

UNIVERSIDADE FEDERAL DE ALFENAS

JOÃO PEDRO COSTA ELIAS

**FROM THE TREE TO THE CONTINENT: DIVERSITY AND DISTRIBUTION OF
VASCULAR EPIPHYTES**

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JOÃO PEDRO COSTA ELIAS

**FROM THE TREE TO THE CONTINENT: DIVERSITY AND DISTRIBUTION OF
VASCULAR EPIPHYTES**

Tese apresentada como parte dos requisitos para obtenção do título de Doutor em Ciências Ambientais pela Universidade Federal de Alfenas. Área de concentração: Ciências Ambientais.

Orientador: Prof. Dr. Flavio Nunes Ramos
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RESUMO

A interação entre espécies e seu ambiente é moldada, entre outros fatores, pela heterogeneidade do *habitat* e condições climáticas. Enquanto fatores naturais influenciam em como as espécies interagem com seu entorno, perturbações antrópicas podem alterar esta interação. No Antropoceno, regiões como a Região Neotropical, considerada uma das mais diversas, enfrentam inúmeras ameaças oriundas das atividades humanas. Portanto, compreender como a degradação do *habitat* em consequência às atividades antrópicas, combinada com o clima, molda a distribuição de espécies é um dos desafios atuais para a conservação das espécies e preservação do *habitat*. Enquanto os efeitos do clima e pressões antropogênicas são relativamente bem estabelecidos para grupos específicos, obter conclusões abrangentes para grupos diversos, porém negligenciados, como as epífitas vasculares, continua sendo desafiador. Desta forma, nesta tese visamos explorar como a distribuição das epífitas vasculares é influenciada pelos a) efeitos da degradação de *habitat* em b) em épocas diferentes. Ainda, c) como o clima influencia em escalas maiores nesta distribuição. Ao explorar em conjunto aspectos ambientais e antropogênicos em diferentes escalas espaciais e temporais, fornecemos informações cruciais para a conservação não só das epífitas, enquanto espécies guarda-chuva, mas também de uma ampla gama de espécies associadas. Em nosso estudo, as mudanças no uso do solo afetaram negativamente as assembleias de epífitas em todas as escalas espaciais e temporais. Em menor escala, a riqueza e composição de espécies entre áreas florestais e degradadas permaneceu relativamente semelhante. Climaticamente, as epífitas mostraram maior diversidade em áreas mais estáveis, com maior disponibilidade de água e temperaturas amenas. Assim, as assembleias de epífitas em paisagens conservadas, com cobertura do solo estável, baixa sazonalidade climática, alta disponibilidade de água e temperaturas amenas, representam comunidades potencialmente diversas que merecem esforços direcionados à preservação. No entanto, áreas com condições distintas destas também possuem potencial, embora limitado, para desempenhar a função de reservatórios de espécies.

Palavras-chave: biodiversidade; estratégias de conservação; impacto humano; interações ecológicas

ABSTRACT

The interaction between species and their environment is shaped by habitat heterogeneity and climatic conditions. While natural factors play a significant role in the dynamics of interactions between species and the surrounding environment, anthropogenic disturbances have the potential to fundamentally alter them. In the context of the Anthropocene, ecologically diverse regions, such as the Neotropics, are considered hotspots of biodiversity but also face substantial threats from human activities. Therefore, understanding how anthropogenic habitat degradation, combined with climatic factors, shapes species distribution is a pressing challenge for the species conservation and preservation of the habitat. While the effects of climate and anthropogenic pressures are relatively well-established for specific groups, drawing comprehensive conclusions remains challenging for diverse yet overlooked groups, such as vascular epiphytes. Thus, this thesis aimed to explore how the distribution of vascular epiphytes is influenced by (a) the effects of degradation in (b) different time periods. Additionally, how the (c) climate influences this distribution at a larger scale. By integrating environmental and anthropogenic aspects, we provide crucial information for the conservation of umbrella species groups, benefiting an even broader range of associated species. In this study, changes in land-cover negatively impacted epiphyte assemblage diversity across all spatial and temporal scales. At the smaller scale, the species richness and composition between forest and degraded areas remained relatively similar. Climatically, epiphytes exhibited higher diversity in more stable areas with increased water availability and mild temperatures. Thus, epiphyte assemblages in preserved landscapes, featuring stable land-cover through the years, low climatic seasonality, ample water availability, and mild temperatures, represent potentially diverse communities deserving targeted preservation efforts. However, areas with conditions distinct from these also have the potential, although limited, to serve as diversity reservoirs.

Key-words: biodiversity; conservation strategies; ecological interactions; human impact

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1 INTRODUCTION

Due to the intricate interactions among variables influencing the spatial distribution of plant species in the tropical regions, a clear and definite general pattern of plant distribution in high-diverse areas remains elusive (Barthlott; Lauer; Placke, 1996; Ferrier *et al.*, 2004). The interaction between species and the environment is closely related to several factors, such as habitat heterogeneity, geological and climatic history, and current climatic conditions (Shmida; Wilson, 1985; Ricklefs, 1987; Field; Wiens; Donoghue, 2004; Jetz; Rahbek; Colwell, 2004; O'brien; Whittaker, 2005; Clarke; Gaston, 2006).

Beyond natural influences, the Anthropocene era introduces pivotal factors that synergically impact plant distribution (Randin *et al.*, 2020). Anthropogenic disturbances, such as croplands and build-up areas expansion, involve many deleterious processes that contribute to habitat degradation (habitat fragmentation, forest gaps, and an increased occurrence of wildfires) (Pivello *et al.*, 2018). The direct effect of human activities not only threatens the equilibrium and functionality of species communities, but also how the species interact with the environment (Adhikari *et al.*, 2020; Pivello *et al.*, 2018; Zanatta *et al.*, 2022). Understanding spatial patterns of biodiversity is a central goal in ecology and biogeography and is crucial for addressing ongoing biodiversity loss due to global change (Newbold *et al.*, 2015; Peters *et al.*, 2019). However, tackling the vast complexity of factors influencing plant species distribution currently necessitates a multidisciplinary approach, encompassing both environmental factors (e.g., climate) and anthropogenic influences (e.g., land cover changes). Additionally, these patterns are often examined based on limited plant collections (occurrence data), although there is growing availability of local documentation of species richness (“alpha diversity”) in recent

times, such as The Global Inventory of Floras and Traits “GIFT” (Weigelt; König; Kreft, 2020).

Even though the general patterns of plant distribution still need assessments, the biodiversity distributional patterns of soil-rooted vegetation in the tropics (e.g., trees and shrubs) are increasingly better understood (Condit, 1995). A combination of habitat heterogeneity and certain historical processes are suggested to explain biodiversity distributional patterns across spatial and geographical scales. Environmental heterogeneity, encompassing both biotic (e.g., functional diversity) and abiotic factors (e.g., climate and topography), frequently demonstrates a positive correlation with local diversity. Nevertheless, the nature of this relationship is significantly contingent on the spatial extent, with specific scales at which fine-grained heterogeneity (i.e., small-scale approach) exhibits a transition from a negative to a neutral association (e.g., Stein; Kreft, 2015). Habitat degradation, in turn, has an even more conspicuous pattern. The spatial and temporal effect of habitat degradation on species is hard to measure since the magnitude of degradation, as well as its effects on species diversity is scale-dependent (Arantes *et al.*, 2018; Mendenhall *et al.*, 2014).

The Neotropics encompass seven out of the world's 17 most diverse countries, yet a substantial portion of its biodiversity, along with the ecosystem services it provides, faces imminent threats of extinction (IPBES, 2018a; b). Habitat degradation, which comprises any process resulting in loss of habitat quality, is one of the biggest threats to species diversity in the Neotropics (IPBES, 2018a). The structural changes in vegetation as a consequence of habitat degradation can drastically alter microclimate and microhabitats, resulting in loss of local species diversity and changes in species composition (Newbold *et al.*, 2015; Senior *et al.*,

2017; Tripathi *et al.*, 2021). Although regional conservation initiatives are active in the Neotropics, their effectiveness and success depend on comprehensive data regarding biodiversity distribution patterns, which are in constant increase (Ferrier *et al.*, 2002).

One of the most conspicuous and least studied components of biodiversity in the tropics is vascular epiphytes. These are structurally dependent vascular plants that root non-parasitically on other plants (mainly trees). Vascular epiphytes can be locally highly diverse. For example, up to 200 epiphyte species can be found in a single tree, whereas this number of tree species may be found in 25 to 50 ha of tropical forest. They are wildly diverse in the Neotropics, where they contribute more to overall vascular plant diversity than in other tropical regions (Gentry; Dodson, 1987; Taylor *et al.*, 2022; Zotz *et al.*, 2021). Globally, they are mainly distributed in the tropics but also in the subtropics and contribute significantly to vascular plant richness, around 9% globally and up to 50% locally (Kelly *et al.*, 2004; Kelly *et al.*, 1994; Zotz *et al.*, 2021). Epiphytes provide many resources to biota, such as habitat for arthropod fauna, nesting site to birds, considered as ‘umbrella’ and “engineer” species, for example, the bird's nest fern *Asplenium* species, and are essential to the ecosystem functioning, e.g., hydrology and nutrient fluxes (Zotz; Hietz, 2001; Stuntz; Simon; Zotz, 2002; Zotz; Reuter, 2009; Gotsch; Nadkarni; Amici, 2016; Phillips *et al.*, 2020; Seidl *et al.* 2020).

The main source of water and nutrients for epiphytes is atmospheric deposition, which highlights their sensibility to atmospheric changes (Gentry; Dodson, 1987; Zotz, 2016). Although many epiphyte species are adapted to non-favorable conditions (e.g., aridity), water restriction correlates negatively with epiphyte species richness, since few species can withstand long periods without

water (Menini Neto *et al.*, 2016; Werner *et al.*, 2011). Temperature limits the latitudinal and elevational distribution of vascular epiphytes (Sylvester; Sylvester; Kessler, 2014; Zotz, 2016). Once occurring in an area under disturbance, several epiphyte species respond quickly to changes in environmental conditions due to habitat degradation, with high rates of species extinction and rarely recovering previous species compositions, even after forest regeneration (Hietzseifert; Hietz; Guevara, 1996; Werner *et al.*, 2011; Cardós *et al.*, 2018). Nonetheless, biodiversity patterns of this hyper-diverse group are scarcely known. Most efforts to understand epiphyte diversity patterns consist of local inventories and predictions (Krömer *et al.*, 2005; Küper *et al.*, 2004). At regional scales, studies exhibit a bias towards specific taxonomic groups (e.g., Orchids and Bromeliads) (Zotz, 2016). However, even at large scales, such as at the subcontinental level (e.g., Neotropics), a comprehensive approach is absent.

Currently, at the local scale, which is the most frequently examined scale, numerous studies have highlighted the importance of distinct tree traits in influencing epiphyte diversity (e.g., Einzmann *et al.*, 2014; Elias *et al.*, 2021; Wagner; Mendieta-Leiva; Zotz, 2015). Trees provide essential microhabitats at a small scale, with distinct microclimatic conditions within different zones of the tree (Murakami *et al.*, 2022). These microclimatic variations, combined with specific tree characteristics, are crucial in shaping and influencing epiphyte species distribution at local scales (Wagner; Mendieta-Leiva; Zotz, 2015; Elias *et al.*, 2021). Nonetheless, limited studies have delved into the configuration of this relationship across different habitat types (e.g., preserved vs. degraded habitats). The prevailing understanding is that host structure and traits influence the distribution of epiphyte diversity even in habitats subjected to human pressures (Zotz, 2007).

Regarding tree host traits, the tree host size have a well defined and positive relationship with epiphyte richness, where bigger trees should harbor larger species richness, mainly by the higher vertical and structural heterogeneity of the host (Cruz *et al.*, 2022; Li *et al.*, 2015). Nonetheless, while our understanding of this relationship across various disturbance levels is limited, it's evident that disturbance alters the dynamics of the association between tree size and epiphyte species richness (Flores-Palacios, Garcia-Franco 2016; Izuddin; Webb, 2015). Flores-Palacios and Garcia-Franco (2006) found a positive and linear relationship between species richness and tree size only in sites with relatively lower disturbance, whereas higher disturbance resulted in a neutral relationship or positive asymptotic one. Similarly, Izuddin and Webb (2015) reported greater epiphyte species richness in larger trees, although the disturbance in the vicinity of the tree host also plays a decisive role. This can lead to reduced species richness when the tree host is situated within anthropogenic landscapes, such as pasturelands.

Relatively few studies have attempted to assess large-scale patterns of vascular epiphytes, mostly including climatic and topography predictors (e.g., Gentry; Dodson, 1987; Küper *et al.*, 2004; Taylor *et al.*, 2022). In these studies, vascular epiphyte species richness at the subcontinental level, i.e. Neotropics has been positively linked to precipitation for the first time by Gentry and Dodson (1978), based on the occurrence of epiphytism in the most diverse families in three forests in Western Ecuador. Thereafter, Kreft *et al.* (2004) supported this hypothesis based on total species richness from 17 sites across Central and South America. Kreft *et al.* (2004) additionally highlighted the importance of seasonality and fog for epiphyte richness. Despite being confined to the Neotropics, these studies offer an incomplete panorama of this extensive biogeographical area. This limitation arises from the

heterogeneity in data collection methods and the predominant taxonomic biases of these investigations. Nonetheless, based on these studies, the effect of variables related to precipitation and cloud cover, as water availability predictors, seems to be key for epiphyte distribution at this large scale, unlike for the soil-rooted vegetation (e.g., Gentry; Dodson, 1987; Küper *et al.*, 2004; Weigand *et al.*, 2020). This can probably be explained by the high dependence of epiphytes on atmospheric water, as they have no access to water sources in the soil, they have diverse adaptations to improve water storage (e.g., pseudobulb) and resistance in periods with low water availability, from poikilohydric to homoiohydric (Kessler *et al.*, 2007).

Aside from the large-scale gradients related to climate, epiphyte distribution at large scales may be related to other factors such as habitat type (e.g., forest, anthropogenic matrices), topographic complexity, and anthropic pressures. For instance, Gentry and Dodson (1987), Küper *et al.* (2004) and Kreft *et al.* (2004) found the highest epiphyte richness at middle elevations, and Küper *et al.* (2004) found the same pattern for endemic species. Regarding the synergistic impact of elevation and habitat degradation, the intensity of disturbance holds significant implications for species composition changes. Nevertheless, these effects vary along an elevation gradient (Guzmán-Jacob *et al.*, 2020). Any level of human disturbance exerts detrimental effects on epiphyte communities, resulting in reduced species richness and alterations in species composition. The consequences are more pronounced in high-diversity habitats, particularly those at middle elevations (Guzmán-Jacob *et al.*, 2022).

Although evaluating the effect of degradation in epiphytes at the local scale is the most common approach, the effect of degradation at larger scales (i.e. landscape) remains elusive. For other taxonomic groups, such as trout and birds, the

impact of landscape degradation frequently triggers significant species extinctions within a particular area, subsequently leading to recolonization from surrounding unaffected regions (Sedell; Gresswell; McMahon, 2015; Nasruddin-Roshidi *et al.*, 2021). However, as epiphytes are a group with many particularities in their relationship with the habitat, these overall conclusions possibly do not apply. For instance, epiphytes are highly dependent on vertical structure heterogeneity, i.e. trees' host stem density and structure (Qureshi; Rawat; Kushalappa, 2009; Ceballos, 2020). Therefore, as habitat degradation at regional scales (e.g., land use change) commonly reduces the complexity of the arboreal strata, epiphyte species may respond quickly with high rates of population decrease and local extinctions of species (Hietzseifert; Hietz; Guevara, 1996; Werner *et al.*, 2011). Additionally, the structural change of landscape also compromises the connectivity between epiphyte species communities, making it unlikely for the communities to recover the previous local diversity and species composition (Cardós *et al.*, 2018).

Although the issue of factors influencing epiphyte distribution at the subcontinental level remains unresolved, the recent assembly of a Neotropical epiphyte database (referred to as the Epiphyte Inventory Group or "EpiG") provides an opportunity to address such inquiries. EpiG is a consortium currently formed by more than 40 collaborators who contribute with datasets of vascular epiphyte inventories as well as pertinent knowledge (e.g., vegetation informatics, biogeography, tree host info, and macroecology). The database comprises data from vascular epiphytes (holo, hemi epiphytes, and nomadic vines/climbers) distributed across nine countries, eight biomes, and 45 WWF Terrestrial Ecoregions out of the 234 recorded for the Neotropics (Olson *et al.*, 2001). This thesis is the first research

to use the EpiG database to explore both environmental (e.g., climate) and human (e.g., land cover changes) influencing Neotropical epiphyte distribution.

We structured this thesis into three chapters, progressively expanding from the tree to the continental scale. The chapters explore the impacts of tree features, human pressures, and climate on Neotropical epiphytes. The first chapter investigated the effects of tree features (i.e. zonation) and habitat degradation (i.e. forest conversion into pasture) in epiphyte communities using a local database collected by me and incorporated in the EpiG database, as well. Expanding the scale from local to subcontinent level, the second chapter explored the habitat degradation effects across spatial (i.e. from site to landscape scales) and temporal scales using part of the EpiG database. Lastly, also at the subcontinental level and with the aid of the EpiG database, the third chapter explores the effect of climate predictors on vascular epiphyte (i.e. water availability and temperature predictors) using all the Neotropical data. All conclusions based on our findings aimed to provide a complex picture of factors influencing the epiphytes, additionally to research questions that could be further answered.

2 ARTICLE 1 - TREE STRUCTURE INSTEAD OF MICROCLIMATIC ONES DETERMINES DIFFERENCES IN VASCULAR EPIPHYTE ASSEMBLAGES BETWEEN FOREST AND PASTURE

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2.1 Abstract

Land cover change threatens biodiversity by reducing epiphyte species richness, altering species composition, and favouring generalist species. Pasture creation can promote the loss of original species, although this loss can be mitigated by maintaining scattered trees to reduce their structural differences with forests and thus retaining a portion of regional epiphyte diversity. We explore the negative effects of land cover change and potential factors promoting similarity of epiphyte assemblages between forests and pastures. We hypothesize that pasture epiphyte assemblages are characterized by low species richness and are dominated by xerotolerant and generalist species, with a species composition nested from the forest community, indicating a degree of overlap. We hypothesize that two main factors drive the similarity between forest and pasture epiphyte assemblages: "structural dependence", whereby trees host similar species on their crowns and trunks independent of habitat, and "microclimatic dependence", where pasture and forest trees are more similar in areas with comparable microclimatic conditions. We found

lower species richness and higher abundance of generalist species in the pasture than in the forest, with differing species composition. However, there was still a significant overlap in species composition between the two habitats, indicating that the epiphyte assemblages in the pasture were nested from the forest assemblages. Pasture and forest trees shared more epiphyte species between crown and trunk zones rather than between shaded and sunlight-exposed zones. Hence, the similarity of vascular epiphyte assemblages between habitats is partially driven by structural factors, where certain epiphyte species preferentially occur in specific tree zones regardless of the microclimate or habitat. Considering these findings, we recommend maintaining scattered trees in pastures to enhance structural complexity (e.g., longer trunks and multiple crown branching), which can foster a proportion of the vascular species from forested areas, thus maintaining the similarity in vascular epiphyte assemblages between habitats.

Keyword: epiphyte conservation, grassland, holoepiphyte, isolated trees, Johansson zones, land-use, phorophyte.

2.2 Introduction:

Human activities leading to habitat degradation are the biggest threats to species diversity in the modern world (IPBES, 2018a). Anthropogenic disturbances, such as land cover change of forests to croplands or pastures, involve many prejudicial processes resulting in habitat degradation (e.g. habitat fragmentation, forest gaps, and an increase in wildfires; Pivello *et al.*, 2018). Habitat degradation threatens the equilibrium and functionality of species assemblages by favouring the invasion of exotic species (Adhikari *et al.*, 2020) and leading to the explosive population growth and posterior hyperdominance of certain native species (Pivello *et al.*, 2018; Zanatta *et al.*, 2022). Therefore, habitat degradation is related to changes in population sizes

and species composition. These compositional changes can be attributed to species turnover, where new species from unaffected surrounding areas colonize degraded areas (Burkle *et al.*, 2015). Additionally, changes may be due to nestedness, whereby environmental filters determine which species from the original species pool may persist and avoid local extinction (Fernandez-Juricic, 2002). However, substitution of species (i.e., turnover) and nestedness can synergistically explain species composition changes (Baselga, 2010).

Pastures have emerged as one of the predominant anthropic land use worldwide, especially in the Americas, occupying the largest proportion of land cover (IPBES, 2018b). Although pastures are structurally more different from the forest than croplands due to the relatively low cover of arboreal strata, cropland management is more intensive and prejudicial for forest regrowth and native species (Schweizer *et al.*, 2022). Therefore, the maintenance and inclusion of arboreal elements (e.g. scattered trees) within pasture matrices could provide some degree of habitat heterogeneity, acting as a refuge and fostering species diversity, making pastures a less stressful landscape (Manning *et al.*, 2009). Scattered trees in pastures may increase the connectivity of some species between forest patches as “stepping stones” (Tiang *et al.*, 2021), which could help to maintain the structures of meta-communities and the regional species pool over time (Siqueira *et al.*, 2017). In addition to their significance in landscape-level conservation, scattered trees are crucial in providing resources to several species, including vascular epiphyte plants (Hietz-Seifert *et al.*, 1996).

