF	3
‘Ferns & lycophytes’			
Aspleniaceae			
Asplenium auriculatum Sw. VGJ 559 UC	2000	DF	1
Asplenium cuspidatum Lam. VGJ 76 UC	1500,2000	OG,DF	10
Asplenium harpeodes Kunze. VGJ 143 UC	1500,2500	OG,DF	12

Asplenium linearifolium Bonap. VGJ 648 CITRO	2500	OG,DF	4
Asplenium monanthes L. VGJ 648 UC	2500	OG,DF,SF	4
Asplenium rutifolium (Bergius) Kunze. VGJ 838 CITRO	2000	DF	1
Asplenium 2500 sp1. VGJ 667 CITRO	2500	OG	1
Schaffneria nigripes Fée. VGJ 286 CITRO	500	OG	1
Blechnaceae			
Blechnum fragile (Liebm.) C.V. Morton & Lellinger. VGJ 181 UC	1500	OG,DF,SF	6
Cystopteridaceae			
Cystopteris diaphana (Bory) Blasdell. VGJ 647 UC	2500	OG	1
Dryopteridaceae			
Elaphoglossum 1500 sp1. VGJ 1 CITRO	1500	OG	2
Elaphoglossum 500 sp1. VGJ 438 CITRO	500	OG	1
Elaphoglossum erinaceum (Fée) T. Moore. VGJ 760 UC	2000	OG,DF	4
Elaphoglossum glaucum T. Moore. VGJ 54 UC	1500,2000,2500	OG,DF,SF	11
Elaphoglossum lanceum Mickel. VGJ 373 UC	2500	OG	6
Elaphoglossum lonchophyllum (Fée) T. Moore. VGJ 23 CITRO	1500	OG	5
Elaphoglossum muscosum (Sw.) T. Moore. VGJ 1000 CITRO	2500	OG	1
Elaphoglossum paleaceum (Hook. & Grev.) Sledge. VGJ 724 UC	2000,2500	OG.DF	5
Elaphoglossum peltatum (Sw.) Urb. VGJ 203 UC	1500,2000,2500	O,SF	6
Elaphoglossum petiolatum (Sw.) Urb. VGJ 693 UC	1500,2000	OG	8
Elaphoglossum pringlei (Davenp.) C. Chr. VGJ 185 CITRO	1500	DF	2
Elaphoglossum sartorii (Liebm.) Mickel. VGJ 625 UC	1500,2000,2500	OG,DF,SF	26
Elaphoglossum vestitum (Schltdl. & Cham.) T. Moore. VGJ 59 CITRO	1500,2000	OG.DF,SF	12
Hymenophyllaceae			
Didymoglossum reptans (Sw.) C. Presl. VGJ 37 UC	1500	OG,DF	15
Hymenophyllum crispum Kunth. VGJ 633 CITRO	2000	DF	1
Hymenophyllum fucoides (Sw.) Sw. VGJ 533 UC	2000,2500	OG.DF,SF	8
Hymenophyllum polyanthos (Sw.) Sw. VGJ 36 UC	1500,2000	OG	6