Vascular epiphytes are an especially highly diverse plant group globally (ca. 10% of plant species; Zotz *et al.*, 2021), structurally dependent plants that root non-parasitically on other plants (mostly trees). The primary source of water and

nutrients for epiphytes is atmospheric deposition, which highlights their sensibility to atmospheric changes (Gentry and Dodson, 1987; Zotz, 2016). They provide many resources to biota (e.g. habitat for arthropod fauna: Stuntz *et al.*, 2002; nesting site to birds: Seidl *et al.*, 2020), may be considered as ‘umbrella’ organisms (e.g. bird's nest fern *Asplenium* spp.: Phillips *et al.*, 2020), and are essential to ecosystem functioning (e.g. hydrology and nutrient fluxes: Zotz and Hietz, 2001; Gotsch *et al.*, 2016). Several epiphyte species respond quickly to changes in environmental conditions due to habitat degradation, with high rates of local extinction (Hietz-Seifert *et al.*, 1996; Werner *et al.*, 2011) and in the case of forests, they rarely recover previous species compositions, even after forest regeneration (Cardos *et al.*, 2018). In general, the conversion of natural areas to human-degraded habitats reduces species richness and abundance of vascular epiphytes (Werner and Gradstein, 2009), with a negative association between epiphyte diversity and degradation intensity (Wolf, 2005). High disturbance intensity has significant implications for species composition, leading to the loss and subsequent replacement of various epiphyte species (Guzmán-Jacob *et al.*, 2020). The replacement process is driven mainly by the colonization and dominance of xerotolerant species, primarily (Larrea and Werner, 2010; Acuña-Tarazona *et al.*, 2015). However, specifically for the conversion of forest into pasture, it is possible to maintain some local diversity, as the scattered trees within the pasture could buffer harsh environmental conditions and host forest specialist species in addition to xerotolerants (Elias *et al.*, 2021). Hence, the presence of scattered trees within pastures can originate relatively comparable and nested epiphyte assemblages, mirroring that found in adjacent forest remnants (Amici *et al.*, 2019). This underscores the significance of these scattered trees as

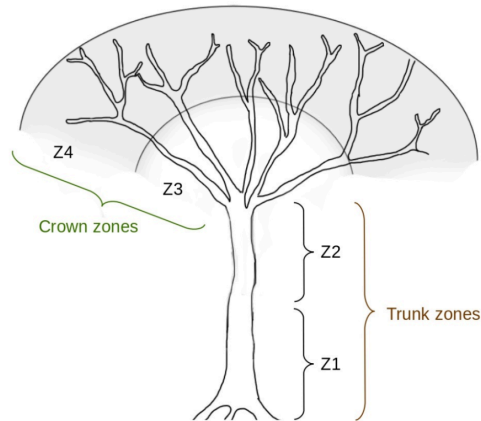
potential mitigation tool in degraded areas, serving as refugia to support epiphyte populations.

Trees provide essential microhabitats at a smaller scale, with distinct microclimatic conditions within different zones of the tree (Murakami *et al.*, 2022). These microclimatic variations, combined with specific tree characteristics (Elias *et al.*, 2021), are crucial in shaping and influencing epiphyte species distribution (Wagner *et al.*, 2015). The tree host size predicts the area available to epiphytes and is positively related to epiphyte species richness and abundance (trunk diameter: Sáyago *et al.*, 2013; total tree height: Flores-Palacios and Garcia-Franco, 2006). Similarly, other characteristics predict microclimate variability (e.g. crown leaf density), resulting in different species composition (Duarte and Gandolfi, 2017; Elias *et al.*, 2021). The differentiation of tree habitats into various zones based on their structural features, including the trunk and crown (Francisco *et al.*, 2019), along with the variation of light intensity and humidity along the vertical gradient of the forest (Krömer *et al.*, 2007), play a crucial role in facilitating a rich diversity of epiphytic species. This stratification enables the provision of a wide range of microhabitats, ultimately fostering favorable conditions for the occurrence and coexistence of many epiphytes within a host tree. However, any processes modifying the environmental conditions surrounding the tree host could change the stratification of the tree. For example, the vertical stratification of trees' microclimate in forest canopies shows that zones closer to the ground tend to be wetter, colder, and less exposed to sunlight and wind (e.g. Li *et al.*, 2015; Cruz *et al.*, 2022). However, reducing the canopy cover (e.g. forest conversion into open matrices, such as pasture) could increase the exposure of these zones to sun irradiation, which could become drier and hotter. As a result, epiphyte species initially found in specific zones of trees may undergo shifts in

their vertical distribution over time due to their preference for particular microclimate conditions. These species might change their occurrence to other zones within the tree that offer similar microclimatic conditions, such as the inner tree crown (Li *et al.*, 2015), or face local extinction (Hylander *et al.*, 2017).

To understand the differences in diversity between vascular epiphyte assemblages from forests and pastures, we hypothesized that (i) pastures would have lower species richness but higher abundance than the forest and the species composition will be nested from the forest composition. We aim to unravel the factors determining the similarity in species composition between habitats. Thus we examined whether the similarity in species composition is (ii) "structurally dependent," wherein both forest and pasture trees harbor comparable species in their crowns and trunks, regardless of microclimate conditions (Fig. 1.a); or "microclimatically dependent," with species composition displaying a high degree of similarity between pasture and forest trees in zones that share similar microclimate conditions, such as shaded or sunlight-exposed areas (Fig. 1.b). However, irrespective of whether the similarity in species composition between pasture and forest trees relies on structural or microclimatic factors, we hypothesized that (iii) the species composition will be consistently more similarity within specific tree zones of a given habitat when compared to the similarity observed among different habitats.

a) Structurally dependent



b) Microclimatically dependent

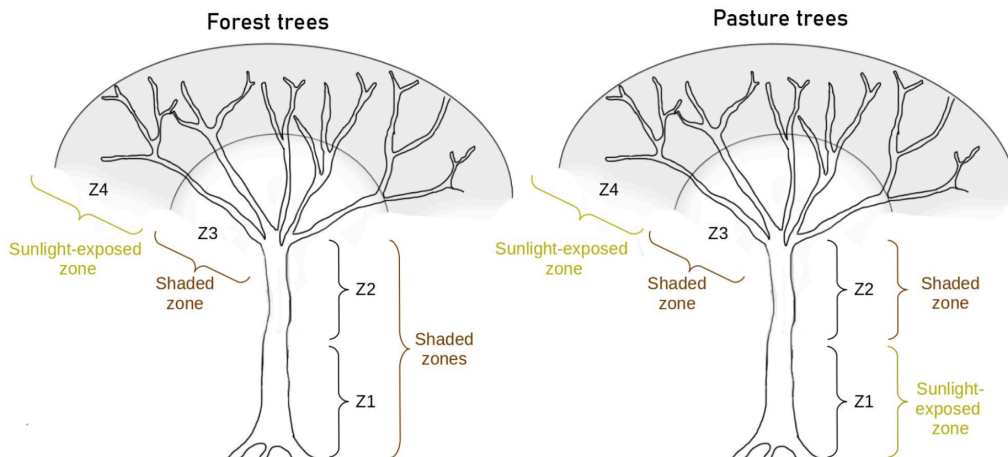


Figure 1: Tree zonation (Z1, Z2, Z3, and Z4) and associated zone groups (a. structural: crown and trunk | b. microclimatic: sunlight-exposed and shaded). Structural zonation follows the same pattern for forest and pasture, while microclimatic zonation is habitat-specific.

2.3 Methods

2.3.1 Study area

We carried out the study in 15 sites located in the municipality of Alfenas, southern Minas Gerais state, Brazil (45°56'49.28"W, 21°25'33.69"S). The region is classified as Seasonal Semideciduous Atlantic Forest and is highly fragmented, where only 9% of the original forest cover remains. The land-use coverage is mainly

pastures (51%), coffee plantations (17%), and annual crops (largely sugarcane and corn, 7%; Olivetti *et al.*, 2015). The region has two marked seasons (warm and wet & cold and dry), with a mean annual rainfall of 1500 mm and annual mean temperature ranging from 17 to 24°C.

We first selected areas that had forest fragments surrounded by pastures containing scattered trees. Second, the landscape around the forest fragment (i.e., a buffer of a 1 km radius around the forest fragment centre) should have between 10 to 50% forest cover to control forest coverage influence. After filtering, we selected 15 areas with forest fragment sizes ranging from 8.3 to 447 ha., elevations ranging from 790 to 1003 m a.s.l., and separated by a minimum distance of 5km (Table 1). All sampled forest fragments have low integrity in relation to the original land cover (i.e. ‘low integrity’ from Forest Landscape Integrity Index; Grantham *et al.*, 2020; Table 1), which means all forest fragments are under high pressure from human activities (i.e. infrastructure, agriculture, and tree cover loss), therefore, heavily and often modified (Fig. S1). The observed mosaic of forest fragments and pasture in the selected areas dated before 1985, the oldest satellite imagery available for the region.

Table 1: Information from the 15 sampled areas. “Paratio”, is a proxy of forest fragment shape complexity, defined as the forest fragment area divided by the perimeter, with higher values representing a more regular shape. “Forest Landscape Integrity Index” (FLII) values of the forest fragments sampled are classified as ‘low integrity’ (i.e. index value between 0 - 6, on a scale of 0 to 10; Grantham *et al.*, 2020).

Area	Code	Longitude	Latitude	Elevation	Pasture trees	Fragment area (ha)	Paratio (ha/m)	FLII
1	H47	-45.5159	-21.6813	874.5	33	40.1	0.011	0.0
2	P21	-45.7622	-21.4365	810.0	11	26.4	0.013	0.0
3	P9	-45.7696	-21.198	897.7	24	58.4	0.014	1.7

			9						
4	MT	-45.8624	-21.500 0	884.5	176	53.1	0.014	0.0	
5	P7	-45.9167	-21.466 7	833.5	67	58.9	0.017	0.0	
6	PZV	-45.9321	-21.146 2	800.5	215	42.6	0.019	5.0	
7	P4	-46.0833	-21.216 7	983	58	263.8	0.012	2.3	
8	P2	-46.1086	-21.046 6	790.0	14	447.2	0.007	0.0	
9	P23	-46.1167	-21.300 0	1003.0	35	8.4	0.02	0.0	
10	PD	-46.1367	-21.441 2	861.0	21	124.9	0.015	3.0	
11	P19	-46.1588	-21.400 1	881.5	56	58.8	0.012	<0.1	
12	P27	-46.1695	-21.335 3	924.5	21	25.7	0.019	0.0	
13	P13	-46.2233	-21.422 0	962.3	49	200.1	0.011	3.3	
14	T3	-46.3301	-21.216 2	876.7	46	13.2	0.031	0.0	
15	T4	-46.3724	-21.285 8	832.8	14	9.9	0.025	0.0	

2.3.2 Data survey

Since the density, distribution and characteristics of trees in forest and pasture were considerably different, we used a specific method of tree sampling according to the habitat. Recognizing the sporadic spatial distribution of trees in pastures, we established 'plots' and standardized our pasture sampling efforts based on area. In contrast, due to the prevalent spatial clustering of forest trees, we standardized our sampling efforts based on the number of trees sampled, and we established 'transects'. In each forest fragment, we randomly allocated four transects of 100 m, separated by at least 50 m among them and at least 50 m from the nearest forest edge. We sampled the closest tree with DBH \geq 10 cm every 10 meters of the

transect, making up 40 sampled trees per forest fragment and totalling 600 surveyed trees in the forest habitat. In the pastures, we delimited a plot of 2 ha (100 x 200m) in each site, placed 3 m from the forest fragment edge, and arranged for it to contain the highest density of scattered trees possible (Fig. S2). We sampled all trees with DBH \geq 5cm inside the plot, ranging from 11 to 215 trees, totalling 840 in pasture habitat (Table 1). We chose the threshold of DBH \geq 5cm for pasture sampling due to the higher prevalence of smaller trees in this habitat (Fig. S3). Although we have chosen specific sampling methods for each habitat type and had different sampling efforts (number of trees), the pasture and the forest had similar sample coverage, allowing comparison of species richness and diversity between habitats (Fig. S4, i.e. sample coverage analysis from 'iNEXT' R package, Hsieh *et al.*, 2022, Chao *et al.*, 2014). However, for abundance analysis, we used the mean abundance (i.e. the sum of the epiphyte individuals divided by the total number of trees per plot) instead of raw values to control the difference in sampling effort.

We sampled all angiosperm epiphytes (excluding hemiepiphyte and nomadic vines, according to Zotz *et al.*, 2021) on each tree by ground observation with binoculars. While ground observations may result in the subsampling of epiphytes, our sampled forests are characterized as semi-deciduous with pronounced dry seasons, significant human disturbance, and are predominantly dominated by short trees (ca. 20m of height). Consequently, our forest exhibits lower epiphyte abundance, frequency, and species diversity. In this ecological context the relative effectiveness of ground-based observations using binoculars is warranted. Similarly, scattered trees in pastures can be easily observed from the ground. Therefore, the chosen sampling method is effective in both forest and pasture environments

We divided the tree into zones based on the tree structure, adapted from Johansson (1974): Z1 as the low trunk (i.e. ground to 1.3m), Z2 upper trunk (i.e. from 1.3 until crown base), Z3 inner crown, and Z4 as the external crown (Fig. 1.a). We quantified epiphyte species richness and abundance per tree zones considering abundance as the total of individual epiphyte stands (i.e. grouped individuals without overlapping roots and leaves; Sanford 1968).

2.3.3 Statistical analysis

To test hypothesis (I), i.e. habitat differences, we compared the species richness and mean abundance (i.e. epiphytes individuals/tree) between pastures and forest fragments using Wilcoxon Test ('stats' R core package; R Core Team, 2022). We used this test because the data were not normally distributed, considering the area as a sample unit, with 30 observations, 15 in pastures, and 15 in forests. For beta diversity analysis, we aggregated the epiphyte data of all pastures and forests, obtaining one value of beta diversity and its components (i.e. nestedness and turnover).

To test for the hypotheses about dependence (II - 'structural,' Fig. 1.a; III - 'microclimatic,' Fig. 1.b), we compared the species composition between habitats for specific zone pairs. Specifically for the structural dependence hypothesis, we considered 'trunk zones' (zones Z1 and Z2) and 'crown zones' (zones Z3 and Z4) for both pasture and forest trees. For the microclimatic dependence hypothesis, we considered 'sunlight-exposed zones' Z1 and Z4 in pasture trees and Z4 in the forest trees, and 'shaded zones' Z2 and Z3 in the pasture trees, and Z1, Z2, and Z3 in the forest trees. While the tree structures may be also influenced by microclimate variability, it is important to emphasize that the criteria for identifying microclimatic zones provide a more precise and effective means of distinction. The delimitation of

microclimatic zones has relied primarily on field observations. Also, these zones are often delimited using a combination of methods, including literature based on microclimatic field measurements (e.g., Woods *et al.*, 2014; Murakami *et al.* 2022) and studies that reach similar conclusions by studying the distribution of epiphytic assemblages within tree zones (e.g., Johansson 1974; Woods *et al.*, 2019; Cruz *et al.*, 2022).

To test hypothesis (III), i.e. species composition is more similar within than among habitats, we aggregated epiphyte assemblages according to the similarity in species composition using presence/absence and performed a cluster analysis using Euclidean distance ('factoextra' R package, Kassambara, 2020). We used non-metric Multidimensional Scaling, Jaccard similarity index as distance metric (NMDS; 'vegan' R package, Oksanen *et al.*, 2022), as a visualization tool to aid in identifying the differences in species composition observed in the cluster analysis, and indicator species analysis ('indicspecies' R package, De Caceres and Legendre, 2009) to identify which species could explain the differences found. In turn, testing hypothesis I and II was complemented by calculating beta diversity and component scores using the 'betapart package' (Baselga *et al.*, 2022). We carried out all the analysis using R programming language (R Core Team, 2022).

2.4 Results

2.4.1 Epiphyte per habitat

We recorded 10,297 epiphyte individuals (359 in the forest and 9938 in the pasture) and 23 epiphyte species (18 in the forest, 16 in the pasture, Table 2, Fig. 2 and 3). Our results partially support the hypothesis (I) since both habitats had similar species richness ($W = 155.5$, $p = 0.07$), but the pastures showed significantly higher

epiphyte abundance than the forest (individuals/tree; $W= 33$, $p=0.001$), as expected. In turn, pasture and forest differed in their species composition (beta-diversity: 0.95%) mostly due to nestedness (0.64, Fig. 4a).

Among the 23 epiphyte species found, 11 (48%) were common for both habitats (Table 2), representing 85% and 90% of the individuals in the forest and pasture, respectively. In the pastures Bromeliaceae was the most abundant family (9306 individuals, 93.6%), especially due to the over-abundance of *T. recurvata* (6799 individuals, 68.4% of total abundance in pastures) and *T. pohliana* (1543, 15.5%). While, in the forests Orchidaceae was the most abundant family (257 individuals, 71.6%), with the two most abundant species: *Polystachya concreta* (125 individuals, 34.8% of total in forest) and *Brassavola tuberculata* (63, 34.8%). Surprisingly, the two most abundant species of pasture and forest are common in both habitats, but with considerable differences in their representation (Fig. 3).

Table 2: Abundance and frequency (i.e. occurrence in the 30 areas, 15 pasture, and 15 forest) of species found. Values within parentheses are the observed value per habitat (forest; pasture). Species in bold are species found in both habitats.

Family	Species	Acronym	Abundance	Frequency
Bromeliaceae	<i>Aechmea bromeliifolia</i> (Rudge) Baker ex Benth. & Hook.f.	Ae.b	21 (5; 16)	4 (2; 2)
	<i>Billbergia porteana</i> Brongn. ex Beer	Bi.p	9 (3; 6)	4 (2; 2)
	Bromeliaceae sp.	Br.sp	9 (9; 0)	1 (1; 0)
	<i>Tillandsia loliacea</i> Mart. ex Schult. & Schult.f.	Ti.l	84 (0; 84)	5 (0; 5)
	<i>Tillandsia pohliana</i> Mez	Ti.p	1555 (12; 1543)	18 (4; 14)
	<i>Tillandsia recurvata</i> (Gaudich.) Baker	Ti.r	6827 (28; 6799)	20 (5; 15)
	<i>Tillandsia</i> sp.1	Ti.sp1	1 (1; 0)	1 (1; 0)
<i>Tillandsia</i> sp.2	Ti.sp2	3 (0; 3)	1 (1; 0)	

	<i>Tillandsia streptocarpa</i> Baker	Ti.s	3 (0; 3)	2 (0; 2)	
	<i>Tillandsia tricholepis</i> Baker	Ti.t	852 (0; 852)	3 (0; 3)	
Cactaceae	<i>Epiphyllum phyllanthus</i> (L.) Haw.	Epip.p	72 (9; 63)	13 (3; 10)	
	<i>Brassavola tuberculata</i> Hook.	Br.t	333 (63; 270)	2 (1; 1)	
	<i>Bulbophyllum chloroglossum</i> Rchb.f.	Bu.c	28 (28; 0)	4 (4; 0)	
	<i>Campylocentrum micranthum</i> (Lindl.) Rolfe	Cam.m	3 (3; 0)	3 (3; 0)	
	<i>Catasetum fimbriatum</i> Rchb.f.	Cat.f	2 (2; 0)	2 (2; 0)	
	<i>Encyclia patens</i> Hook.	En.p	2 (2; 0)	1 (1; 0)	
	<i>Epidendrum pseudodiforme</i> Hoehne & Schltr.	Epid.p	8 (1; 7)	2 (1; 1)	
Orchidaceae	<i>Gomesa pubes</i> (Lindl.) M.W.Chase & N.H.Williams	Go.p	9 (9; 0)	1 (1; 0)	
	<i>Gomesa varicosa</i> (Lindl.) M.W.Chase & N.H.Williams	Go.v	51 (1; 50)	3 (1; 2)	
	<i>Oncidium</i> sp.	On.sp	2 (0; 2)	2 (0; 2)	
	<i>Polystachya concreta</i> (Jacq.) Garay & H.R.Sweet	Po.c	225 (125; 100)	9 (6; 3)	
	<i>Trichocentrum pumila</i> (Lindl.) M.W. Chase & N.H. Williams	Tr.p	135 (56; 79)	7 (4; 3)	
Piperaceae	<i>Peperomia tetraphylla</i> Hook. & Arn.	Pe.t	96 (35; 61)	3 (1; 2)	

2.4.2 Epiphyte per zones

Regarding the species distribution per zone, *Polystachya concreta* (Orchidaceae) was the only species found throughout the whole tree in the forest, while in pasture three *Tillandsia* species (i.e. *T. pohliana*, *T. recurvata*, and *T. tricholepis*; Bromeliaceae) and *Epiphyllum phyllanthus* (Cactaceae) were found occurring in all zones (Fig. 2). However, considering these species' occurrence in the opposite habitats, *P. concreta* occurred only in crowns zones in pasture trees, while in forest trees the *T. recurvata* and *E. phyllanthus* occurred throughout all zones except in the most shaded one (i.e. Z1), and *T. pohliana* only in the intermediate zones (i.e. Z2 and Z3).

Regarding species with restricted distribution, this was the case in the forest for *Gomesa varicosa* (Orchidaceae) and *Peperomia tetraphylla* (Piperaceae) which occurred only in the tree trunks; however, in the pastures we found them occurring in the trunks and crowns of trees. We did not find species restricted to tree trunks in pasture trees, while for the crowns, we found four crown-exclusive species in forests and seven in pastures. *Epidendrum pseudodiforme* (Orchidaceae) occurred only in tree crowns in both habitats, and three of the crown-exclusive in pastures also occurred in forest tree trunks (i.e. *P. concreta*, *Trichocentrum pumila*, and *Bilbergia porteana*).

Regarding the microclimate zones, only forests harboured species restricted to sunlight-exposed zones, although it was one species with relatively low abundance (*Encyclia patens*, Orchidaceae; 2 individuals). Regarding species restricted to shaded zones, we found 12 in forests and only two in pastures. Curiously, from the 12 species restricted to shaded zones in forests, six of them occurred in sunlight-exposed zones in pasture trees. Only *Bilbergia porteana* (Bromeliaceae) was strictly restricted to shaded zones in both habitats.

2.4.3 Epiphyte diversity between habitats

We found differences in epiphyte species composition between tree structures and microclimate zones (Fig. 4.b). Differently from the overall beta diversity (hypothesis I), which was mainly due to nestedness, the compositional differences between the trunks, shaded, and sun-light zones of habitats were largely due to species turnover.

Regarding the degree of similarity, we found that assemblages on tree structures, in pastures and forests, were more similar (mean beta-diversity: 0.89 [trunk 0.83, crown 0.96]) than those on microclimate zones (mean beta-diversity:

0.93 [shaded 0.90, exposed 0.95]). Therefore, although assemblages on structures and microclimate zones were relatively highly dissimilar (i.e. beta-diversity score higher than 0.75), our data supports hypothesis II of similarity being largely structurally than climatically dependent.

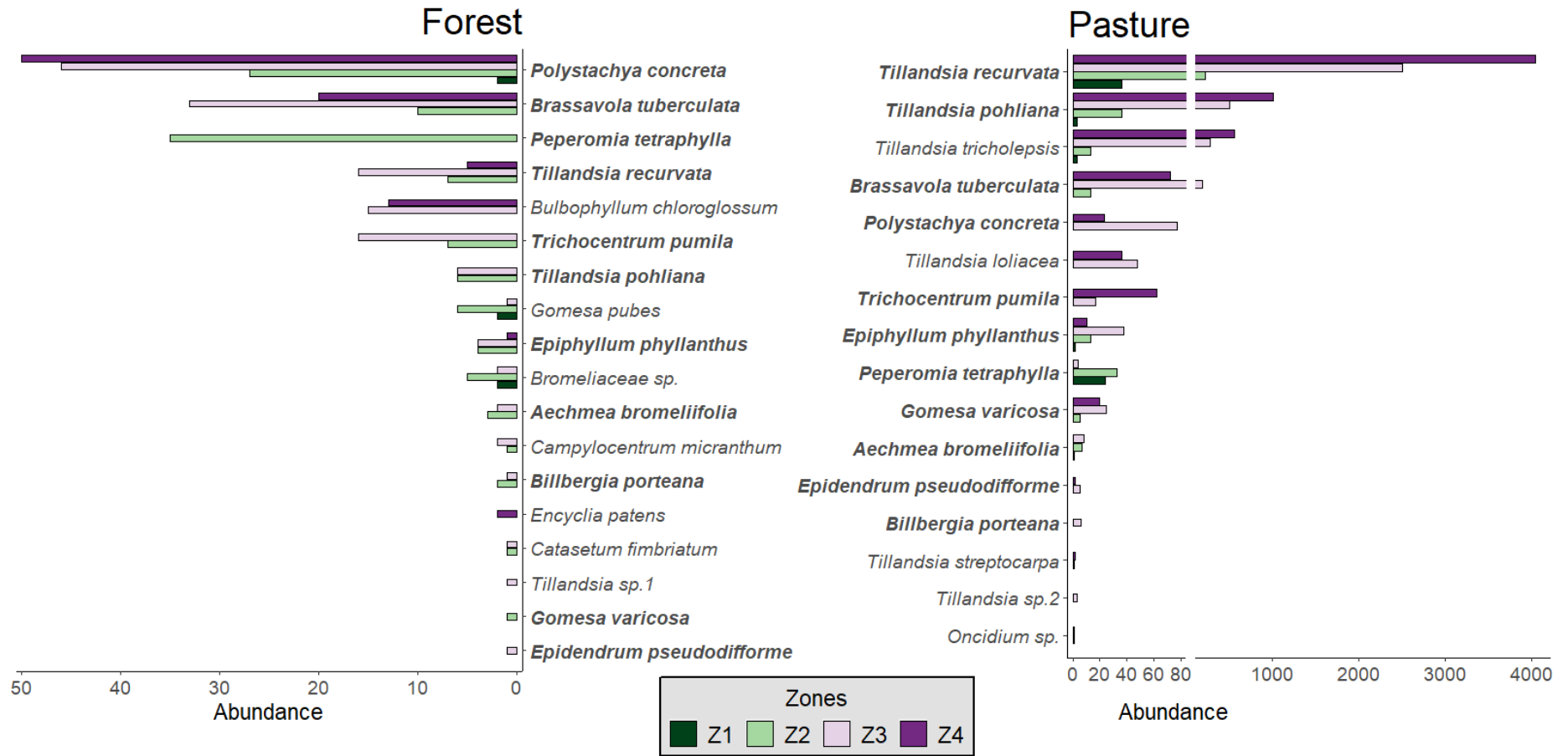


Figure 2: Epiphyte species abundance per zone in each habitat. Species in bold are species found in both habitats.

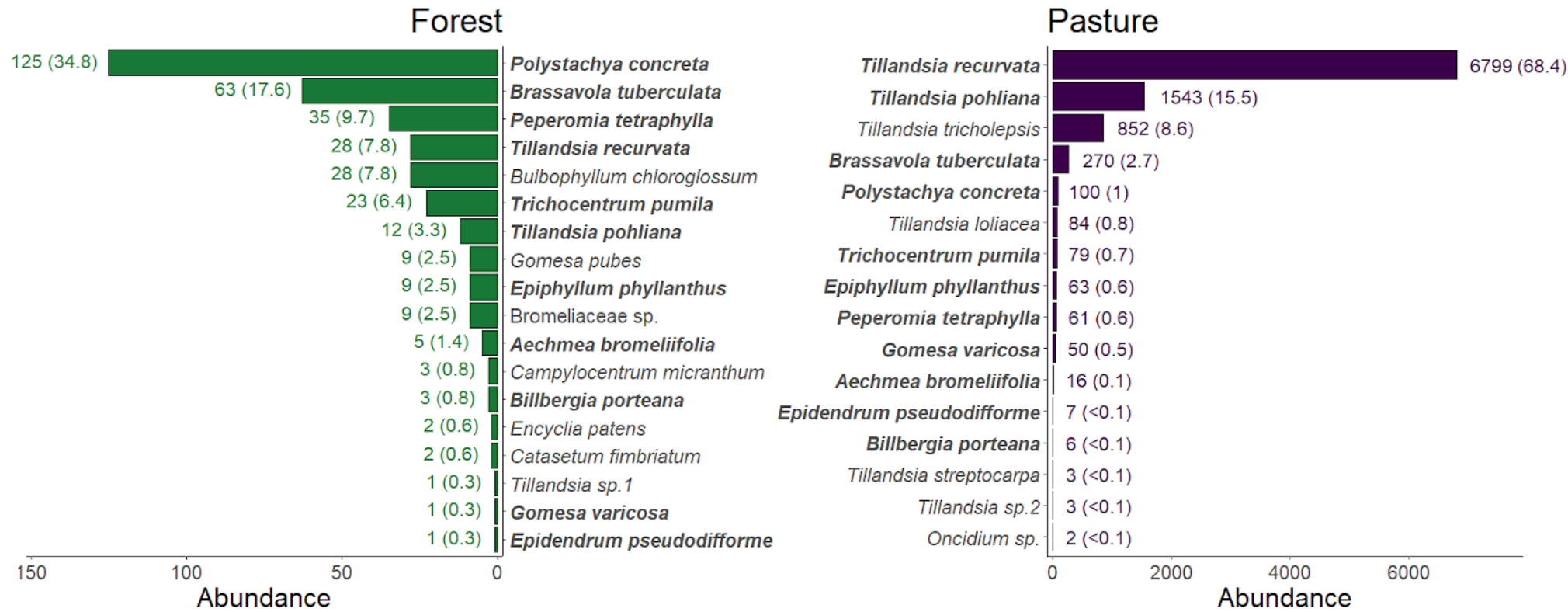


Figure 3: epiphyte species abundance per habitat. Values in parenthesis are the percentage of specific species individuals to the total. Species in bold are species found in both habitats.

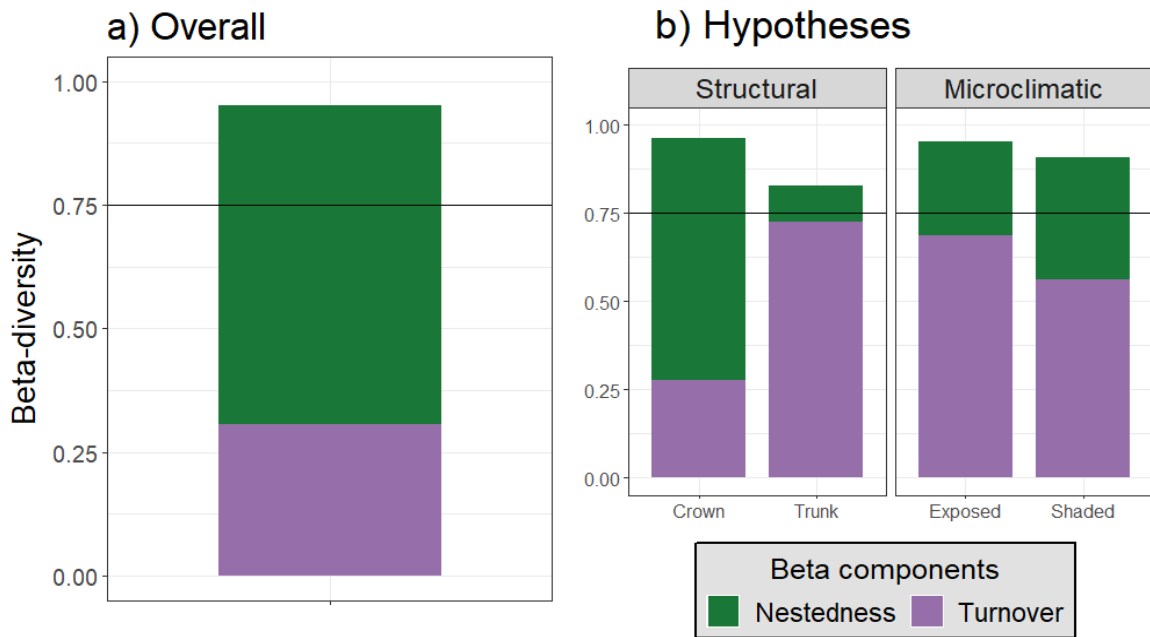


Figure 4: Comparison of species composition dissimilarity between habitats for the overall (a) and by hypotheses (b).

Lastly, our data provides partial support for hypothesis (IV). For tree structures (trunk and crown), the similarity is higher within each habitat, as expected. The species occurring in the trunk and crown of forest are indeed more similar among them than those occurring in the trunk and crown of pasture trees (Fig. 4.a, cluster). *Bulbophyllum chloroglossum* and *Gomesa pubes* were significantly associated with the crown and trunk of forest trees, respectively (Fig. 5). Forests host more exclusive species, which contributed to the high similarity among forest structures (Fig. 2, Fig. 4.a, NMDS plot), especially *Gomesa pubes*, Bromeliaceae unident., *Campylocentrum micranthum*, and *Catasetum fimbriatum*, are forest-exclusive species occurring in both trunks and crowns. However, for microclimatic zones (shaded and sunlight-exposed), shaded zones of forest trees were more similar, in species composition, to assemblages occurring in microclimatic zones in pastures than to assemblages on exposed zones of forest trees (Fig. 4.b, cluster). This

counterintuitive pattern is mainly due to the species *Tillandsia pohliana*, which was significantly associated with both shaded and exposed zones in pasture trees (Fig. 6) but restricted to shaded zones in forest trees (Fig. 2). Additionally, *Peperomia tetraphylla*, *Trichocentrum pumila*, *Aechmea bromeliifolia*, and *Gomesa varicosa* occurred strictly in shaded zones in forest trees, but we found those species in both shaded and exposed zones in pasture trees, which could also result in higher similarity between shaded zones of forest trees and both zones in the pasture (Fig. 4.b, NMDS plot).

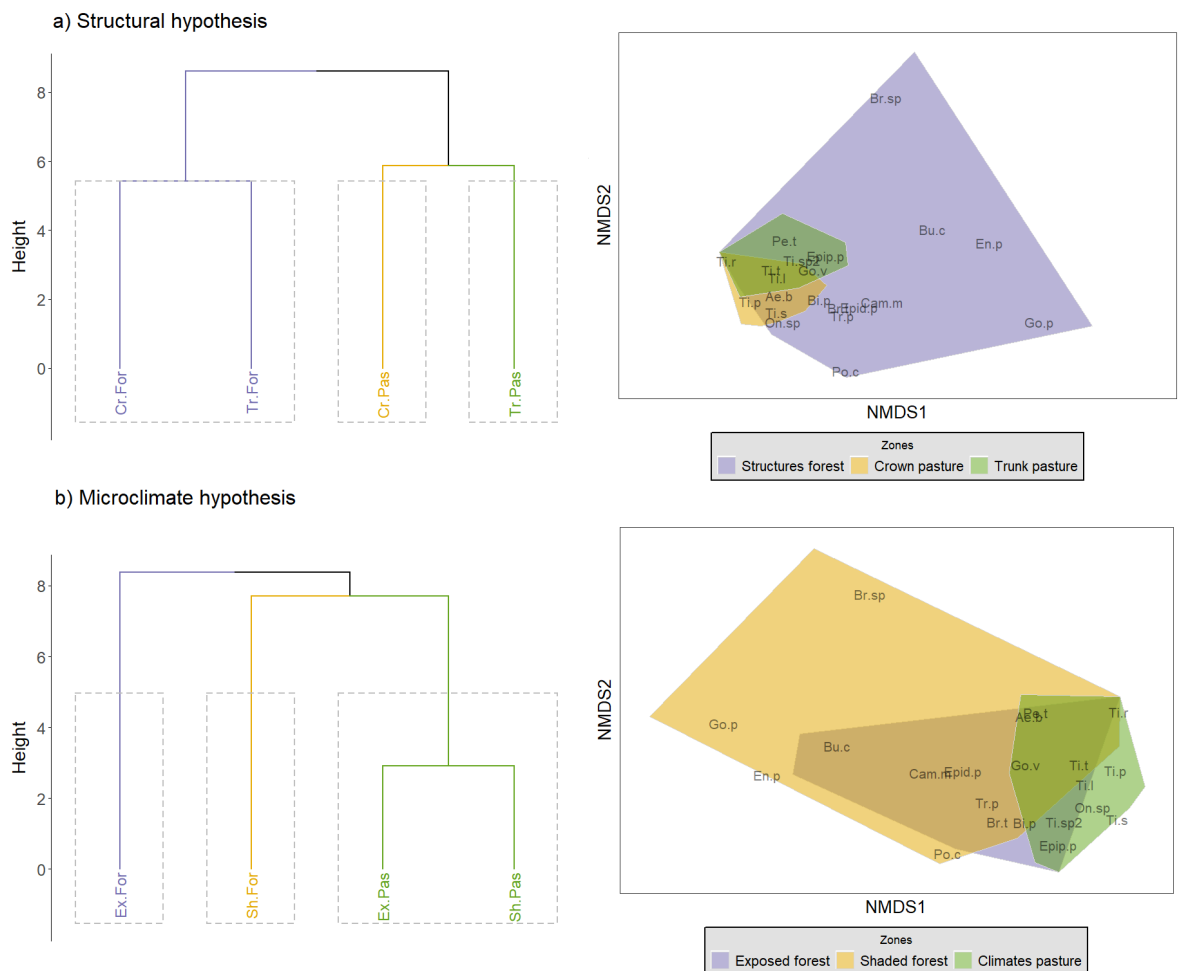


Figure 5: Similarity of species composition between assemblages on (a) structures (Cr. for crowns and Tr. for trunks) and (b) microclimatic zones (Ex. for exposed and Sh. for shaded) among habitats (For for forests and Pas for Pastures). The dashed squares in cluster plots, and colors in both cluster and

NMDS plots, indicate the zone groupings with high dissimilarity in species composition. “Structures forest” are both the trunk and crown of forest trees, which had similar species composition according to the cluster analysis, whereas “Climates pasture” are both shaded and exposed pasture trees.

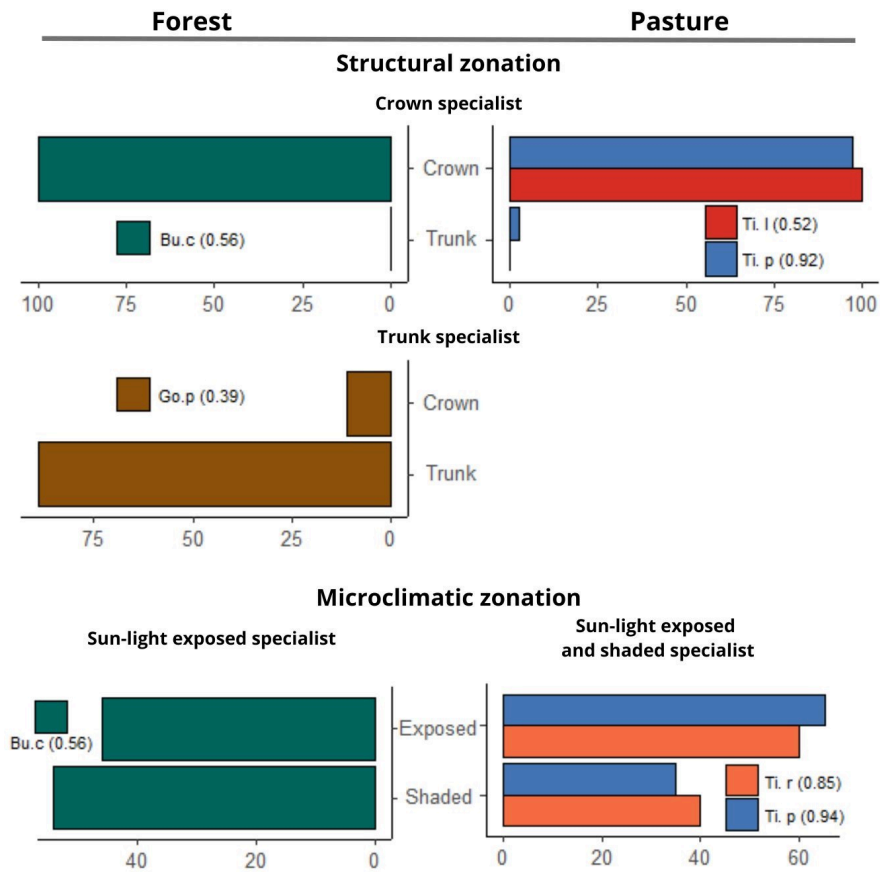


Figure 6: Species significantly associated (i.e. indicator analysis $p < 0.05$) with each tree zonation (structural: crown and trunk | microclimatic: sun-light exposed and shaded), and their relative abundance for the zone groups (i.e. percentage on the x-axis). Species acronyms are available in Table 2. Values in parenthesis are the ‘stat’ values of the association, where higher values indicate a stronger association between the species and the zone group in which it specializes. “Ti. r” and “Ti. P” are specialized in both sun-light exposed and shaded zones of pasture trees.

2.5 Discussion

We observed the expected negative impact of land cover conversion from forest to anthropogenic areas on epiphyte assemblages. Consistent with previous studies (e.g. Werner, 2011), our results showed lower species richness and distinct species

composition in pastures compared to forests. However, both habitats shared a relatively high proportion of species (48%), with somewhat lower species richness in the forest fragments and with epiphyte assemblages in pastures nested from the forest fragments. We found more epiphyte individuals in pastures than in forests, primarily due to the over-abundance of xerotolerant and generalist species such as *Tillandsia spp.* Despite these substantial differences, the species composition showed greater similarity between pasture and forest trees in terms of structural zones (crown vs. trunk) than microclimatic conditions (shaded vs. sunlight-exposed). This higher similarity in composition according to structures can be attributed to certain epiphyte species that exhibited significantly higher occurrence in either the crown or trunk of host trees, regardless of the habitat (e.g. *Peperomia tetraphylla* in the tree trunk, *Brassavola tuberculata* and *Polystachya concreta* in the tree crown). However, while structural factors were important for similarity, similarity in species composition was generally higher between tree zones, within the same habitat, than between habitats.

Any anthropogenic process worsening habitat quality is expected to have a negative effect on vascular epiphyte assemblages (e.g. forest clearance: HietzSeifert *et al.*, 1996; habitat loss and fragmentation: Cardos *et al.*, 2018). Forest conversion into anthropogenic matrices is well-defined as harmful to most plant species (Vellend, 2003), including vascular epiphytes (Werner, 2011). The removal of arboreal strata leads to drastic changes in the local climate (Holl, 1999; Jucker *et al.*, 2018), while the new coverage of anthropogenic matrices implies the introduction of non-natural processes and their consequences (e.g. high chemical input reducing pollinator activities [Ramos *et al.*, 2018] and soil quality [Passinato *et al.*, 2021]). The first observed impact in the epiphyte community is local species extinction, with only a

few species filtered for and persisting in the community, followed by a high colonization and abundance increase of xerotolerant and generalist species (Acuña-Tarazona *et al.*, 2015). Our findings align with previous studies (e.g. Hietz-Seifert *et al.*, 1996; Larrea and Werner, 2010; Einzmann *et al.*, 2016; Guzmán-Jacob *et al.*, 2020), showing a minor decline in species richness but significant alterations in species composition. The loss of species, reflected by nestedness, played a crucial role in shaping these changes, with a high contribution to the overall patterns observed.