Hymenophyllum tegularis (Desv.) Proctor & Lourteig. VGJ 652 UC	2000,2500	OG	9
Hymenophyllum trapezoidale Liebm. VGJ 512 CITRO	2500	OG	3
Trichomanes capillaceum L. VGJ 21 UC	1500	OG,SF	30
Vandenboschia radicans (Sw.) Copel. VGJ 714 CITRO, VGJ 718 UC	2000	OG,DF	2
Lycopodiaceae			
Diphasiastrum thyoides (Humb. & Bonpl ex Willd.) Holub VGJ 350 UC	2500	SF	1
Huperzia cuernavacensis (Underw. & F. E. Lloyd) Holub. VGJ 832 CITRO	2000	DF	3
Huperzia pringlei (Underw. & F. E. Lloyd) Holub. VGJ 705 CITRO	2000	OG,SF	4
Huperzia taxifolia (Sw.) Trevis. VGJ 85 CITRO	1500	OG	3
Phlegmariurus cuernavacensis (Underw. & F.E. Lloyd) B. Øllg. VGJ 346 UC	2500	SF	1
Phlegmariurus pringlei (Underw. & F.E. Lloyd) B. Øllg. VGJ 498 UC	2500	OG,DF	6
Lygodiaceae			
Lygodium venustum Sw. VGJ 602 CITRO	0	SF	2
Polypodiaceae			
Campyloneurum amphostenon (Kunze ex Klotzsch) Fée. VGJ 472 UC	2000,2500	OG,DF,SF	14
Campyloneurum angustifolium (Sw.) Fée. VGJ 193 CITRO	1500,2500	OG,DF	8
Campyloneurum phyllitidis (L.) C. Presl. VGJ 271 CITRO	500,1000	OG,DF	20
Cochlidium linearifolium (Desv.) Maxon ex C. Chr. VGJ 344 UC	2000,2500	OG,DF,SF	10
Galactodenia delicatula (M. Martens & Galeotti) Sundue & Labiak. VGJ 766 UC	2000	SF	1
Goniophlebium furfuraceum (Schltdl. & Cham.) T. Moore. VGJ 52 CITRO	500,1000,1500,2000	OG,DF,SF	30
Melpomene leptostoma (Fée) A. R. Sm. & R.C. Moran. VGJ 55,82 UC	1500,2000	OG,DF,SF	5
Melpomene pilosissima (M. Martens & Galeotti) A. R. Sm. & R. C. Moran. VGJ 510 UC	1500,2000	OG	8
Melpomene xiphopteroides (Liebm.) A. R. Sm. & R. C. Moran. VGJ 58 UC	1500,2000,2500	OG,SF	16
Microgramma nitida (J. Sm.) A. R. Sm. VGJ 294 UC	0,500,1000	OG,DF,SF	12
Niphidium 500 sp1. VGJ 257 CITRO	500	OG	4
Pecluma atra (A. M. Evans) M. G. Price. VGJ 302 CITRO	500,1000	OG,DF,SF	20

Pecluma dispersa (A. M. Evans) M. G. Price. VGJ 428 UC	1000	OG,DF	6
Pecluma divaricata (E. Fourn.) Mickel & Beitel. VGJ 252 CITRO	500	OG	7
Pecluma hartwegiana (Hook.) F. C. Assis & Salino. VGJ 359, 491 UC	2000,2500	OG,DF,SF	19
Pecluma liebmannii (C. Chr.) A. R. Sm. & Carv. -Hern., comb. nov. VGJ 550 UC.	2500	OG,DF,SF	16
Pecluma longepinnulata (E. Fourn.) F. C. Assis & Salino. VGJ 29, 561 UC	500,1500	OG,SF	11
Pecluma plumula (Humb. & Bonpl. ex Willd.) M. G. Price. VGJ 321 UC	1500	OG,SF	5
Pecluma 2500 sp1. VGJ 389 CITRO	2500	DF,SF	8
Pecluma sursumcurrens (Copel.) M. G. Price. VGJ 19 UC	1500	OG,DF,SF	12
Phlebodium areolatum (Humb. & Bonpl. ex Willd.) J. Sm. VGJ 98 CITRO	1000,1500,2000	OG,DF,SF	35
Phlebodium pseudoaureum (Cav.) Lellinger. VGJ 120 UC	1000,1500,2000	OG,DF,SF	31
Pleopeltis acicularis (Weath.) A. R. Sm. & T. Krömer, comb. nov. VGJ 318 UC.	1000	SF	4
Pleopeltis angusta Humb. & Bonpl. ex Willd. var. stenoloma (Fée) Farw. VGJ 121 UC	1500	OG,DF,SF	36
Pleopeltis complanata (Weath.) E. G. A. Hooper. VGJ 123 CITRO	1500	OG	1
Pleopeltis crassinervata (Fée) T. Moore. VGJ 107 UC	1000,1500,2000	OG,DF,SF	47
Pleopeltis mexicana (Fée) Mickel & Beitel. VGJ 618, 619 UC	2000,1500	OG,DF,SF	34
Pleopeltis plebeia (Schltdl. & Cham.) A. R. Sm. & Tejero. VGJ 81,99, 144 UC	1500,2500,3000,3500	OG,DF,SF	55
Pleopeltis polylepis (Roemer ex Kunze) T. Moore. VGJ 355 UC	3000,3500	OG,DF	25
Pleopeltis polylepis (Roemer ex Kunze) T. Moore var. interjecta (Weath.) E. A. Hooper. VGJ 386, 645 UC	2500	OG,DF	44
Pleopeltis polylepis (Roemer ex Kunze) T. Moore var. polylepis. VGJ 127 UC	1500	OG	8
Pleopeltis polypodioides (L.) E. G. Andrews & Windham. VGJ 701 CITRO	2000	OG	2
Polypodium cf. fraternum VGJ 480 CITRO	2500	DF,SF	3
Polypodium fraternum Schltdl. & Cham. VGJ 623 CITRO	2000	OG	6
Polypodium collinsii Maxon. VGJ 4 CITRO	1500	OG	3
Polypodium furfuraceum Schltdl. & Cham. VGJ 437 CITRO	500,1000	OG,DF,SF	30