While croplands exhibit a structural resemblance to forests, the absence or low intensity of management in the pasture matrix generally has a minor detrimental impact on local species (Carneiro *et al.*, 2016a; Carneiro *et al.*, 2016b, Tiang *et al.*, 2021). The retention of arboreal elements such as scattered trees or tree groups within the pasture has the potential to support some portion of the local epiphyte diversity (Einzmann *et al.*, 2016; Elias *et al.*, 2021; Hietz *et al.*, 2022). The presence of these trees in the pasture matrix can contribute to the preservation of ecosystem services and aid in landscape-scale mitigation efforts (Manning *et al.*, 2009; Siqueira *et al.*, 2017). We found a few epiphyte species which were forest specialists occurring on pasture trees (see Elias *et al.*, 2021 for the species classification) but with evident domination of xerotolerant and generalist species, which is commonly observed in degraded and disturbed habitats (Einzmann and Zotz, 2017b; Elias *et al.*, 2021). This dominance of a few species, associated with the decrease in host tree availability, may indicate a saturation of epiphytes on pasture trees. However, scattered trees in pastures are observed to be not fully occupied by epiphyte individuals (personal observation, Einzmann and Zotz, 2017b), indicating that the main limitations to epiphyte occurrence in a pasture are reaching the scattered trees

(Cascante-Marín *et al.*, 2008) and surviving under unfavorable environmental conditions (Einzmann and Zotz, 2017a).

Assuming that generalist epiphyte species can occur widely under any environmental conditions, the main difference in species composition among forests and anthropogenic areas is the occurrence of sensitive and forest-specialist species. Given the non-random association of epiphytes with their host trees, the presence of "good host trees" in the pasture—trees characterized by rugose bark and a dense leaf cover in the crown (Elias *et al.*, 2021)—can facilitate the occurrence of not only generalist species but also specialized forest species. This highlights the importance of having suitable host trees in pastures to support a broader range of epiphyte species. As a result, pasture trees may potentially harbor a significant representation of the regional epiphyte diversity (e.g. Oliveira *et al.*, 2015; de Carvalho *et al.*, 2020). Conversely, forest remnants that experience high human pressure are likely to support a lower number of epiphyte species compared to preserved forests (e.g. human-managed secondary forests: Böhnert *et al.*, 2016; Carvajal-Hernandez *et al.*, 2017). Any degree of human disturbance has detrimental effects on epiphyte assemblages, leading to decreased species richness and changes in species composition (Guzmán-Jacob *et al.*, 2020). Nonetheless, in our study area, the high similarity of epiphyte assemblages among forest remnants and the pasture areas may be due to the relatively high epiphyte diversity in pastures due to the conservation of "good host trees" (Elias *et al.*, 2021), and to lower than expected epiphyte diversity in the surrounding forests as consequence of high human pressure (Böhnert *et al.*, 2016; Carvajal-Hernandez *et al.*, 2017).

Regarding the similarity in species composition among habitats, we observed a greater resemblance of epiphyte assemblages from tree structures (i.e., trunk and

crown) compared to microclimate zones (i.e., shaded vs sunlight-exposed). Specifically, we found that the trunks exhibited the highest similarity in epiphyte composition between forest and pasture. Epiphytes are a highly diverse group, taxonomically and functionally (Zotz *et al.*, 2021; Hietz *et al.*, 2022). The complexity of a single host tree offers various microhabitats across its surface and vertical stratification, leading to a positive relationship between host tree complexity and epiphyte species diversity (Izuddin and Webb, 2015; Woods *et al.*, 2019). The tree trunk and crown serve as distinct substrates for different epiphyte species, thereby supporting unique assemblages (Woods *et al.*, 2019; Cruz *et al.*, 2022). The trunk is commonly used by epiphyte species that require more moist habitats, this zone is closer to the soil and relatively protected from wind and light exposure, especially in forest habitats (Li *et al.*, 2015). For instance, species of tank bromeliads are commonly observed on tree trunks, sustained by elevated humidity levels (Cruz *et al.*, 2022) and the accumulation of water and organic matter, which serve as nutrient sources (Benzing and Renfrow, 1974). Our study also revealed a relatively great abundance of tank bromeliads (*Billbergia porteana* and *Aechmea bromeliifolia*) in the trunk zones, particularly on forest trees. In turn, the crown tends to have more surface available to epiphyte species, which could represent higher variability of microhabitats (Annaselvam and Parthasarathy, 2001), potentially hosting high representativeness of local epiphyte diversity (Azuma *et al.*, 2021). The complexity of crowns is directly linked to the mechanical support, allowing a higher occurrence of big-sized epiphyte individuals and an accumulation of epiphyte stands (i.e. cluster of epiphytic individuals, which make it difficult to differentiate individuals numbers; Sanford 1968; Annaselvam and Parthasarathy, 2001; Izuddin and Webb, 2015). In addition to providing a larger surface area for epiphyte colonization, the crown of a

tree exhibits significant microclimate variation and a heterogeneous habitat (Anhuf and Rollenbeck, 2001; Murakami *et al.*, 2022). It accommodates a diverse range of species, from water-dependent ones in the inner crown, characterized by higher moisture levels, milder temperatures, and relative shade, to xerotolerant species in the outer crown, facing drier, hotter, and more exposed conditions (e.g. Cruz *et al.*, 2022). Although specific regions within the crown have distinct microclimatic conditions, microclimate variation in the crown is ephemeral, fluctuating daily and/or annually (Murakami *et al.*, 2022). As a result, epiphyte species inhabiting the crown often exhibit functional adaptations that enable them to thrive under a wide range of climatic conditions, such as reduced leaf area (Guzmán-Jacob *et al.*, 2020) and smaller individual size (Nitta *et al.*, 2020), as well as specialized structures for water storage, like pseudobulbs (Ng and Hew, 2000). For example, atmospheric *Tillandsia* species are highly abundant in tree crowns (Chaves *et al.*, 2016), as well as in degraded habitats (Flores-Palacios, 2016; Einzmann and Zotz, 2017b), mainly through drought-tolerance and CAM photosynthesis (Crassulacean acid metabolism).

Although the stratification of epiphytes in the tree is also influenced by microclimatic conditions (e.g. Cruz *et al.*, 2022), the stratification based on microclimate is not quite clear as for structures (Sanger and Kirkpatrick, 2016). The vertical stratification of microclimate, relatively well established for forest habitats, describes a stratification of the water availability and light exposure from the ground to the outer canopy (e.g. Didham and Ewers, 2014), which could influence the occurrence of specific species groups (e.g. Lepidoptera [Schulze *et al.*, 2001]; termites [Roisin *et al.*, 2006]; birds [Rajaonarivelo *et al.*, 2021]). However, the same tree zone could have different microclimate conditions (Sanger and Kirkpatrick, 2016), as well as show a high variation of microclimate according to the phenology of

the tree species (i.e. tree deciduousness; Einzmann et al., 2015; Murakami *et al.*, 2022). Since the distribution of epiphytes in the host tree is highly dependent on the microclimate, this high variability within the same tree zone could lead to the co-occurrence of epiphyte species from different functional groups in the same zone (Sanger and Kirkpatrick, 2016). However, despite the microclimatic variation, we observed certain species predominantly occurring in specific microclimate zones within both habitats (pastures and forests). For instance, *Peperomia tetraphylla* and *Aechmea bromeliifolia* were predominantly found in shaded zones; although they also occurred in sunlight-exposed zones on the trunks of pasture trees. These species occurrences in zones hypothetically not favorable (i.e. sunlight-exposed) suggest a high association of these species with tree trunk substrate structure, independently of microclimate conditions, but also a possible methodological issue, whereby microclimate zonation in pasture trees requires a finer resolution to identify the actual climate stratification (see Murakami *et al.*, 2022).

Lastly, although similarity among habitats was slightly more structurally dependent, species composition among tree zones within a same habitat was generally higher. Forest epiphyte species (i.e. species highly abundant and widely distributed in the forest trees) are sparsely found in pasture trees, but frequently restricted to the crown, with their species richness and abundance positively associated with tree crown volume (Elias *et al.*, 2021). Host trees surrounded by anthropogenic matrices could have a contraction of favorable microclimate zones (i.e. similar to forest microclimate) from the outer zones to inner zones, which could restrict the occurrence of some epiphyte species to the inner crown (De Beenhouwer *et al.*, 2015). Indeed we identified three epiphyte species occurring throughout the whole tree in the forest, but restricted to crowns in pasture trees. Additionally, we

found widespread species like *T. loliaceae* (pasture exclusive) and *Tillandsia pohliana* as indicators of tree crowns in pasture trees. Generalist epiphytes often exhibit high abundance in trees within human-modified landscapes (Einzmann and Zotz, 2017b). Specifically, in crowns, their presence is more pronounced (Chaves *et al.*, 2016), and their abundance is positively related with the size and complexity of the crown area (Izuddin and Webb, 2015; Elias *et al.*, 2021). If crowns of pasture trees are not saturated with epiphyte individuals (Einzmann and Zotz, 2017b), these species can overpopulate them, thus becoming indicator species for tree crowns in anthropic areas.

However, in terms of microclimate zones, we observed a higher similarity in species composition between shaded zones of forest trees with pasture assemblages than with sunlight-exposed zones of forest trees. From the 11 species shared by the habitats, six were restricted to shaded zones in the forest but occurring in sunlight-exposed zones in pasture trees. Despite the variation in microclimates, the presence of epiphytes on the trunk suggests that substrate structure may play a more significant role in determining their occurrence (Zotz, 2007; Cruz *et al.*, 2022). An interesting example is *Tillandsia pohliana*, which indicates both shaded and sunlight-exposed zones in pastures, but only occurred in shaded zones in the forest, contributing significantly to this unexpected finding. As explained by Sanger and Kirkpatrick (2016), epiphyte species with different functional characteristics can coexist in the same tree zone due to microclimate variability. Given the highly variable light exposure among pasture trees, which results in a heterogeneous light environment across the tree surface, the same species may occur in different tree zones as these zones may have similar light exposure (e.g. Ventre-Lespiaucq *et al.*, 2017).

2.6 Conclusion

Zotz (2007) concluded that epiphyte stratification in tree hosts is poorly predicted specially by pre-established tree zonation schemes, as epiphyte distribution is more related to substrate features and forest structure (i.e. branches diameter, height above ground, and inclination) than to zones schemes. Although crowns and trunks tend to have high structural specificities, this structural heterogeneity is not necessarily present in all trees. However, using tree structures such as trunk and crown allowed us to find consistent results in line with previous findings. Although, regarding our microclimate division, we found conspicuous results. While our hypotheses were partially supported by our findings, even when considering the theoretical and literature-based aspects of our microclimatic zonation, we propose additional explanations: 1) the high degradation of forest fragments may result in microclimatic conditions more similar to that on pastures than what is expected for a forest, and 2) the microclimate stratification of pasture trees requires a finer division due to their highly variable microclimate (see Murakami *et al.*, 2022 for more details). Nevertheless, despite the pasture hosting only fewer epiphyte species than the forest, mostly xerotolerant ones, we observed a nested composition, indicating that the pasture trees harbour an important share of the epiphyte diversity from forest assemblages. This highlights the importance of pasture trees as crucial contributors to the regional epiphyte species pool and underscores their potential as tools for mitigation efforts to avoid species losses in the landscape. Maintaining and planting scattered trees in pastures (see Table S1 for key tree host species in our study area), with increased structural complexity (e.g. longer trunks and greater crown branching), can maintain some forest species in the landscape, mitigating the diversity erosion by frequent anthropic disturbance.

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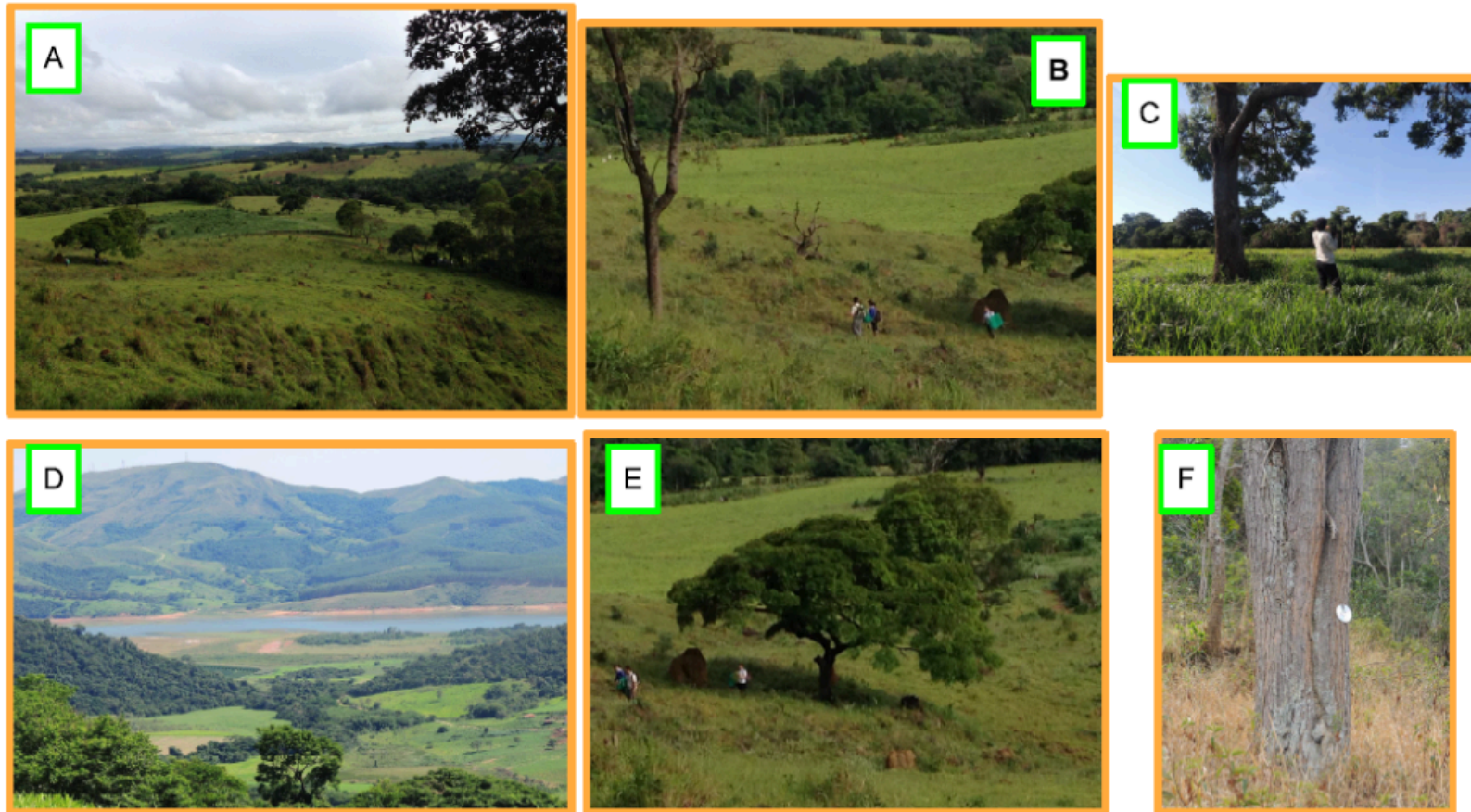


Figure S1: Landscape overview of the study area. Images A to D provide a comprehensive perspective of the remaining forest fragments amidst the pasture matrix dotted with scattered trees. Images E and F offer a closer examination of these scattered trees within the pastures. Photos by Flavio N. Ramos.

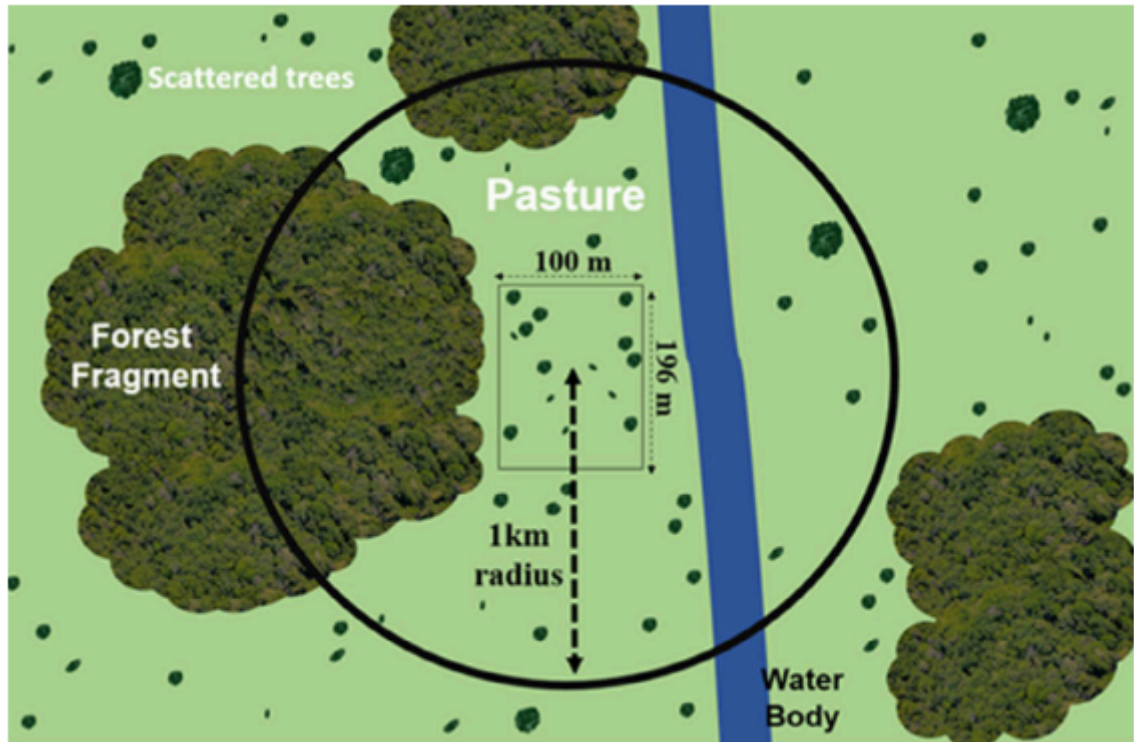


Figure S2: example of pasture sampling strategy in pastures. All plots were 100×196 m (1.96 ha) and placed at a maximum distance of 3 m from the forest fragment edge. The plot format was based on the smallest pasture included in the study, which was limited by a water body. Each pasture was selected following the criterium of having 10–50% of plot area covered by forest inside a buffer with 1 km of radius, centralized in the plot.

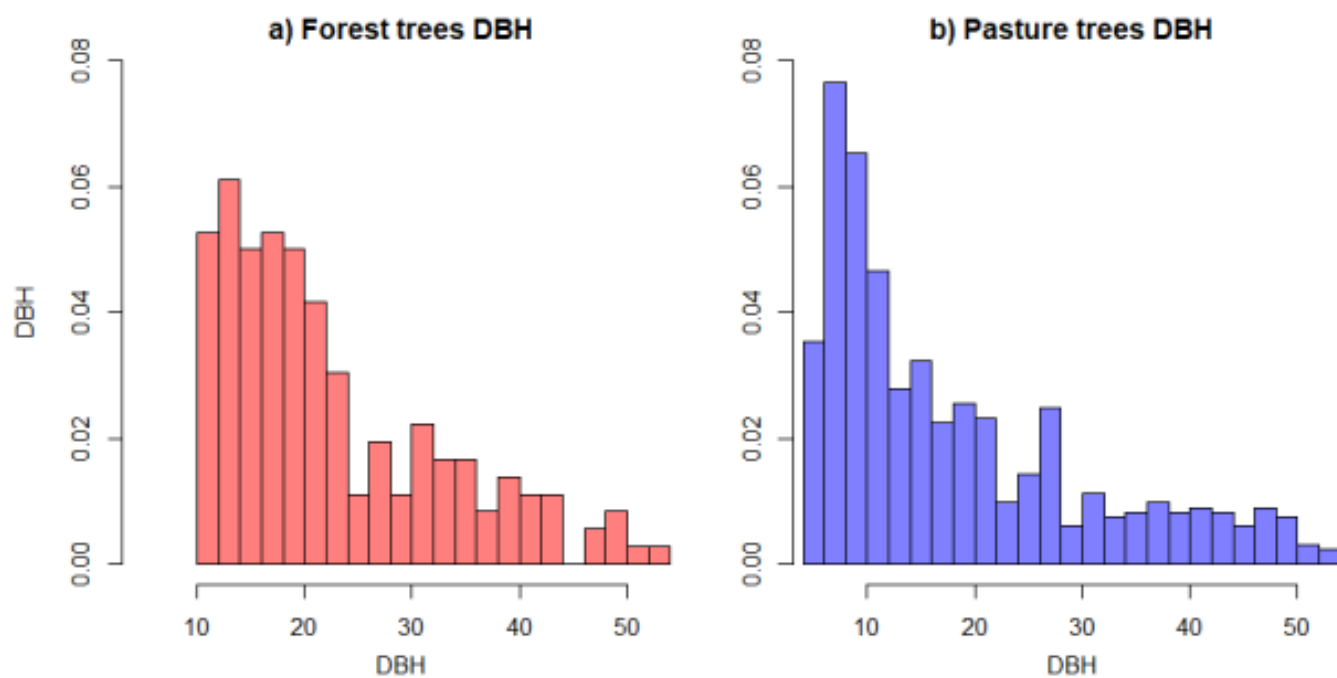


Figure S3: distribution of DBH groups for both forest (a) and pasture (b). While the distribution of larger trees (DBH >30 cm) is similar between the two habitats, there is a notably higher frequency of trees with approximately 10 cm of DBH in pastures compared to forests. Therefore, we included smaller trees (DBH 5-10 cm) in our pasture sampling due to their higher prevalence in this habitat.

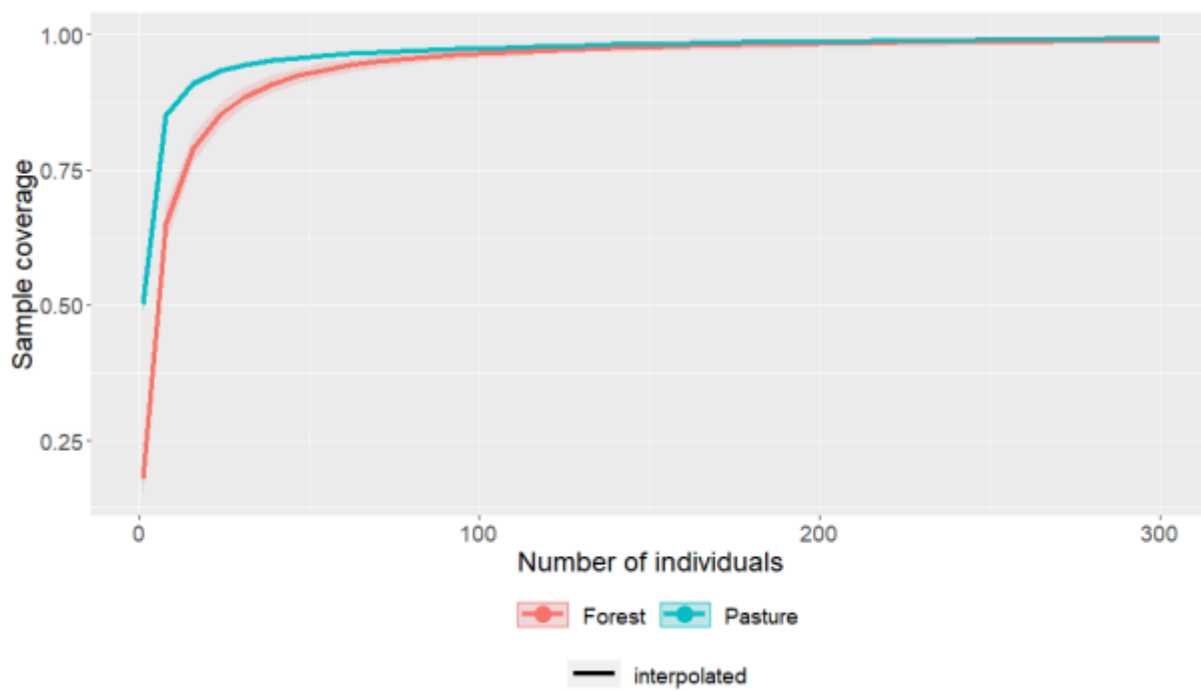


Figure S4: sample coverage of forest and pasture sites. Both curves indicate adequate coverage of epiphyte assemblages.

Table S1: Epiphyte species richness (Epiphyte spp.) and species composition on each tree host species within the pasture areas. The column “n” indicates the number of individuals sampled of each host tree species. Acronyms for epiphyte species are provided in Table 2. Out of the 840 host trees within the pasture, only 238 (28.3%) could be identified at least until the genus level, and these are included in this table.

Tree host species	n	Epiphyte species presence/absence																
		Epiphyte spp.	Ti. r	Ti. p	Ti. t	Ti. l	Ti. s	Ti.sp 2	Epip. p	Br.t	Po. c	Go. v	Epid. p	Tr. p	Pe. t	Ae. b	Bi. p	On.s p
	6																	
<i>Maclura tinctoria</i> (L.) D. Don ex Steud	3	11	1	1	1	1	0	1	1	0	1	0	0	1	1	1	0	1
	1																	
<i>Machaerium villosum</i> Vogel	5	8	1	1	1	0	0	0	1	0	0	0	0	1	1	1	1	0
	2																	
<i>Platypodium elegans</i> Vogel	2	5	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	1
<i>Casearia sylvestris</i> Sw.	11	5	1	1	0	0	0	0	1	0	1	0	0	0	0	1	0	0
<i>Handroanthus chrysotrichus</i> (Mart. ex A.DC.)																		
Mattos	7	5	1	1	0	1	0	0	1	0	1	0	0	0	0	0	0	0
<i>Siparuna guianensis</i> (Aublet.)	7	5	1	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0
<i>Terminalia glabrescens</i> Mart.	6	5	1	0	0	0	0	0	1	1	0	1	1	0	0	0	0	0
<i>Platycamus regnellii</i> Benth.	1	4	1	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0

3 ARTICLE 2 - SPATIAL AND TEMPORAL LAND-COVER CHANGES EFFECT ON VASCULAR EPIPHYTE ASSEMBLAGES ACROSS THE NEOTROPICS

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3.1 Abstract

The Neotropics, known for its high biodiversity, faces significant threats from habitat degradation, mainly due to human activities. Anthropogenic degradation leads to loss of quantity and quality of habitat, affecting species diversity and composition, ecosystem services, and ecological interactions. Spatially, while local degradation may lead to high extinction rates, larger-scale degradation limits dispersal and connectivity between populations. Therefore, the scale from which the degradation is originated may define the extent and intensity of their effect. Similar to the spatial approach, the temporal scale also is crucial, once the temporal gap between the degradation event and the consequence could be different according to the species

and also the diversity metrics (e.g., species richness, diversity, and individual abundance). In this study, we explored the impact of habitat degradation on vascular epiphytes (i.e., plants that grow non-parasitically on other plants) across the Neotropics from different spatial and temporal scales. We found that the influence of land cover on epiphyte diversity varied across spatial and temporal extents. Larger spatial extents and longer-term dynamics were more influential in explaining species richness, while current land cover was more influential for abundance. Degradation had complex effects, with negative impacts at small spatial extents but positive effects at larger extents, particularly in natural and semi-natural habitat patches. Arboreal cover showed mixed effects, with both positive and negative associations with epiphyte diversity across different site types. Overall, habitat degradation has significant implications for epiphyte diversity, affecting richness and abundance differently across spatial and temporal scales. Understanding these dynamics is crucial for effective conservation strategies in the face of ongoing habitat degradation in the Neotropics.

Key-words: Diversity, Habitat degradation, Neotropics, Spatial and temporal effects, Vascular epiphyte

3.2 Introduction

Habitat degradation, which comprises any process resulting in loss of habitat quality, is one of the biggest threats to species diversity in the Neotropics (IPBES 2018b). The structural changes in vegetation following degradation can drastically alter microclimate and microhabitats (Senior et al. 2017), resulting in loss of local species diversity and changes in species composition (Newbold et al. 2015, Senior et al. 2017, Tripathi et al. 2021). Habitat degradation is detrimental to well-functioning

ecosystem services (e.g., production of water, carbon sequestration and storage, and erosion; Carlson et al. 2017, Concostrina-Zubiri et al. 2017), ecological interactions (Potapov et al. 2020, Hemprich-Bennett et al. 2021), and species functional diversity (Carneiro et al. 2016). Consequently, the habitat could become permanently vulnerable, being susceptible to cascade effects after the degradation (e.g., invasions of exotic species, Adhikari et al. 2020), compromising the resilience and recovery capacity of the ecosystem (Tang et al. 2020).

The natural disturbance events, leading to habitat degradation (e.g., El Niño, Ingram and Dawson 2005; extreme drought or heat, Elst et al. 2017), are historical and the consequences in the biota can be buffered by species adaptation as a result of previous events, if the event is not extreme. However, habitat degradation as a consequence of anthropic activities tends to change the habitat more drastically, intensely, and fastly than natural ones, being the conversion of natural and preserved habitat to agricultural land the most common anthropic pressure (IPBES 2018a). Anthropic habitat degradation involves many direct non-natural processes (e.g., habitat fragmentation and loss of connectivity, Dai et al. 2019; chemical inputs, Gallardo 2014; introduction of invasive species, Adhikari et al. 2020), which could imply indirect effects such as loss of biodiversity (Heinrichs et al. 2016), substantial carbon enrichment (Rappaport et al. 2018), and the endangerment of ecosystem services (Cancio et al. 2016).

The spatial effect of habitat degradation on species richness and abundance is hard to measure since the magnitude of degradation, as well as its effects on species richness, are scale-dependent (Mendenhall et al. 2014, Arantes et al. 2018). The degradation could be local, decreasing the habitat quality within a habitat patch; and/or regionally at bigger scales, compromising the connectivity among habitat

patches and communities in a landscape. Although the degradation at a local scale could result in high extinction of species at a given locality, some species can recolonize the affected area from surrounding ones, assuming that the habitat patches are still connected and environmentally favorable (Sedell et al. 2015, Nasruddin-Roshidi et al. 2021). However, if the degradation occurs at large scales, dispersal becomes more limited due to the loss of connectivity between populations and communities (e.g., Zimmerman et al. 2022). Nonetheless, the definition of local and regional scales of degradation effects depends on the biology of resident and focal species. If the habitat degradation occurs to a large enough spatial extent to result in loss of connectivity and isolation of species communities, to the point where it is possible to spatially differentiate the communities (e.g., decrease in sharing species, Gray et al. 2004), that extent could be considered as regional for those species.

Additionally, the effect of landscape degradation is also influenced by the characteristics of the habitat patch, such as conservation status and environmental conditions (e.g., water bodies, humidity, temperature, soil). A community could be inserted within a preserved habitat site, but surrounded by degraded landscapes. Therefore, the pressure from the degradation in the surrounding landscape could be partially (or totally) buffered by the characteristics maintained within the habitat patch (e.g., presence of tall trees and canopy cover within the habitat patch: Hazwan et al. 2022, Cudney-Valenzuela et al. 2023). Contrarily, if the habitat patch is degraded (e.g., forest with high canopy openness: Cudney-Valenzuela et al. 2023), or inserted in non-favourable environmental conditions (e.g., non-adequate heat and shade; Poniatowski et al. 2018), the degradation from surrounding areas could have a heightened negative effect, consequently selecting and benefiting more tolerant and

generalist species, and increased rates of specialist species loss (e.g., Lebigre et al. 2022; generalist species: Einzmann and Zotz 2017).

Studies examining the impact of habitat degradation on plant diversity tend to focus on local scales, such as degradation within forest patches (e.g., Ceballos 2020). However, this local approach may obscure the consequences at larger scales. In addition to spatial extents, it is crucial to address the temporal scale. The time lapse between a degradation event, such as a change in land cover, and its effect on the biota can vary depending on the species and habitat (Ladányi et al. 2016, Li et al. 2017). In the short term, resistant and tolerant species (e.g., bird species from open areas, Jirinec et al. 2022) increase their population size after the degradation, while sensitive species (e.g., forest specialists, Levey et al. 2023) show a decrease. As a result, the initial impact of degradation events is predominantly demographic, influencing the size and dynamics of specific species populations (Plass-Johnson et al. 2016), particularly those directly reliant on altered environmental conditions (e.g., desalination affecting annual salt pioneer plants, Ladányi et al. 2016). Furthermore, long-term dynamics reveal significant community-level changes, primarily stemming from short-term population shifts. The loss of native species and the invasion of exotic species post-degradation can trigger an extensive cascade effect, altering the composition of the community (e.g., Moncayo-Estrada et al. 2012) and disrupting ecological interactions (e.g., parasitism, Vidal-Martinez and Wunderlich 2017). Consequently, a comprehensive understanding of both spatial and temporal dimensions is essential for effective conservation strategies in the face of habitat degradation.

The Neotropics, a highly-diverse area comprising the tropical region of South America, Central America, and south of Mexico, is one of the most species-diverse

realms worldwide (Raven et al. 2020). However, the Neotropics have many of the most highly degraded ecoregions of the world, mainly caused by the expansion of the agricultural frontier. The cropland extent in the Americas has greatly increased in the last 300 years, transforming the cover of some native regions into ~90% cultivation areas (IPBES 2018b). Even though many initiatives are carried out to preserve habitat in the Neotropics, e.g., expansion of protected areas, the scenario of increased biodiversity loss risk persists (Laurance et al. 2012). Therefore, it is crucial to understand the effect of anthropic habitat degradation on diversity across many scales to improve the efficiency of resources and actions spent in conservation by politicians and decision-makers.

Our hypothesis posits that the influence of each land cover type on plant species richness and abundance varies across spatial and temporal scales. Specifically, we predict that site naturalness (i.e. the degree of conservation status of the habitat patch, from natural [i.e., preserved at the original state] to degraded [i.e., completely changed and under anthropic influence]) strongly affects richness at small extents, while degradation at landscape scale has a greater impact at large extents. In the case of canopy cover (e.g., forest and shrubland), we expect a positive correlation between spatial extent and its influence on species richness. Additionally, water body cover is expected to consistently exert a positive influence. Lastly, specifically for each naturalness category (i.e. natural, semi-natural, and anthropic), we expect degradation to have a negative effect on plant diversity for natural sites, while neutral or positive for semi-natural and anthropic sites, which are already degraded and the species community resistant to degradation; and canopy cover will have a positive effect in all natural sites. Our temporal hypothesis suggests a stronger impact on plant abundance over a shorter period (e.g., present), reflecting

demographic effects before influencing overall species diversity, therefore, richness being mainly influenced by long-term dynamics (e.g., 10 years).

To comprehensively understand the spatial and temporal impacts of land cover, we used vascular epiphyte species as a model group, analyzing a large Neotropical database (Mendieta-Leiva et al. 2020). Vascular epiphytes (hereafter only “epiphytes”), mechanically-dependent plants that root non-parasitically on other plants never reaching the soil, are one of the most diverse species groups of the tropics (Taylor et al. 2022). Epiphyte plants have a closer dependency on the atmosphere, being the atmospheric deposition their main source of water and nutrients (Gentry and Dodson 1987). Regarding the habitat, epiphytes are highly dependent on vertical structure heterogeneity, i.e. trees' stem density and structure (Page et al. 2009, Ceballos 2020). Since habitat degradation commonly reduces the complexity of arboreal strata, or even removes it, epiphyte species respond quickly, with high rates of species local extinctions after the degradation (Werner et al. 2011), and are unlikely to recover to previous species composition (Cardos et al. 2017). Due to the quick and clear response to degradation in comparison to other plants (e.g., trees and shrubs), epiphyte species are an interesting group to explore the consequences of habitat degradation on biodiversity (e.g., Page et al. 2009, Ceballos 2020).

3.3 Methods

3.3.1 Data description

The data was obtained from the Epiphyte Inventory Group Database (EpiIG-DB v 1.0; Mendieta-Leiva et al. 2020). EpiIG-DB comprises Neotropical vascular epiphyte data (including hemiepiphytes [with early life stages epiphytically but establishing contact with the soil later], nomadic vines/climbers [germinating terrestrially and climbing up

the support with flexible stem], according to classification from Zotz et al. (2021). In total, EpiG includes 18,142 observations (10,553 trees and 7,589 plots) from 77 datasets, sampled in natural (i.e. forests and/or savannas composed of native species), semi-natural areas (i.e. forest and/or grassland composed of non-native species, secondary grasslands, and heathlands in forest biomes), and anthropogenic areas (i.e., vegetation types highly different of the natural vegetation areas) according to Bruelheide et al. (2019).

We used a subset of the EpiG-DB, only including trees where all vascular epiphyte taxa (i.e. Angiosperms and Pteridophytes) were sampled with abundance data (number of individuals or 'stands' following Sanford, 1968, thereafter termed abundance). We selected only holopiphytes and hemiepiphytes (excluding nomadic vines/climbers classified according to Zotz et al. (2021) identified to species level. We spatially aggregated the subset of trees into 30 arc-second grid cells (~ 1 km; *site* extent), and selected grids with at least five trees sampled. The threshold of five trees was chosen based on a good balance between sample sufficiency, the number of grids available for the analysis, and the number of sites' naturalness for each classification (i.e. natural, semi-natural, and anthropic).

To guarantee the inclusion of all spatial and temporal extents in our analysis, we specifically chose grids that were sampled after 2002 (more information in the “degradation metrics” section). We ended up with a total of 2,778 trees (26.3% of EpiG tree relevés) distributed in 97 grids cells across 16 Neotropical ecoregions (based on WWF classification – Olson et al. 2001), comprising 65,095 epiphyte individuals from 764 epiphyte species. For each grid, richness was defined as the sum of species within the grid and abundance as the total of epiphyte individuals.

3.3.2 Degradation metric

We defined habitat degradation as the amount of area covered by non-natural land use (e.g., cropland, urban environment) instead of natural cover (e.g., forest, shrublands, and flooded vegetation), therefore, at landscape level. To define the land cover, we used the rasters from Copernicus Climate Change Service (Buontempo et al. 2022), which includes land cover annually from 1992 to 2020 with a relatively high spatial resolution (pixels with a horizontal resolution of 300m). We consider as degraded areas the pixels classified into “Cropland rain-fed”, “Cropland irrigated or post-flooding”, “Mosaics cropland / natural vegetation”, and “Urban areas”, being the degradation metric the sum of all these groups. For the arboreal cover, we summed all pixels identified as tree cover, shrubland, and the mosaic of trees and shrubs, flooded and not flooded. Lastly, we quantified the number of pixels identified as water bodies as an additional land cover class.

3.3.3 Multi-extent approach

To explore the effect of habitat degradation using a multi-extent approach, we define extents that capture a wide degradation gradient for our studied areas. For the spatial approach, we set five spatial extents, with buffers of 1km, 1.5km, 2km, 3km, and 5km in diameter, surrounding the center coordinates of the grid. We quantified the degradation for each spatial extent by aggregating the number of pixels classified as degraded areas within each buffer.

For the temporal approach, we set three extents: “present”, “five years”, and “ten years”. We considered in “present” the degradation quantified for the year of sampling, while “five years” and “ten years” considered the difference of each land cover from the present to five and ten years before the year sampling date, respectively. Therefore, since the values of five and ten years are relative to the

present, the values were possibly negative, if the specific land cover reduced the amount in a time window, or positive if increased. With the exception of water, we obtained the land-cover values of five and ten years for both degradations and arboreal cover. Additionally, none of the 1km buffers had water cover, resulting in the inclusion of water cover only in the 1.5km, 2km, 3km, and 5km extents.

3.3.4 Statistical analyses

To assess the importance of each land cover and naturalness of the sampled site in epiphyte species richness and abundance across extents, we used variance partitioning analysis ('variancePartition' R package; Hoffman and Schadt 2016). For that, we performed a variance analysis for each spatial extent (i.e., five variance analyses), including the three temporal extents for the respective spatial extent, in addition to the naturalness and number of sampled trees. Naturalness is part of the hypothesis, a fixed factor, whereas the inclusion of the number of trees was only to measure the influence of sampling effort in the final pattern. We considered the "most important" predictors which explained more of the variance for the epiphyte response metrics (species richness and abundance).

Additionally, to explore the significance and direction of the effects (i.e. positive and negative), we performed Generalized linear mixed models ('GLMM'), with Negative Binomial distribution ('glmmTMB' R package, Brooks et al. 2017), including all spatial and temporal extents as fixed effects in the full model. We included the number of sampled trees as random effect, in addition to the ecoregion, to control the variance generated from the sampling effort. Therefore, the full model had 49 predictors (19 land cover for "the present", 15 for "five years", and 15 for "ten years"), and two random effects (ecoregion and sampling effort). In order to reduce the number of predictors, we performed a multicollinearity test ('performance' R package;

Lüdecke et al. 2021), removing all predictors with moderate and high correlation (i.e. $VIF \geq 5$ and ≥ 10 , respectively), starting to the predictors with higher VIF, until the model conserved only low correlated predictors (i.e. $VIF < 5$). Then, with the remaining predictors, we performed a stepwise procedure ('buildmer' R package; Voeten 2023), first checking if the model converged ('order' direction), then carrying out a backward elimination to select the predictors. We reduced only the fixed effects, assuming all predictors had the same chance to be significantly associated with the epiphyte metrics, and conserved both random effects in the final model.

In order to test the hypothesis of natural and semi-natural sites being similarly influenced by land cover, while anthropic sites are differently affected, we performed a GLMM analysis for all grids together, and for three grids subsets: 1) grids with natural sites (hereafter 'NAT'), 2) semi-natural sites (hereafter 'SNAT'), and 3) anthropic sites (hereafter 'ANT'). All analyses were carried out in the R software, version 4.3.1 (R Core Team, 2023).

3.4 Results

3.4.1 Variance explained across extents

While a notable portion of the variance in species richness and abundance remained unexplained, increasing the size of the spatial scale (2, 3 and 5 km) considerably increased the explained variance in species richness. Abundance, on the other hand, was particularly well accounted for at scales of 2 and 5 km (Figure 1; Table 1). Sampling effort, indicated by the number of sampled trees (Figure 1; gray bars), contributed only minimally to the variance in species richness, while for abundance the contribution was relatively high at large spatial scales (3 and 5 km). This suggests that variations in sampling effort among grid cells had a limited impact on the overall pattern (Table 1; *Sampling effort* values).