Polypodium hartwegianum Hook. VGJ 842 CITRO	3000	SF	29
Polypodium lepidotrichum (Fée) Maxon. VGJ 52 UC	1500	DF	2
Polypodium plebeium Schltdl. & Cham. VGJ 25 CITRO	1000,1500,2000,2500	OG,DF,SF	75
Polypodium plesiosorum Kunze. VGJ 377, 387 UC	2000,2500	OG,SF	10
Polypodium polypodioides (L.) Watt. VGJ 115 CITRO	0,1500,2500	OG,DF	10
Polypodium puberulum Schltdl. & Cham. VGJ 139, 347, 373 UC	1500,2000,2500	OG,DF,SF	26
Polypodium 1500 sp1. VGJ 5 CITRO	1500	OG	1
Polypodium 1500 sp2. VGJ 109 CITRO	1500	SF	5
Polypodium thyssanolepis A. Braun ex Klotzsch. VGJ 51 CITRO	1500	OG	1
Polytaenium lineatum (Sw.) J. Sm. VGJ 71 CITRO	1500	DF	3
Serpocaulon falcaria (Kunze) A.R. Sm. VGJ 177 UC	1500,2000,2500	OG,DF	29
Serpocaulon triseriale (Sw.) A.R. Sm. VGJ 214 UC	500,1000	DF,SF	8
Stenogrammitis prionodes (Mickel & Beitel) Labiak. VGJ 763, 765 UC	2000	OG,SF	4
Terpsichore asplenifolia (L.) A. R. Sm. VGJ 32 CITRO	1500	DF	1
Pteridaceae			
Scoliosorus ensiformis (Hook.) T. Moore. VGJ 721 UC	2000,2500	OG,DF	6
Vittaria graminifolia Kaulf. VGJ 338 UC	1500,2000,2500	OG,DF,SF	27
Psilotaceae			
Psilotum complanatum Sw. VGJ 738 UC	1500,2000	OG,SF	3

Table A2. Results of statistical analyses for (nested ANOVA). Analysis of Variance (ANOVA), function *aov* results of comparisons between species richness (^{0}D), Shannon (^{1}D) and Simpson (^{2}D) along the elevation and forest-use intensity. Bold values are statistically significant at < 0.05.

	Species richness (^{0}D)		**Shannon (^{1}D)**		**Simpson (^{2}D)**	
	F-value	**P-value**	**F-value**	**P-value**	**F-value**	**P-value**
Elevation	$F_{7,96} = 73.23$	**< 0.001**	$F_{5,72} = 91.62$	**< 0.001**	$F_{5,72} = 89.96$	**< 0.001**
Elevation/FUI	$F_{16,96} = 2.52$	**< 0.001**	$F_{12,72} = 3.28$	**< 0.001**	$F_{12,72} = 3.58$	**< 0.001**

Table A3. Results of multiple comparisons of means using Tukey Contrasts**.** Multiple comparisons are between vascular epiphyte species richness (^{0}D), Shannon (^{1}D) and Simpson (^{2}D). diversities respectively in every forest-use intensity and each elevation. Abbreviations: Old-growth forest (OG), degraded forest (DF), and secondary forest (SF).