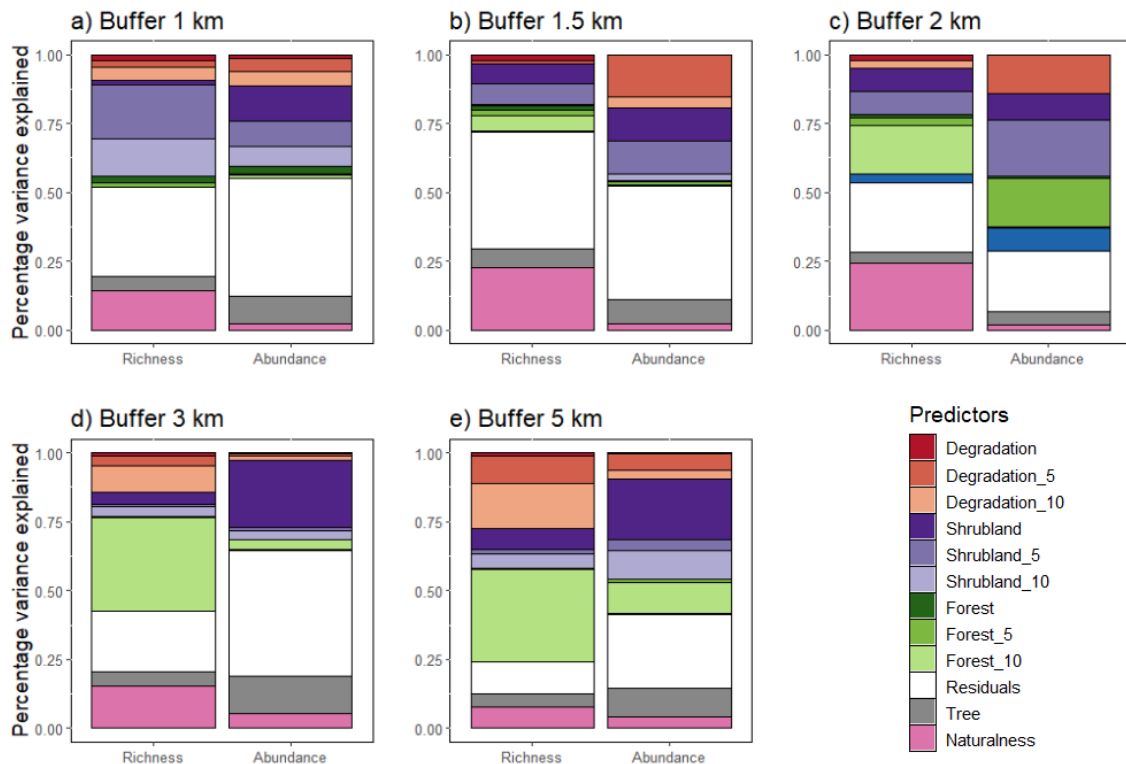


Figure 1: Percentage of variance of epiphyte richness and abundance explained by land-cover predictors, water (blue bars), naturalness (pink bars), and number of sampled trees (tree, gray bars) across scales. Here, all predictors within each spatial scale were included in the analysis. The darkest shade of degradation (red bars), forest (green bars), and shrubland (purple bars) corresponds to the present, intermediate shades to 5 years, and lighter shades to 10 years.

Regarding the spatial scope, land cover increasingly explained more of the variation in species richness with increased observation area (Figure 1; Table 1). In terms of arboreal cover, we observed that while shrubland cover predominantly explained the variance in richness in smaller areas (1 and 1.5 km), forest cover gained prominence at larger extents (3 and 5 km). In the context of degradation, site naturalness was the primary driver of species richness in smaller areas (1, 1.5 and 2 km), as anticipated. However, degradation cover became equally important at a larger extent (3 km) and eventually surpassed naturalness in significance at a big extent (5 km). Conversely, the variance of abundance was predominantly associated with shrubland cover across all extents - although relatively less at a extent of 2 km -

with minor contributions from forest and degradation factors. Notably, naturalness played a negligible role in explaining abundance across all extents.

Table 1: Percentage of variance explained by all predictors for species richness (spp) and abundance (abd) across spatial extents (1, 1.5, 2, 3 and 5 km) and temporal scales (present, 5 and 10 years previously). High values (i.e., ≥ 0.1) from the land-cover predictors are highlighted in red.

		1 km		1.5 km		2 km		3 km		5 km	
		Spp	Abd	Spp	Abd	Spp	Abd	Spp	Abd	Spp	Abd
Degradation	Present	0.02	0.01	0.02	<0.01	0.02	<0.01	0.01	<0.01	0.01	<0.01
	5 years	0.03	0.05	0.01	0.15	<0.01	0.14	0.04	0.01	0.09	0.06
	10 years	0.05	0.05	<0.01	0.04	0.03	<0.01	0.09	0.01	0.17	0.03
Shrubland	Present	0.01	0.12	0.07	0.12	0.08	0.09	0.05	0.24	0.07	0.22
	5 years	0.19	0.09	0.08	0.12	0.08	0.20	<0.01	0.01	0.01	0.04
	10 years	0.13	0.07	<0.01	0.02	0.01	<0.01	0.04	0.03	0.05	0.1
Forest	Present	0.02	0.03	0.01	<0.01	0.03	0.17	<0.01	<0.01	<0.01	<0.01
	5 years	0.01	<0.01	0.02	0.01	0.02	0.17	<0.01	<0.01	<0.01	0.01
	10 years	<0.01	0.01	0.05	<0.01	0.17	<0.01	0.34	0.04	0.33	0.11
Naturalness	-	0.14	0.02	0.23	0.02	0.24	0.02	0.15	0.05	0.08	0.04
Water	-	-	-	<0.01	<0.01	0.03	0.08	<0.01	<0.01	<0.01	<0.01
Sampling effort	-	0.05	0.1	0.07	0.09	0.04	0.05	0.05	0.13	0.04	0.11
Residuals	-	0.32	0.42	0.42	0.41	0.25	0.21	0.22	0.45	0.11	0.27

In terms of the temporal approach, the land cover conditions from 5 and 10 years preceding the year of epiphyte sampling have proven to be more influential in explaining the variation of species richness than the current state of land cover, which is aligned with our hypothesis (Figure 1; Table 1). The majority of the variance in richness is significantly attributed to long-term dynamics (i.e. 10 years), particularly shrubland at a small scale (i.e., 1 km), forest at larger extents (2, 3 and 5 km), and degradation at the largest extent (5 km). Conversely, when it comes to abundance, the current land cover plays a more consistent role, with shrubland cover in the

present explaining a large proportion of the abundance variance across all extents - except at the intermediate extent (2 km), when forest cover in the present rises as one of the main explaining factors.

3.4.2 Effect explained across extents

In general, the impact of land use on epiphyte diversity was more pronounced at larger extents (3 and 5 km) compared to smaller extents (1 and 1.5 km) (see Table 2). Temporary wise, the influence of current land cover was less frequent than that of long-term dynamics, particularly over 10-year periods. Interestingly, the effects of land cover on smaller spatial extents (1.5 and 2 km) were significantly linked to epiphytes only in the present, while larger extents had an effect in the context of long-term dynamics (5 and 10 years). Consistent with our temporal hypothesis, species richness was more influenced by longer-term dynamics than abundance, showing two more associations with the land-cover dynamic over a 10-year period.

Regarding each site's naturalness, we observed a positive association between degradation and epiphyte richness in natural sites, contrary to our initial hypothesis, while anthropic sites exhibited a negative association. Also contrary to expectations, negative associations were found between epiphyte richness and arboreal cover in both natural and anthropic sites. However, for water, we observed the expected positive effects.

Table 2: GLMM results of the land-cover predictors for each diversity metric (i.e. Spp = species richness, Abd = abundance) and each naturalness category. Only significant associations between the predictors and diversity metric are shown (coefficients and SD in parenthesis). Red values indicate negative association between the predictors and epiphyte metrics.

	Temporal	Spatial	Natural		Semi-natural		Anthropic	
			Spp	Abd	Spp	Abd	Spp	Abd
Degradation	Present	1.5km	-	-	-	-	-0.28 (0.08)	-0.41 (0.12)
		5km	-	0.27 (0.12)	-	-	-	-

	5 years	3km	-	0.46 (0.07)	-	-	-	-
	10 years	5km	-	-	-0.28 (0.06)	-	0.26 (0.09)	0.62 (0.12)
Shrubland	5 years	5km	-0.38 (0.13)	-	-	-	-	-
	10 years	5km	0.53 (0.21)	-	-	-	0.38 (0.13)	0.49 (0.17)
Forest	Present	1.5km	-	-	-	-	-0.33 (0.1)	-0.52 (0.14)
	10 years	3km	-	-0.7 (0.26)	0.26 (0.11)	-	-	-
Water	-	2km	-	0.66 (0.22)	-	-	-	-
	-	5km	-	-	-	-	0.13 (0.06)	0.21 (0.08)

3.5 Discussion

We identified a significant association between degradation and epiphyte diversity across various spatial and temporal extents. In general, land cover at large spatial extents (3 and 5 km) accounted for a significantly greater portion of the variability in epiphyte species richness, a trend that is not as evident for abundance. The intermediate spatial extent (2 km) explained a larger portion of the variability in abundance. Regarding degradation, the naturalness class (i.e. natural, semi-natural, anthropic) of the site played a more significant role in determining both epiphyte richness and abundance at small extents. In contrast, degraded land cover emerged as a more influential factor at large extents. Apart from the variability explained, degradation had conspicuous effects on epiphyte diversity across scales (temporal and spatial) and naturalness of the site. In general, degradation had a negative effect at small spatial extents, while it was positive at large extents (except for species richness in semi-natural sites), while arboreal cover (forest and shrubland cover) exhibited no clear pattern. Over time, the escalation of degradation in long-term dynamics (5 and 10 years) indicated an increase in epiphyte species richness and abundance in both natural and anthropogenic areas. Conversely, the rise in degradation in semi-natural areas was associated with a decrease in epiphyte species richness. In contrast, arboreal cover (forest and shrubland cover) yielded more conspicuous results in natural sites (i.e. both positive and negative effects), and

a well-defined pattern in semi-natural and anthropogenic areas (i.e. always positive or negative for each arboreal cover type). The increase in arboreal cover long-term consistently led to an increase in epiphyte species richness and abundance. Comparing diversity metrics, we observed a greater influence from long-term dynamics on epiphyte species richness than on abundance, as anticipated.

The overall impact of habitat degradation is expected to be predominantly negative for biodiversity (Soh et al. 2019). The ongoing changes in land cover emerge as the main concern regarding habitat degradation and its impact on species (Ayyad 2003), mainly due to the effects triggered from the degradation itself. The consequences of land cover changes not only involve a negative effect and an overall decrease in species diversity but also encompass positive influences on a few species. The dominance of tolerant species after degradation poses a significant issue resulting from habitat degradation (Pueyo et al. 2008, Babyesiza et al. 2023), as well as an increased likelihood of affected communities being invaded by exotic species (Cattau et al. 2010, Merson et al. 2019). We observed a positive effect of degradation on epiphyte diversity, particularly in terms of abundance in natural sites. When a natural and preserved site undergoes degradation, there is an anticipated increase in the populations of tolerant and generalist epiphyte species, notably *Tillandsia* spp. (e.g., Flores-Palacios and Garcia-Franco 2006, Einzmann and Zotz 2017, Elias et al. 2021). This increase could potentially lead to an overall rise in assemblage abundance.

In the framework of long-term dynamics, once the community is dominated by a few species, it may undergo a homogenization of functional diversity, even when maintaining a relatively similar number of species (Li et al. 2017). The functional homogenization potentially compromises the habitat resilience and the capacity to

recover the species pool previous to the degradation (de Juan et al. 2014, Nasruddin-Roshidi et al. 2021). Therefore, while abundance could be overall positively influenced by degradation, the species richness is expected to decrease, followed by a functional homogenization (Ibarra and Martin 2015, Smith et al. 2020). We found a decrease in species richness as a consequence of degradation in semi-natural sites over long-term dynamics, while there was a positive effect in anthropogenic sites. Once a site retains few preserved aspects, i.e., semi-natural sites, it is expected that those sites harbor a few forest-specialist species, which are still sensitive to habitat degradation (e.g., (Liu et al. 2010, Brüggeshemke et al. 2022). Therefore, although not as strongly negative as in natural sites, the species occurring in the semi-natural sites are equally negatively affected by degradation, as we observed. On the other hand, the prevalence of generalist species in degraded sites is higher than in natural and semi-natural ones (Julliard et al. 2006, Prati et al. 2022). Once the degraded site also presents degraded areas in the landscape surrounding it, it is more likely to receive more generalist species from associated nearby habitat patches, increasing not only in abundance but also slightly in the number of species, with changes in composition (Julliard et al. 2006, Godó et al. 2017).

We observed both the anticipated positive effects and unexpected negative effects of arboreal cover on epiphyte species richness and abundance. The negative effect of increased forest cover in anthropic sites aligns with expectations, once sites are degraded they are typically dominated by xerotolerant and generalist species, not as widely abundant in forest habitats as in the degraded ones (Einzmann and Zotz 2017). For natural sites, the negative association between the increase in forest cover and epiphyte abundance may be attributed to the reduced availability of open

habitats within forest patches, resulting in a decline in the abundance of xerotolerant and open-environment-adapted epiphytes within forest and natural sites (Coote et al. 2008, Ventre-Lespiauq et al. 2017). However, although plausible, this strong observed association is possibly not solely explained by this factor.

Concerning shrubland, the impact of shrubland cover dynamics on epiphyte species richness was negative in short-term dynamics but positive in the long-term. Shrublands, being more open environments compared to forest habitats, can accommodate both epiphyte generalists and xerotolerant species, as well forest species (e.g., Michel et al. 2010, Aragon et al. 2015). However, shrublands generally host less diversity than forest habitats, with specific functional types (Simijaca et al. 2023). If the expansion of shrubland coverage is associated with the forest habitat, there may be an increase in the regional species pool richness due to increased habitat heterogeneity at landscape scales (e.g., de la Rosa-Manzano et al. 2019, Morales-Linares et al. 2022). Nonetheless, if the expansion continues and potentially results in a decrease in forest cover, leading to landscape homogenization, the regional species pool could shrink, becoming restricted to species found in shrublands. However, while plausible, further analyses are required to confirm this secondary hypothesis.

In general, we emphasize the contribution of both small and large spatial extents to epiphyte assemblage diversity. While large spatial extents consistently show associations with both epiphyte species richness and abundance, small extents are crucial to complement our understanding of the effects of land-cover dynamics on epiphyte diversity. In terms of degradation, the naturalness of the site is highly significant at smaller scales, with degraded land-cover becoming more influential for epiphyte diversity at larger scales. In temporal terms, both short and long-term

dynamics contribute, but notably, short-term dynamics play a more decisive role in abundance, while long-term dynamics have a greater impact on species richness and potentially influence species composition. Therefore, we recommend investigating land-cover effects across various spatial extents and temporal scales, with an emphasis on larger spatial extents and temporal scales as they appear to be more influential on vascular epiphyte assemblages. By extending conservation efforts to larger scales and considering the degradation of land-cover dynamics over the last 10 years; these efforts not only benefit epiphytes, as “umbrella” species, but also encompass all directly and indirectly associated species.

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4 ARTICLE 3 - LARGE-SCALE NEOTROPICAL EPIPHYTE RICHNESS IS DRIVEN BY CLIMATE AND INDIRECTLY THROUGH ABUNDANCE

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4.1 Abstract

1. Understanding the mechanisms underlying spatial patterns of biodiversity is crucial given current scenarios of climate change and landscape modification. One potential driver of species richness is the energy available, which could influence it directly or indirectly through abundance. The latter is the central prediction of the more-individuals hypothesis (MiH). However, climate can also directly affect diversity, and disentangling direct and indirect abundance-driven climate effects is challenging. We expected geographic patterns of diversity to be strongly related to climate because epiphytes are coupled to climatic conditions.

2. We modelled climatic drivers of vascular epiphyte diversity in the Neotropics and analysed diversity patterns. We constructed structural equation models exploring the effect of climatic predictors on species richness and abundance and the relationships between richness and abundance. The analysis was conducted for all epiphyte species together and for orchids, bromeliads and Pteridophytes separately.

3. Climate variables predicted abundance and species richness partially in opposite directions. Abundance responded more strongly to climate than species richness for all epiphyte species and taxonomic groups. Abundance was positively related to species richness for all groups except for bromeliads; however, species richness was always more strongly related to the climatic variables than to abundance, refuting the hypothesis that the climatic effect on species richness is mediated by abundance.

5. *Synthesis:* We demonstrate that the mechanisms behind diversity patterns differ between taxonomic groups. Although the effect of climate on species richness was not mediated by abundance, as predicted by the MiH, abundance was positively related to species richness. This positive effect of abundance on species richness, in line with the MiH, provides an essential step to understanding the mechanisms leading to large-scale patterns of epiphyte diversity in the Neotropics.

Keywords: biodiversity, cloud cover, more-individuals hypothesis, Neotropics, precipitation, temperature, vascular epiphytes.

4.2 Introduction:

Understanding the spatial patterns of biodiversity is a central goal in ecology and biogeography and is crucial to deal with ongoing biodiversity loss due to global change (Newbold et al., 2015; Peters et al., 2019). Several factors may explain

plant-diversity gradients globally, such as habitat heterogeneity (Ricklefs, 1987; Shmida & Wilson, 1985); geological and climatic history (Jetz, Rahbek, & Colwell, 2004; Ricklefs, 1987); and contemporary climatic conditions (Clarke & Gaston, 2006; Field, O'Brien, & Whittaker, 2005; Wiens & Donoghue, 2004). Although these factors may act synergistically, some studies have shown that contemporary climate, particularly water and energy dynamics, play a dominant role in determining diversity for angiosperms and other vascular plants (Francis & Currie, 2003; Kreft & Jetz, 2007).

One important productivity-related hypothesis to explain biodiversity patterns is the "more-individuals hypothesis" (MiH - Srivastava & Lawton, 1998), which predicts that the higher the energy available in an environment the higher the biomass or number of individuals which may allow equilibrating population sizes thereby reducing the probability of local extinction. Thus providing a mechanistic link between abundance and species richness (Srivastava & Lawton, 1998; Wright, 1983; Clarke and Gaston, 2006). First, the term "energy" needs to be clarified. In contrast to consumers, for which available energy may be defined by their food (i.e. primary productivity for herbivores and prey biomass for carnivores), the "energy" available to plants consists primarily of light, or more specifically photosynthetically active radiation (PAR); the small fraction of PAR used by plants is strongly regulated by water availability and temperature, therefore plant diversity is not correlated to light or determined temperature and water availability alone (Clarke & Gaston, 2006). Thus, the usefulness of the MiH to understand plant diversity patterns has been questioned because of the difficulty in defining available energy for plants and linking it to an increase in biomass and/or abundance and to a subsequent increase in species richness (Clarke & Gaston, 2006). Although the general importance of climatic

predictors as drivers of plant diversity is well established (e.g. for trees: Currie et al., 2004; Šímová et al., 2011; for ferns and lycophyte: Weigand et al., 2020), the link through abundance has been shown in some cases (e.g. Currie et al 2004, Pautasso and Chiarucci 2008, Simova et al 2011), thus there is use in the MiH to understand plant diversity patterns. Therefore, the use of climate-related variables as energy proxies is justified in this case. Current studied patterns for plants are biased towards some taxonomic groups or life forms, such as trees or terrestrial plants. Other ecologically important groups, such as vascular epiphytes, remain strongly under-represented in global databases and, consequently, drivers of their diversity patterns, at a large-scale, which may well differ from those of e.g. trees, are much less understood.

Vascular epiphytes are structurally dependent plants that root non-parasitically on other plants (mostly trees); they are most abundant in the tropics but are also found in the subtropics (Zotz, 2016). Epiphytes contribute significantly to vascular-plant richness, ca. 9-10% globally (Taylor et al., 2022) and up to 50% locally (e.g. Kelly, Tanner, Lughadha, & Kapos, 1994). They also fulfil critical ecological functions in the ecosystems they inhabit (e.g. provide resources and habitat for arthropod fauna, Stuntz, et al. 2002; nesting site to birds, Seidl et al. 2020) and influence forest hydrology and nutrient fluxes (Gotsch, Nadkarni, & Amici, 2016; Mendieta-Leiva et al., 2020; Zotz & Bader, 2009; Zotz & Hietz, 2001).

Epiphyte diversity is considered to be primarily determined by climatic factors because epiphytes have no direct contact with the soil and are thus strongly coupled with the atmosphere, from which they capture water and nutrients via depositions (Feild & Dawson, 1998). Therefore, when looking at trait syndromes, epiphytes clearly distinguish themselves from trees and most non-epiphytic herbs, mainly in

traits related to water relations (Hietz et al., 2022). Although many epiphyte species are adapted to non-favourable conditions (e.g. aridity), water restriction correlates negatively with epiphyte species richness since few species can withstand long periods without water (Menini Neto, Furtado, Zappi, de Oliveira, & Forzza, 2016; Werner, Koster, Kessler, & Gradstein, 2011). Temperature limits the latitudinal and elevational distribution of vascular epiphytes (Sylvester, Sylvester, & Kessler, 2014; Zotz, 2016). At a global scale, temperature constraints epiphytes to the subtropics and more so to the tropics (Taylor et al. 2022). Regionally, at higher elevations, low temperatures and frost events limit the occurrence and growth of several plant species (e.g. Clarke & Gaston, 2006; Keil & Chase, 2019). Extreme high temperatures can restrict epiphyte distribution by increasing water stress, especially in seasonally dry environments (Benzing, 1990; Zotz & Hietz, 2001). Climatic conditions known to promote epiphyte diversity are intermediate temperatures and precipitation/humidity with low seasonal variation (Gentry & Dodson, 1987; Hernández-Rojas et al., 2020; Kreft, Koster, Küperr, Nieder, & Barthlott, 2004; Krömer, Acebey, Kluge, & Kessler, 2013; Taylor et al., 2022). More specifically, at regional scales, it has been shown that there is a positive relation between total annual precipitation and cloudiness with the abundance and species richness of epiphytic plants (e.g. Kessler, Kluge, Hemp, & Ohlemuller, 2011; Zotz, 2016). These insights regarding the relationship between climatic-related variables and epiphytes are based on a few regional studies. To date, there is no overall understanding of how climatic drivers determine epiphyte diversity patterns at a large scale, e.g., the whole of the Neotropics. Data at a continental scale has become recently available (Mendieta-Leiva et al., 2020), allowing us to test whether local patterns hold at continental or larger scales.