Elevation	Forest-use intensity	Species richness (^{0}D)				Shannon (^{1}D)				Simpson (^{2}D)			
		Estimate	Standard error	t-value	P-value	Estimate	Standard error	t-value	P-value	Estimate	Standard error	t-value	P-value
0 m	DF vs OG	-0.07	0.25	-0.28	0.96	-0.02	0.24	-0.11	0.99	0.02	0.23	0.09	1.00
	SF vs OG	-0.30	0.25	-1.23	0.46	-0.21	0.24	-0.88	0.66	-0.13	0.23	-0.55	0.85
	SF vs DF	-0.23	0.25	-0.95	0.62	-0.18	0.24	-0.78	0.72	-0.15	0.23	-0.64	0.80
500 m	DF vs OG	0.01	0.25	0.05	1.00	0.03	0.24	0.12	0.99	0.04	0.23	0.17	0.98
	SF vs OG	-0.63	0.25	-2.55	0.06	-0.63	0.24	-2.67	0.05	-0.63	0.23	-2.75	0.04
	SF vs DF	-0.64	0.25	-2.60	0.06	-0.66	0.24	-2.79	0.04	-0.67	0.23	-2.92	0.03
1000 m	DF vs OG	-0.07	0.10	-0.73	0.75	-0.04	0.09	-0.43	0.90	-0.01	0.08	-0.07	1.00
	SF vs OG	-0.27	0.10	-2.74	0.04	-0.27	0.09	-3.12	0.02	-0.26	0.08	-3.11	0.02
	SF vs DF	-0.20	0.10	-2.01	0.15	-0.23	0.09	-2.69	0.05	-0.25	0.08	-3.04	0.03
1500 m	DF vs OG	-0.35	0.09	-3.73	0.01	-0.38	0.10	-3.99	0.005	-0.41	0.10	-4.22	0.003
	SF vs OG	-0.45	0.09	-4.89	0.001	-0.50	0.10	-5.21	0.001	-0.53	0.10	-5.37	0.001
	SF vs DF	-0.11	0.09	-1.16	0.50	-0.12	0.10	-1.21	0.47	-0.11	0.10	-1.15	0.50
2000 m	DF vs OG	-0.08	0.23	-0.36	0.93	-0.14	0.22	-0.65	0.80	-0.20	0.22	-0.91	0.64
	SF vs OG	-0.26	0.23	-1.16	0.50	-0.34	0.22	-1.53	0.31	-0.40	0.22	-1.87	0.19
	SF vs DF	-0.18	0.23	-0.80	0.71	-0.20	0.22	-0.88	0.66	-0.21	0.22	-0.96	0.62
2500 m	DF vs OG	-0.05	0.22	-0.22	0.97	-0.06	0.22	-0.28	0.96	-0.09	0.22	-0.40	0.92
	SF vs OG	-0.56	0.22	-2.56	0.06	-0.58	0.22	-2.62	0.05	-0.60	0.22	-2.69	0.05
	SF vs DF	-0.51	0.22	-2.35	0.09	-0.52	0.22	-2.34	0.09	-0.51	0.22	-2.29	0.09
3000 m	DF vs OG	0.14	0.23	0.61	0.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	SF vs OG	0.14	0.23	0.61	0.82	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	SF vs DF	0.00	0.23	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
3500 m	DF vs OG	0.00	0.20	0.00	1.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	SF vs OG	-0.42	0.20	-2.12	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00
	SF vs DF	-0.42	0.20	-2.12	0.13	0.00	0.00	0.00	0.00	0.00	0.00	0.00	0.00