A more favourable climate (e.g. higher water availability and mild temperatures) may affect diversity by allowing more individuals to coexist, in contrast to marginal climates where only specialist species (e.g. drought-tolerant, frost-tolerant) could survive (Chu et al., 2019; Sylvester et al., 2014). However, favourable conditions, i.e. those allowing high primary productivity and high numbers of individuals, may lead to reduced diversity because of strong competition (e.g. Sammul, Oksanen, Mägi, & Lundberg, 2006), which implies that the MiH may not be supported in those conditions as expected (Furness, Garwood, Mannion, & Sutton, 2021). For epiphytes, by contrast, competition is thought to be of lesser importance, because of the dynamic nature of the substrate (Spruch et al 2019). For instance, old growth (ca. 20 years old) palm trees showed no sign of saturation of epiphyte individuals under favourable environments (e.g. primary rainforest, Zotz and Vollrath 2003), indicating low competition for space among epiphyte species in favourable climate. The strong association with climate related variables and the implied negligible effect of competition make vascular epiphytes especially interesting to test the predictions of the MiH since the positive effects of more individuals on species numbers may not be counteracted by the negative effects of increased competition. The MiH may thus be a useful framework for understanding patterns of epiphyte diversity.

To test the MiH for the diversity of vascular epiphytes, we modelled the direct and indirect relationships of climate predictors (i.e. energy proxies in the MiH conception) with vascular epiphyte diversity at the Neotropical scale. The specific aim of this study was to test the following hypotheses for vascular epiphytes (hereafter only epiphytes): there is a positive relationship between (i) species richness and (ii) abundance with energy (i.e. water availability and temperature); (iii) an additional

positive and direct relationship between species richness and abundance; and (iv) a stronger relationship between abundance and energy, as well as between species richness and abundance, than the direct relationship between species richness and energy variables. Additionally, we assessed whether the climatic influence on epiphyte diversity differs amongst the most species-rich groups: Orchidaceae, Bromeliaceae, and Pteridophytes. We expected that variables important for diversity and their effect may differ amongst these groups, due to their ecophysiological particularities (Crayn, Winter, & Smith, 2004; Zotz & Asshoff, 2010).

4.3. Materials and Methods

4.3.1 Data preparation

We obtained the epiphyte data from the Epiphyte Inventory Group database (EpiG-DB v 1.0; Mendieta-Leiva et al., 2020; see Table S1 in Supporting Information). This EpiG-DB comprises data of vascular epiphytes on 18,142 relevés (10,553 trees and 7,589 plots) from 77 datasets. We used a subset of EpiG-DB restricted to trees sampled in natural (i.e. forests and/or savannas composed of native species and preserved in the natural stage) and semi-natural areas (i.e. forest and/or grassland also composed of non-native species, but keeping the spatial structure of the natural stage), according to Bruelheide et al. (2019). This selection excluded data from plantations, plot-based (instead of tree-based) datasets, or those reporting only presence/absence or frequency (instead of abundance). We included trees for which data at the epiphyte species or morphospecies level is available and includes epiphyte abundance (number of individuals or 'stands' following Sanford (1968), thereafter termed individuals). Within these trees, we included only holoepiphytes and hemiepiphytes (classified according to Zotz et al., 2021). After

subsetting the data, a total of 4,292 host trees (40.1% of the trees in the EpIG database; 73% from natural and 27% from semi-natural areas), with 113,569 epiphyte individuals (42.5% of EpIG) were analysed. These belonged to 1,175 epiphyte species (37.8% of EpIG), of which 21% were morphospecies from 41 families.

We spatially aggregated trees into 30 arc-second grid cells (~ 1 km) distributed across 22 ecoregions (based on WWF classification – Olson et al., 2001) in the Neotropics. To avoid spurious results, we included only grid cells that contained a sufficient number of trees for the analyses (sampling effort). The threshold of 10 host trees for sampling effort was a good balance between sample sufficiency and the number of grid cells available for the analyses; a larger threshold would have resulted in a drastic reduction of the number of grid cells, while a lower threshold would have increased random variation, and also did not drastically increase the number of grid cells. This aggregation and filtering resulted in 69 grid cells containing 4,215 host trees and 102,163 epiphyte individuals (see Figure S1 and S2). Richness was defined as the total number of epiphyte species, and abundance as the total number of epiphyte individuals in a grid cell. We tested for spatial autocorrelation of epiphyte species richness and abundance within our grids, there was no discernible spatial autocorrelation, suggesting an absence of any underlying spatial distribution pattern (i.e. $p < 0.05$ from Moran's test; 'ape' R package [Paradis & Schilep, 2019]).

We carried out analyses for all epiphyte species and, separately, for the three particularly species-rich epiphyte taxonomic groups, representing 73.6% of all epiphyte species and 85.6% of all individuals: Orchidaceae, Bromeliaceae, and Pteridophytes (Table 1). Beside being the most diverse groups for vascular

epiphytes, these three groups are the main division for vascular epiphyte species according to crucial differences in traits, being “stomatal density abaxial”, “guard cell length”, “leaf water content” and concentration of leaf nutrients (e.g., nitrogen, phosphorus) the most distinguishing traits for this separation (Hietz et al., 2021).

TABLE 1. Summary of the data used for the analyses for all epiphyte species and groups. The number of grid cells shows the number used for the analyses, i.e. those grid cells with ten or more trees with adequate epiphyte data. The number of trees (sampling effort), species richness, and abundance (number of individuals) represent the sum within the grid cells. Values in parentheses are the percentage of data used in the particularly species-rich epiphyte taxonomic groups from all species.

	Number of grid cells	Number of trees	Epiphyte species richness	Epiphyte abundance
All species	69	4215	1175	102,163
Orchidaceae	48 (69.6)	1820 (43.2)	479 (40.1)	29,752 (29.1)
Bromeliaceae	54 (78.2)	2390 (56.7)	136 (11.6)	34,555 (33.8)
Pteridophyte	53 (76.8)	2142 (50.8)	250 (21.3)	23,142 (22.6)

4.3.2 Climatic variables

For large-scale analyses, these climate factors usually are measured by mean annual temperature and precipitation, or actual evapotranspiration (Clarke & Gaston, 2006; Currie, 1991), in the sense of climate predictors as energy proxies allowing a higher abundance and possibly a higher diversity. We selected the predictors for the models from a total of 22 environmental variables (Table 2). We used the 19 climate variables from the CHELSA global climate database V1.2 (Karger et al., 2017;

available at <http://chelsea-climate.org/>) to characterise precipitation and temperature conditions. Additionally, we included "Mean Annual Cloud Cover Frequency" (Wilson & Jetz, 2016), "Global Aridity Index" (Trabucco & Zomer, 2019), and "Potential Evapotranspiration" (PET; Trabucco & Zomer, 2010). Climate variables were extracted per 30 arc-second grid cells.

4.3.3 Selection of climatic variables

We selected climatic variables for the analysis based on their importance for epiphyte diversity according to the empirical literature (total of 22 climate predictors, Table 2). To reduce the number of climate predictors, we first evaluated the importance of the variables in determining the main axes of variation in a Principal Component Analysis, and selected the main predictors for each axis (i.e. explaining at least 25% of the variation [PC1, PC2 and PC3]; see Table S2). Second, we selected only non-correlated predictors from the previous selected. The criterias to select the non-correlated predictors were: 1) If a priority predictor (*bold predictors*, Table 2) was correlated with a non-priority, we selected the priority one; 2) if two priority predictors were correlated, we selected the predictor with higher order PCA axis value. The selected predictors and the criteria used in the selection are available in the Table S3.

TABLE 2. List of climatic predictors used for variable selection and their source. Priority variables, i.e. those known to be important for epiphyte richness according to empirical studies, are in bold italics.

Climatic predictors	Data source
<i>Annual precipitation (APr)</i>	Karger et al. (2017)
<i>Mean annual cloud cover frequency (ACF)</i>	Wilson & Jetz (2016)
<i>Mean annual air temperature (MAT)</i>	Karger et al. (2017)
<i>Global Aridity Index (GAI)</i>	Trabucco & Zomer et al. (2019)
<i>Precipitation seasonality (PrS)</i>	Karger et al. (2017)
<i>Temperature seasonality (TeS)</i>	Karger et al. (2017)

<i>Potential evapotranspiration (PET)</i>	Trabucco & Zomer et al. (2019)
Precipitation amount of the wettest month (PrWeM)	Karger et al. (2017)
Precipitation amount of the driest month (PrDrM)	Karger et al. (2017)
Mean monthly precipitation amount of the wettest quarter (MPrWeQ)	Karger et al. (2017)
Mean monthly precipitation amount of the driest quarter (MPrDrQ)	Karger et al. (2017)
Mean monthly precipitation amount of the warmest quarter (MPrWaQ)	Karger et al. (2017)
Mean monthly precipitation amount of the coldest quarter (MPrCoQ)	Karger et al. (2017)
Mean daily maximum air temperature of the warmest month (MTeWaM)	Karger et al. (2017)
Mean daily minimum air temperature of the coldest month (MTeCoM)	Karger et al. (2017)
Mean daily mean air temperatures of the wettest quarter (MTeWeQ)	Karger et al. (2017)
Mean daily mean air temperatures of the driest quarter (MTeDrQ)	Karger et al. (2017)
Mean daily mean air temperatures of the warmest quarter (MTeWaQ)	Karger et al. (2017)
Mean daily mean air temperatures of the coldest quarter (MTeCoQ)	Karger et al. (2017)
Mean diurnal air temperature range (MDT)	Karger et al. (2017)
Isothermality (Iso)	Karger et al. (2017)
Annual range of air temperature (ART)	Karger et al. (2017)

4.3.4 Statistical analyses

We used structural equation models to explore the direct and indirect effects of climatic variables on epiphyte richness and abundance ('piecewiseSEM' R package – Lefcheck, 2016). The Piecewise SEM expands upon the traditional SEM by including nonlinear equations for non-normal response variables. For the SEMs, we built generalised linear mixed models (GLMMs), with Poisson distributions, using the selected climatic variables (see the Table S3) to explain the variation of (a) species richness and (b) abundance for each group (all species, orchids, bromeliads, and

Pteridophytes). The models were built using the 'lme4' R package (Bates, Machler, Bolker, & Walker, 2015). Climatic variables were specified as fixed effects, while ecoregion (WWF classification – Olson et al., 2001) was specified as a random effect in order to control for regional effects (e.g. historical events) as the grid cells were aggregated in ecoregions. The number of sampled trees and the mean DBH of trees within a grid cell were included as fixed effects to control for the influence of sampling effort, following Wolf, Gradstein, & Nadkarni (2009). Also, for the richness model, we included abundance as a fixed effect to test hypotheses three and four (influence of abundance on species richness), besides the climatic influence.

For each of the models specified, all continuous predictors were standardised to mean 0 and standard deviation 1. We built bootstrap confidence intervals by resampling, i.e. taking random subsets of our grid cells, 1000 times using the 'boot' R package (Davison & Hinkley, 1997; Canty & Ripley, 2021). To extract standardised path coefficients, we used the "piecewiseSEM" package (Lefcheck, 2016). All analyses were carried out with R Statistical Software, version 3.6.1. (R Core Team, 2021).

4.4. Results

Our results suggest that the MiH does not explain large-scale diversity patterns of vascular epiphytes in the Neotropics. Generally, water availability-related variables positively affected epiphyte abundance and richness, while the effect of temperature-related variables on species richness and abundance was mostly negative (Figure 1 and Figure 2; see Table S4). Although the expectation that the effect of *climatic variables on abundance* would be stronger than of *abundance on richness* was generally the case, the expectation that these effects would be stronger than the effect of *climatic variables on richness* was not the case for all epiphyte

species and per taxonomic group. That is, abundance did not mediate the effect of climatic variables, the energy proxies, on species richness. Moreover, contrary to the expectation that water availability-related predictors would have the strongest effect on epiphyte diversity, the climatic predictors with the strongest effect on diversity were temperature-related variables for all epiphyte species and the taxonomic groups. Finally, for all epiphyte species, all seven climatic predictors included in the model (i.e. three related to water availability and four related to temperature) affected species richness and/or abundance, except for temperature seasonality (Figure 1 and Figure 2a).

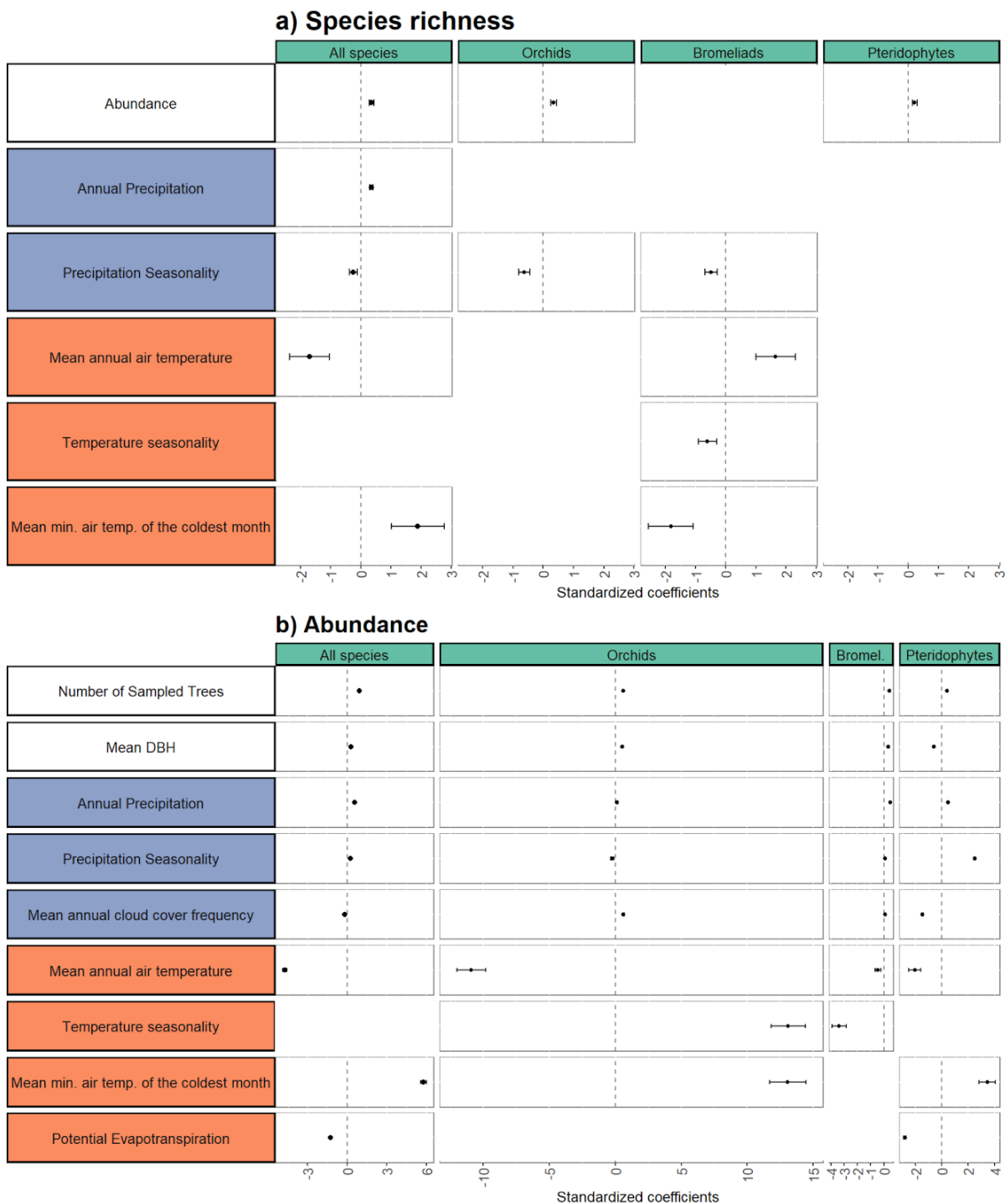


FIGURE 1. Results from GLMMs illustrate the relative importance of climatic variables in explaining species richness and abundance. Standardised coefficients are shown, and the sign of the estimate shows the direction of the effect. Error bars show bootstrap confidence intervals, indicating significant effects when not overlapping with zero. Mean DBH and sampling effort (number of sampled trees in the grid cell) are variables related to the methodology – clearly, grid cells with a higher sample effort

and larger trees yielded higher abundances, while richness effects were found only for all species (positive with mean DBH) and Pteridophytes (negative with sample effort).

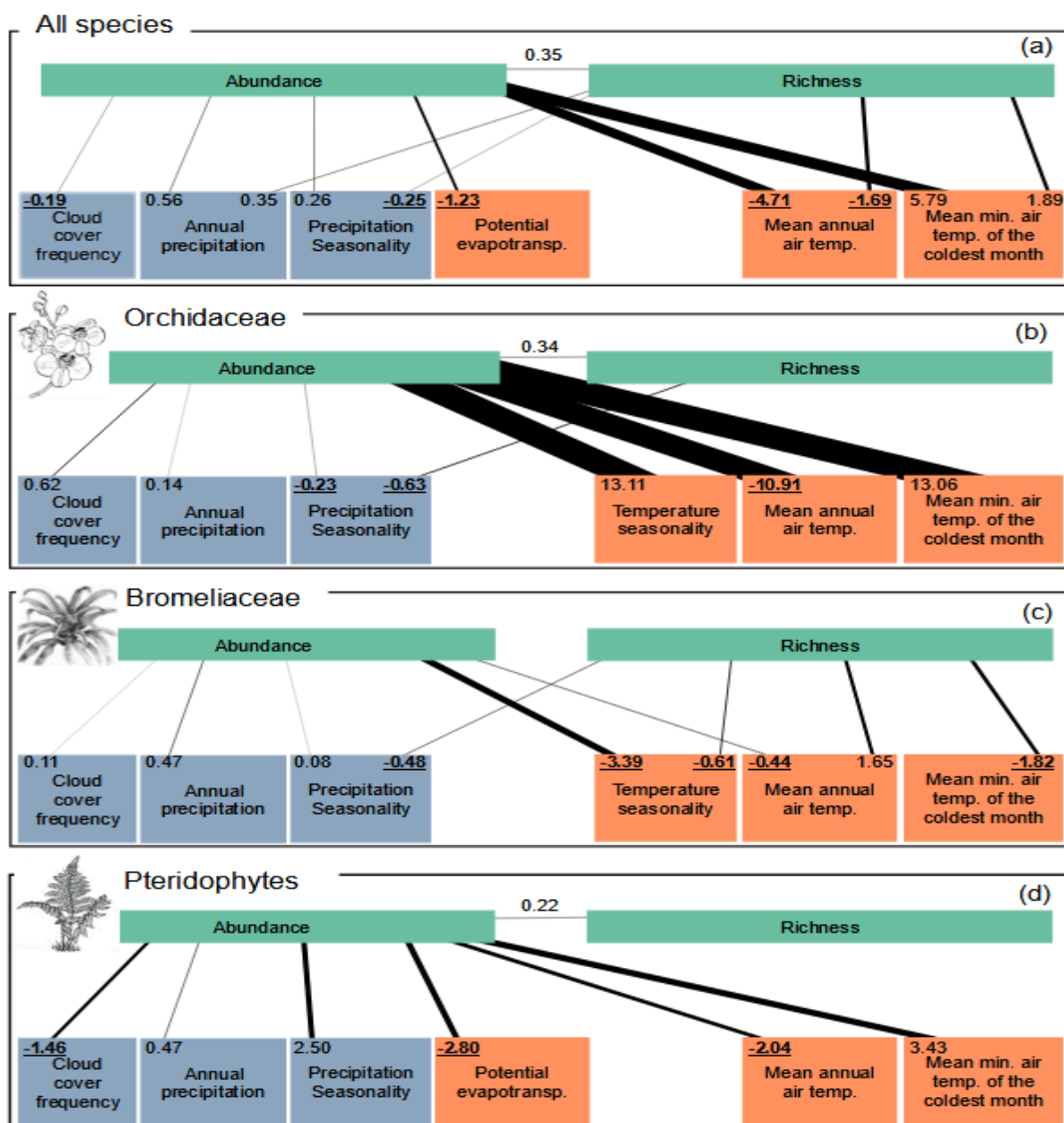


FIGURE 2. Structural equation models for a) all epiphyte species, b) Orchidaceae, c) Bromeliaceae, and d) Pteridophytes. The blue boxes show "water availability predictors" and orange boxes show "temperature predictors", and the green boxes show epiphyte species richness and abundance. The widths of the arrows indicate the strength of the effect, as shown also by the numbers, which are standardised path coefficients (positive values indicate positive relationships; negative values [bold and underlined] indicate negative relationships). Detailed model outputs with bootstrap confidence intervals can be found in Figure 1 and Table S4.