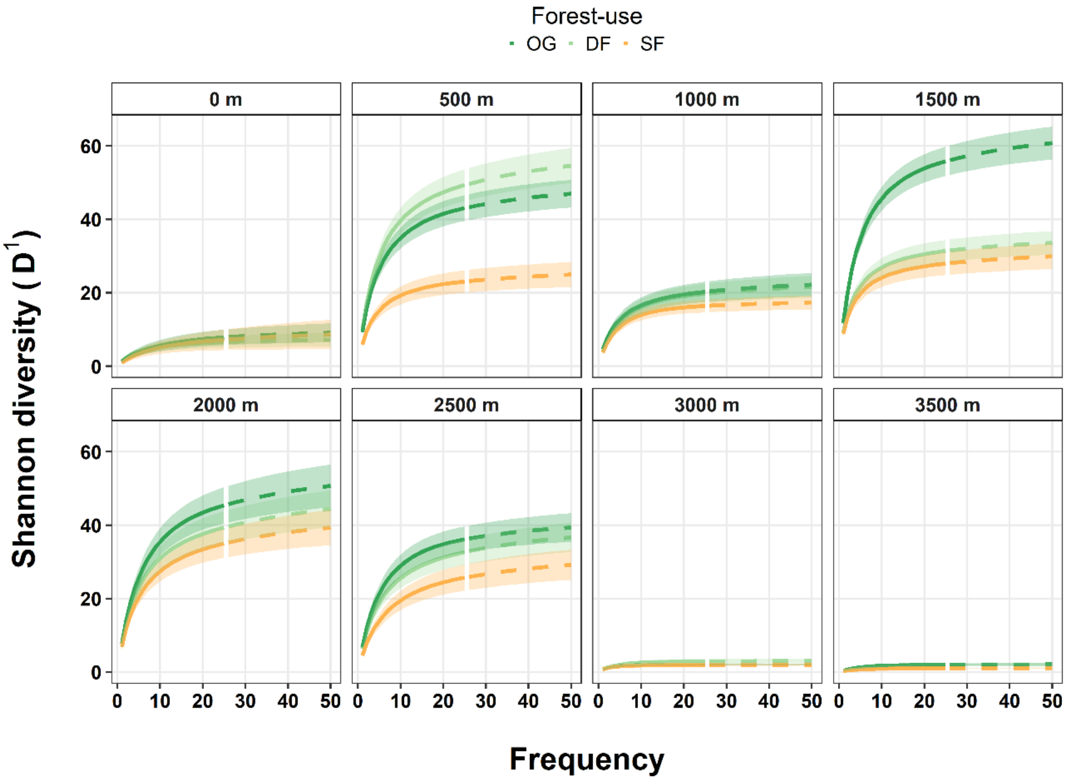

Figure A1. Species accumulation curves Shannon diversity. Species accumulation curves based on incidence data for species diversity, showing rarefaction (solid lines) and extrapolated (dashed lines) curves for Shannon diversity Hill numbers (^{1}D), n= 5 plots per forest-use intensity across the eight study sites. Confidence intervals 95 % (shaded areas). Abbreviations: Old-growth forest (OG, dark green), degraded forest (DF, light green) and secondary forest (SF, orange).

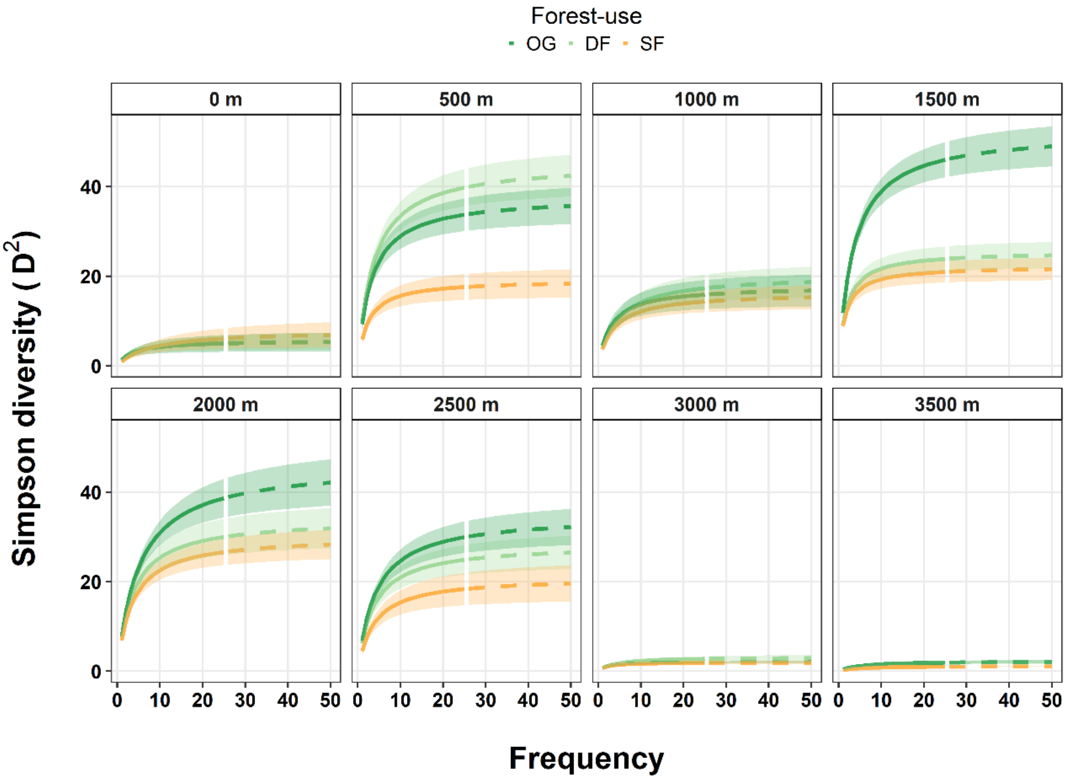

Figure A2. Species accumulation curves Simpson diversity. Species accumulation curves based on incidence data for species diversity, showing rarefaction (solid lines) and extrapolated (dashed lines) curves for Simpson diversity Hill numbers (2D), n= 5 plots per forest-use intensity across the eight study sites. Confidence intervals 95 % (shaded areas). Abbreviations: Old-growth forest (OG, dark green), degraded forest (DF, light green) and secondary forest (SF, orange).

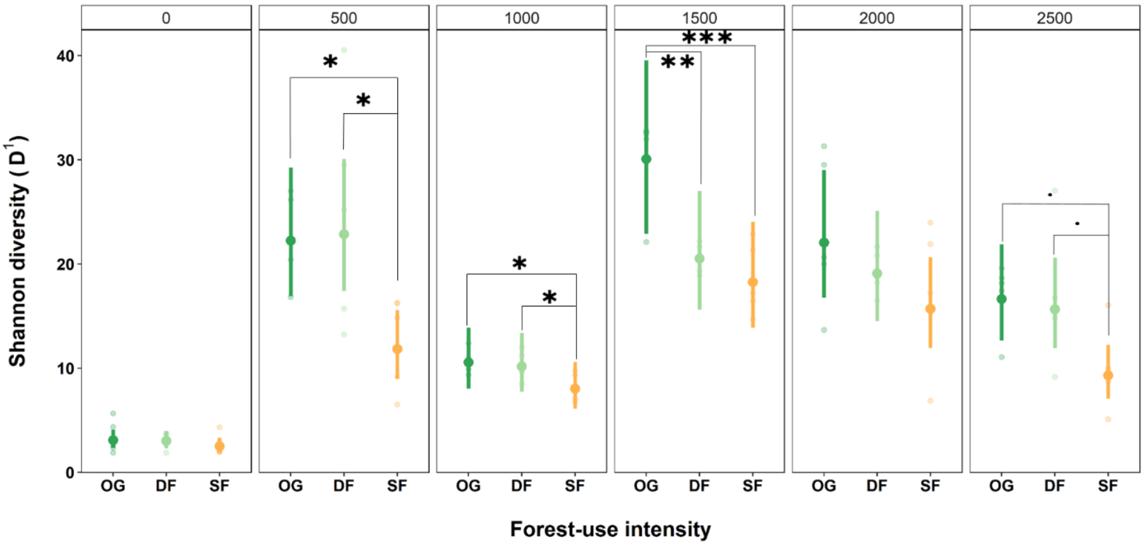

Figure A3. Results of statistical analyses for (nested ANOVA). Variation in Shannon diversity, (^{1}D) across different levels of forest use-intensity at each study site. Confidence intervals showed with color bars. Significant differences indicated with '.' 0.1, '*' 0.05, '**' 0.01. ANOVA/Tukey's Honest Significant Differences. Abbreviations: Old-growth forest (OG, dark green), degraded forest (DF, light green), and secondary forest (SF, orange).

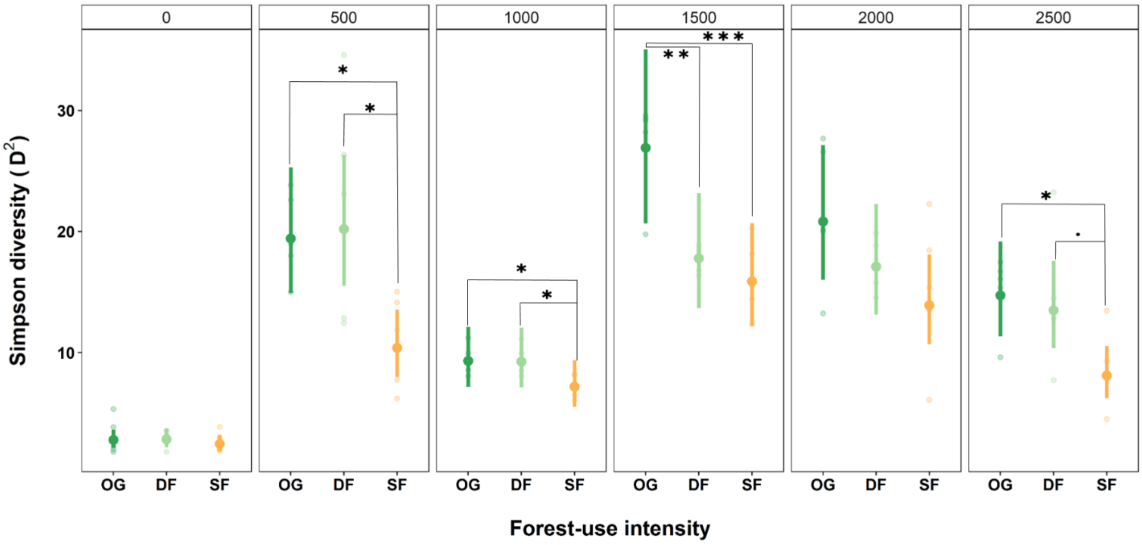

Figure A4. Variation in Simpson diversity (2D) across different levels of forest use-intensity at each study site. Confidence intervals showed with color bars. Significant differences indicated with '.' 0.1, '*' 0.05, '**' 0.01. ANOVA/Tukey's Honest Significant Differences. Abbreviations: Old-growth forest (OG, dark green), degraded forest (DF, light green), and secondary forest (SF, orange).

B Supplementary information to Chapter 2

Table B1. Variance partitioning of the random effects for each morphological trait model: Leaf area, leaf density, specific leaf area (SLA), and leaf dry matter content (LDMC). Numbers are the estimated variances of the random-effects terms in each linear mixed-effects model for morphological leaf traits. Calculations were performed using the 'VarCorr' function in the 'lme4' R package (Bates et al., 2015).

Random effects	*Leaf area*	*Leaf density*	*SLA*	*LDMC*
Individual : (species : family)	0.0308	0.107	0.178	0.0946
Species : family	0.420	0.233	0.550	0.296
Family	0.526	0.560	0.0976	0.526
Residual	0.0136	0.0996	0.174	0.0843

Table B2. Variance partitioning of the random effects for each chemical leaf trait model: Leaf nitrogen; leaf phosphorus, leaf nitrogen-to-phosphorus ratio (leaf N:P), leaf nitrogen isotope ratio (δ^{15}N, and leaf carbon isotope ratio (δ^{13}C). Numbers are the estimated variances of the random-effects terms in each linear mixed-effects model for chemical leaf traits. Calculations were done using the 'VarCorr' function in the 'lme4' R package (Bates et al., 2015).

Random effects	*Leaf nitrogen*	*Leaf phosphorus*	*N:P*	*$\delta^{15}N$*	*$\delta^{13}C$*
Species : family	0.291	0.185	0.0751	0.305	0.589
Family	0.253	0.507	0.214	0.185	0.0734
Residual	0.457	0.308	0.711	0.510	0.338

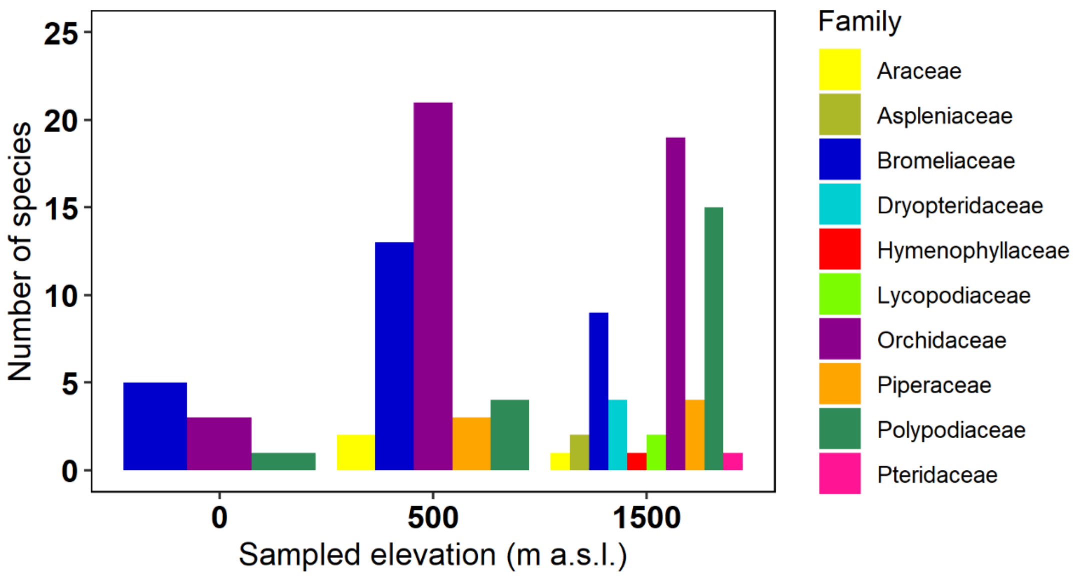

Figure B1. Number of species per family at each sampled elevation.

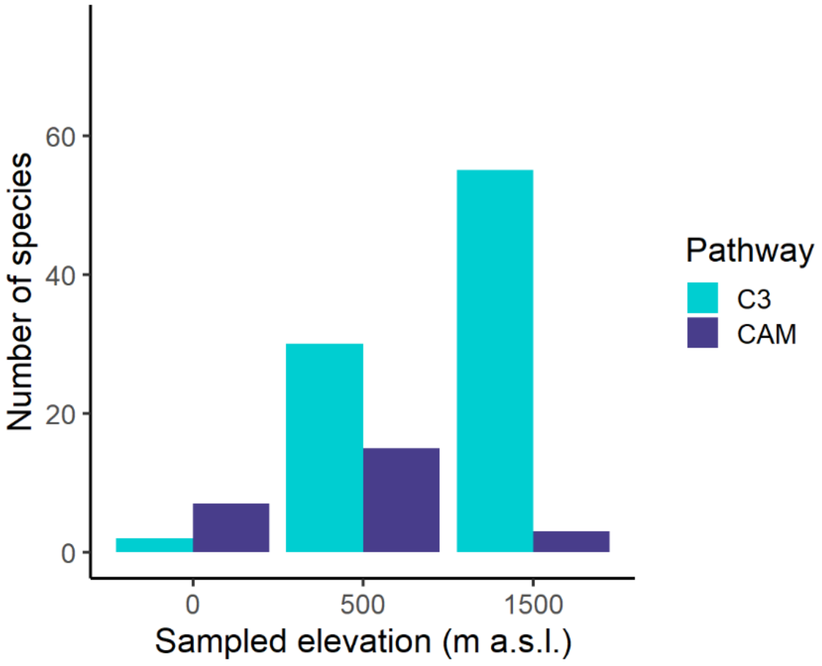

Figure B2. Number of species with CAM and C3 photosynthetic pathway at each sampled elevation.