Temperature-related variables had the strongest effect on species richness and abundance when looking at all epiphyte species and the taxonomic groups, with comparable effects on species richness and abundance in all groups except for orchids, for which the effect was relatively much stronger than on other groups. Differences in their effect on the response variables were shown by the mean annual air temperature which varied greatly in terms of direction and strength; its effect on species richness was linear and negative, while in abundance it was unimodal, with the lowest abundance at ca. 16 °C (Figure 3). Also, the mean daily minimum air temperature of the coldest month was positively related to abundance and species richness, although with differing size effects, whereby they started increasing above ca. 10 °C (Figure 3). Finally, potential evapotranspiration had a negative but relatively small effect, although only in abundance.

The three predictors of water availability were significantly related to abundance and species richness, except for cloud cover frequency for species richness. Annual precipitation showed the strongest effect on species richness and abundance amongst water-related predictors, in both cases, with a positive and linear relationship. Precipitation seasonality was negatively associated with species richness, as expected. However, for abundance, the effect of precipitation seasonality was positive, although relatively weak. Similarly, contrary to the expectation, the effect of cloud cover frequency was slightly negatively related to epiphyte abundance. In addition to the effects of the climatic variables, abundance was also positively related to species richness for all epiphyte species.

Overall, for the taxonomic groups, temperature predictors influenced the abundance of all groups, and each temperature predictor had a consistent effect (positive or negative) across groups. However, considering the effect on species

richness, only Bromeliaceae was affected by temperature-related variables reflecting high values: regions with high annual mean temperature, the warmest, coldest month, and non-seasonal temperature had more bromeliad species. Considering water-related predictors, annual precipitation was always positively related to the abundance of epiphyte groups, while precipitation seasonality had opposite directions in its effect; it was always negatively related to species richness (orchids, bromeliads); however, high precipitation-seasonal places notably harbour more individuals of Pteridophytes. Although temperature seasonality had an opposing effect on abundance for bromeliads (positive) and orchids (negative), predictions showed a comparable increase of individuals in very low and high precipitation-seasonal areas, although very mild on bromeliads in contrast to orchids (Figure 3). Finally, cloud cover frequency had a positive relationship with the abundance of orchids and bromeliads but a relatively strong negative association with Pteridophyte abundance. Additionally to the effect of climatic variables, abundance was positively associated with the species richness of orchids and Pteridophytes, but not with bromeliads.

Some results were unexpected. For example, there was a negative effect of cloud cover frequency and a positive effect of potential evapotranspiration on abundance for all epiphyte species, although both are relatively weak (Figure 2a). However, these results are clearly driven by the abundance of Pteridophytes (Figure 2d). Additionally, mean diameter breast height was positively associated with abundance, except for Pteridophytes, for which the relationship was negative, although the effect was small.

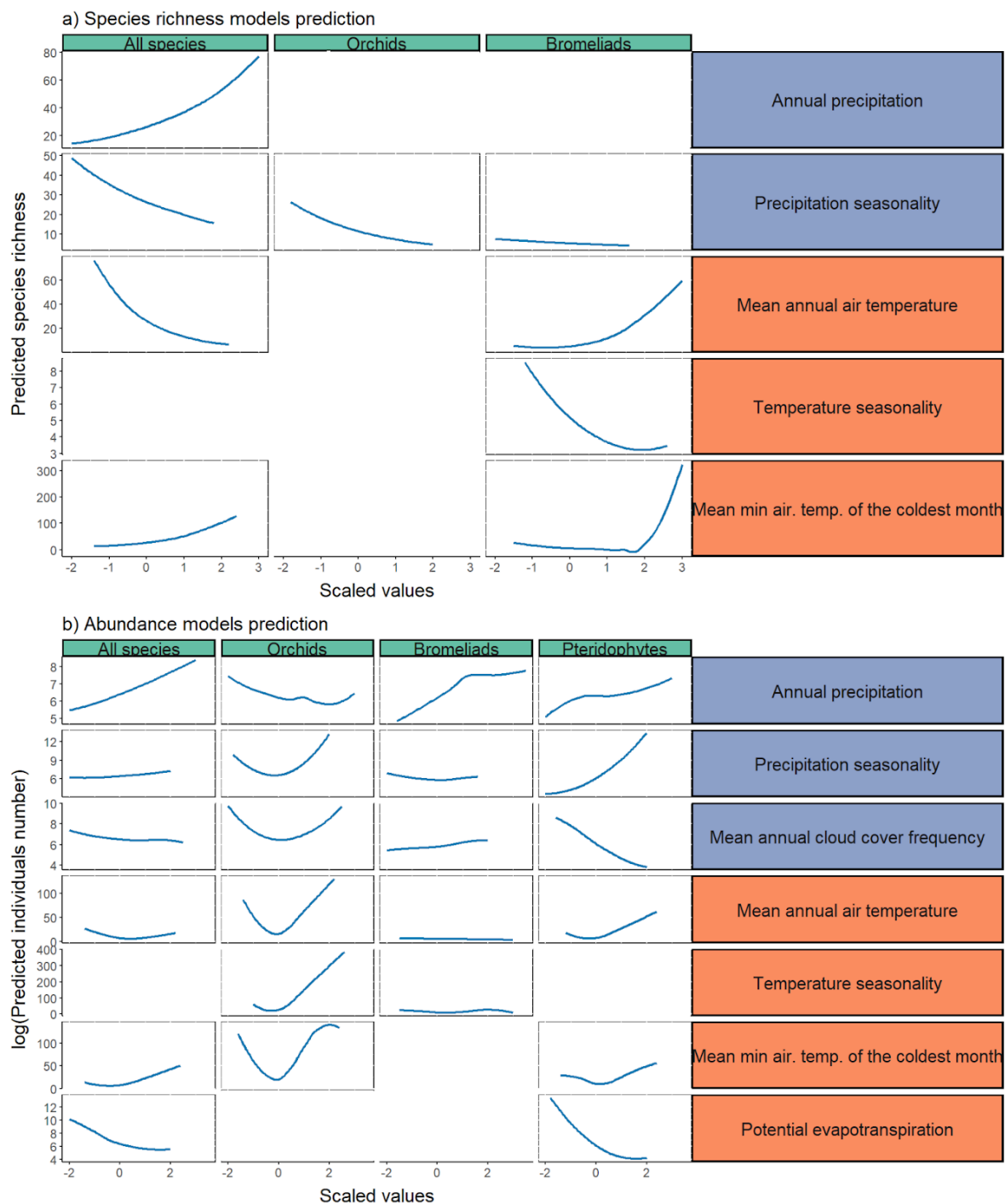


FIGURE 3: GLMMs predictions of (a) species richness and (b) abundance models bootstrap. The predictions are limited to real value ranges of climate predictors, but presented as scaled values.

4.5 Discussion

Our study is one of the few testing the MiH for plants and the first to test it for vascular epiphytes. Our findings did not support the MiH for vascular epiphytes.

Climatic variables had the strongest effect on *abundance*; however the relationship between *abundance* and *richness* was not stronger than that between *climatic variables* and *richness*. Although abundance had a positive effect on species richness, but not for bromeliads, the direct influence of climate remained more important than the indirect effect via abundance for all species, orchids, and bromeliads. However, for Pteridophytes, there could be an indirect effect of climate through abundance, although a link between climate and richness was not apparent.

For plants, the MiH has been tested on trees, shrubs, and understory herbs, for which independent and positive relationships between climatic predictors and species richness and abundance were relatively consistent (Chu et al., 2019; Currie et al., 2004; Dormann et al., 2020; Šimová et al., 2011). For instance, a global study on trees found climatic variables as the best predictors of richness (e.g. minimum temperature and precipitation), while productivity metrics performed poorly (Šimová et al., 2011). Vascular epiphyte richness, thus, can be compared to richness of terrestrial vegetation at a large scale, since we found a consistent relationship between species richness and abundance of epiphytes with temperature- and water-related variables. In most cases, the mechanistic link between richness and energy proxies (such climatic variables for terrestrial vegetation), was not abundance (or otherwise productivity), although the findings are not consistent. For instance, an increase in the number of individuals may result in higher richness for trees at a regional (e.g. Currie et al. 2004; Pautasso and Chiarucci, 2008) and at a global scale (i.e. Šimová et al 2011); however, the main mechanistic link generally were climatic variables (Šimová et al. 2013). Our results were similarly inconsistent, since more individuals indeed represent more species (except for bromeliads), although, similarly

to trees (i.e. Currie et al., 2004), the climatic variables had the strongest effect on richness.

Our study at the Neotropical scale reinforces findings from local to regional-scale studies pointing out the important role of moderate temperatures, but also water availability for vascular epiphyte species richness (i.e. Gentry & Dodson, 1987; Kreft et al., 2004; Weigand et al., 2020, Hernández-Rojas et al., 2020; Kessler, 2002; Krömer et al., 2005).

Gentry & Dodson (1987) were the pioneers in highlighting annual precipitation as a promoter of high local epiphyte richness across the Neotropics. Based on the species richness of local florules from forests in Ecuador, Costa Rica and Panama, along a gradient of precipitation, they concluded that vascular epiphytes decrease more drastically in drier areas than any other habit group does. Although we showed that increasing precipitation in amount but decreasing in seasonality leads to an increase in richness, the effect size was on average six times smaller than that of mean annual air temperature. Therefore, it is clear that water availability has a moderate but complementary effect on epiphyte richness; the pattern, in the case of precipitation seasonality, was strongly influenced by orchids, which has been observed for epiphyte richness elevational patterns (Kreft et al. 2004). This complementary effect of humidity-related variables was much less for abundance, as the difference in the strength of the effect between the variables with the strongest effects was ten fold.

Gentry and Dodson (1987) proposed the “middle elevational bulge” whereby epiphytes have a general tendency to be better represented between 1000 and 2000 m asl., with certain latitudinal variation or heterogeneity. Kreft et al. (2004) used occurrences from 16 inventories of epiphytes in Neotropical forests to show the

positive and negative correlation between epiphyte richness and mean annual precipitation and number of dry months (< 100 mm precipitation), respectively. Kreft et al. (2004) were the first to produce evidence supporting the rainfall-diversity hypothesis from Gentry and Dodson (1987), and further suggested precipitation seasonality as an equally important factor; although our findings support very well these previous conclusions, we put forward temperature related variables as the most important factor driving epiphyte richness at the Neotropical scale, but with a certain degree of uncertainty. At a smaller scale, both Kessler (2000) and Krömer et al. (2005) comprehensively sampled elevational gradients in the Bolivian Andes and identified respective local peaks of richness supporting the “mid-elevation bulge” theory; already discussed the limiting role of low temperature at higher elevations. This observation underscores the significant role of temperature as the primary driver behind the influence of elevation. Nonetheless, as epiphytes are highly diverse regarding functional adaptations, specific epiphyte groups followed a different trend than the overall. Krömer et al. (2005) found orchids and ferns as the most species-rich group, but their contribution to the overall richness changed across the elevational gradient: While orchids are especially abundant in lowlands (hot and wet areas), ferns are dominant at 4000 m.a.s.l. (dry and cold areas). This interplay between specific group adaptations and environmental factors underscores the complex dynamics driving the distribution and diversity of epiphytes across elevational, as well as moisture and temperature, gradients.

Weigand et al. (2019) uncovered a consistent link between water availability and temperature with the species richness of fern and lycophyte across spatial scales (i.e. ranging from smaller plot sizes [300–500 m²] to a larger regional context [7,666 km² grid cells]). Regarding water availability predictors, precipitation (i.e.

“precipitation of the warmest quarter”) is positively associated with species richness at both plot and regional levels, while cloud cover (i.e. “mean annual cloud cover”) emerged as a significant factor at plot level, contributing to greater species diversity by serving as an alternate water source. For temperature, higher temperature during the growing season increases the species richness at both plot and regional level, while “Isothermality” displays a positive relationship with species richness at the plot level.

Similarly to Weigand et al. (2019) for ferns, Kessler (2002) also identified a joint influence of temperature and humidity predictors explaining the variance of epiphytic bromeliads diversity. Sites with higher annual precipitation support a richer diversity of bromeliad; conversely, temperature exhibits a consistently adverse influence on both diversity and distribution patterns. The number of frost days have the negative and stronger effect on species richness, indicating the extreme low temperature as the main factor restricting epiphytic bromeliads occurrence. Similarly, mean annual temperature has an overall negative effect on species richness, but this effect is mostly resulted by the lower diversity found in both extremely low and extremely high temperatures. These findings imply the existence of a non-linear relationship between epiphyte diversity and temperature, following the same pattern for the elevation influence. Specifically, the optimal point for epiphyte diversity is intermediate elevations, followed by a decrease in diversity as moves towards both lower and higher elevation (Kessler 2002).

While the overarching trend suggests that higher water availability and mild temperatures are the optimal conditions for epiphytes, their high diversity represents a challenge in establishing a general pattern. Addressing this complexity, Hernández-Rojas et al. (2020) confirmed that water availability (measured by

precipitation and cloud cover) and temperature (comprising annual mean and seasonality) shape the distribution pattern of both terrestrial and epiphytic fern species. However, the influence from climate on distribution varies according to the range size of species area occurrence. While species with restricted distributional range are mainly found in climatically stable and humid habitats, wide-spread species are clearly favored by heightened temperature seasonality and drier conditions.

According to our models' predictions, abundance should rise strongly above a coldest-month temperature of about ca. 12°C and is slightly negatively affected below ca. 6°C, these predictions set a clear boundary of minimum temperature for epiphyte abundance. For species richness the prediction is only similar in that it should rise strongly above a coldest-month temperature of about ca. 12°C. Our model predictions provide specific understanding about the climatic factors determining current epiphyte abundance and richness. Although the highest biomass (a currency of abundance) of vascular epiphytes ever estimated was in tropical montane cloud forests of Colombia and Costa Rica (see within Gómez González et al., 2017), with minimum temperatures reaching the lower limits of the boundaries predicted, these forests also present very high humidity levels. Although not previously shown at such a large scale, our results are consistent with local and small-scale studies (e.g. Gómez González et al., 2017; Hernández-Rojas et al., 2020). At the population level, "extremely" low temperatures may filter out species with tropical origin and largely distributed in warmer climates (Hernández-Rojas et al., 2020). At the country scale, high elevations and humid habitat conditions favor the occurrence of fern species with restricted ranges (Hernández-Rojas et al., 2020). These range-restricted species, also known as narrow endemics (e.g. Médail and Baumel, 2018), sustain overall diversity (Mittermeier et al., 2011); which may speak rather for low

temperatures.

Climatic stability is one of the hypotheses to explain tropical diversity. The term refers to paleo-climatic stability from an evolutionary perspective, which allows for speciation and maintenance of species with small geographical ranges (Fine, 2015), as found for trees (Stropp et al., 2009) and palms (Kristiansen et al., 2011). Current climatic stability, i.e. intra-annual climatic stability, may be partially correlated with long-term inter-annual variation and has been found to positively influence species richness for terrestrial and epiphytic ferns (e.g. Hernández-Rojas et al., 2020; Tuomisto, Zúquim, & Cardenas, 2014; Weigand et al., 2020), orchids (Zhang et al., 2015), as well as plant species richness overall (Chu et al., 2019; Shen et al., 2012). Our results differ from that of terrestrial ferns and lycophytes in Amazonia, for which annual rainfall seemed an important factor for richness, not so for abundance (Tuomisto, Zúquim, & Cardenas, 2014; Weigand et al., 2020), instead, abundance is likely to indirectly influence pteridophyte epiphytic richness.

The effect of temperature-related predictors on species richness was single-handedly driven by Bromeliaceae, while precipitation-related variables had a shared effect on more than one group, as expected considering the ecology and water-dependence of vascular epiphytes (Gentry & Dodson, 1987; Zotz, 2016). Differences in the direction of the effect of temperature variables on bromeliad richness may be explained by the different strategies of the species belonging to different subfamilies, while Bromelioideae species may be favoured by elevated temperature, Tillandsioideae species may be negatively affected (Muller, Albach, & Zotz, 2018). Temperature seasonality - although non-significant for all species - showed contrasting effects on the richness and abundance of epiphyte groups (positively on orchids' abundance, and negatively on bromeliads' richness and

abundance). Although population of some bromeliads species are able to inhabit areas with high temperature seasonality, by resisting the warmest season, other factors such as light exposure and high rainfall seasonality could negatively affect them and consequently their occurrence in those seasonal areas e.g. Campos Rupestres (Chaves, Leal, & de Lemos, 2018). It is key to highlight that the negative effect of temperature seasonality on Bromeliads was over five times larger on richness than on abundance, which suggests that the filter may be stronger early stages of establishment instead of later ones, e.g. dispersal and germination and that bromeliads have species specific ecological niches. Our database has a larger number of sites which are not disturbed, therefore, species which are well adapted to stable environments are overrepresented. In the case of orchids, the positive effect of temperature seasonality may be explained by the phenotypic plasticity strategies developed by certain species and genera, e.g. species belonging to the *Phalaenopsis* genera modify floral and reproductive traits as a response to changes in temperature (i.e. inflorescence size, flowering period and number of flowers, Blanchard & Runkle, 2006); and *Caladenia robinsonii* increases germination rates at specific levels of temperature seasonality (Janissen, Lawrie, & Huynh, 2022).

Concerning the effect of water-related predictors on species richness, only precipitation seasonality showed a general negative effect on all species and taxonomic groups (i.e. orchids and bromeliads). This pattern highlights the importance of water availability, but mainly of supply stability, for vascular epiphyte richness. Since vascular epiphytes are strongly coupled with the atmosphere due to their habit (Zotz 2016), and epiphyte richness has been linked to water-related variables (e.g. Taylor et al., 2022), it is still senseful that the stability, or lack of water accessibility throughout the year would limit epiphyte richness (Gentry & Dodson,

1987; Kreft et al., 2004). On the other hand, precipitation seasonality had a positive effect on all species abundance, which is probably led by the positive effect on Pteridophytes alone, which is over 10 times larger than that on all species. Although on orchids had a negative, but relatively weaker, association. Seasonality in water availability is well established to negatively affect vascular epiphyte species, however, specific epiphyte species rely on mechanisms to optimise water consumption, as well as to capture and retain water, during dry seasons (Li et al., 2020). A wide range of Pteridophyte species shows a complex set of desiccation strategies (i.e. from poikilohydric to homoiohydric; Kessler, 2007), which allows a higher abundance of those species, especially dry areas (Proctor & Tuba, 2002). Regarding bromeliads species, differences in water storage capacity between ecophysiological forms (i.e. tank vs atmospheric) may play a role in determining distribution at the local scale, for instance, along the vertical moisture gradient of the forest (Reyes-García, Griffiths, Rincón, & Huante, 2008; Wagner, Bogusch, & Zotz, 2013). Atmospheric bromeliads, as drought-adapted species, are commonly observed with relatively high abundance in dry habitats, such as dry forests (Siaz-Torres et al., 2021) and pastures (Elias, Mortara, Nunes-Freitas, van den Berg, & Ramos, 2021), and high water-availability seasonal habitats (González-Salvatierra, Pena-Rodríguez, Reyes-García, De la Barrera, & Andrade, 2021). Our results suggest that the response of epiphyte diversity to water availability restriction is clearly taxa- and response variable dependent.

Our results indicate that energy availability, as indicated by the proxies here used: the climatic variables, has a direct and independent effect on the total number of individuals and species richness, and not as postulated by the MiH. Nonetheless, climatic factors: mainly temperature-related variables in combination with

precipitation-related variables, are important factors driving large-scale patterns of epiphyte diversity. The correlation between species richness and energy or productivity is not consistently linear, and is highly variable, particularly among plant species (Simova et al. 2013, Kessler et al. 2014). For instance, while Chu et al. (2019) found that climate affects tree species richness, on a global scale, through individual abundance, fern richness, in Ecuador, was not related with ecosystem productivity (Kessler et al. 2014). The last authors supposed that the small scale of the study and the ecosystem proxy chosen could be the reason. In turn, Simova et al (2011) found that tree abundance was a weaker correlation with its richness. In the present study, we also find no alignment with some MiH postulated using vascular epiphyte species on large scale study, using many climate variables as proxy. We found that epiphyte richness was more strongly influenced by energy/climate variables than their abundance.

These patterns could be detected in spite of the coarse resolution of the analysis and the incomplete coverage of the data. Both finer-scale analyses, better capturing landscape-scale climatic, abundance, and richness gradients, and a higher and more balanced coverage of the Neotropics may reveal an even stronger association between drivers and responses. Therefore, we strongly recommend both higher epiphyte inventories and collection to decrease the gaps and bias from sampling (Araújo & Ramos, 2021), as well as the continued compilation of datasets with better spatial coverage and with standardised sampling (Mendieta-Leiva et al., 2020) to allow more comprehensive analyses. Because of the current and future scenarios of anthropogenic disturbance, including global climate change, that can alter the productivity and abundance of many different communities around the planet

(Walther, 2010), it is vital to understand the relationship between climate, land use, and diversity in order to predict future biodiversity changes (Miko & Storch, 2015).

We do not find full support for the MiH on vascular epiphytes. Although abundance had a significant and positive effect on species richness (except for bromeliads), as the third MiH postulation, the main effect of climate can not be considered as mainly through abundance for all epiphyte species, Orchidaceae and Bromeliaceae. The fourth postulation, i.e. the effect of variables related to temperature on richness may be mediated through abundance, was only confirmed for the Pteridophytes, since the climate effect was exclusively through abundance. There were differences both in the strength and direction of climatic variables effects for different groups, and the effects of abundance on species richness were group-specific. This variability between groups indicates that analysing climatic relationships for all species from a taxa (e.g. trees, epiphytes) can provide general insights but may mask group-specific patterns. For epiphytes, we suggest that future studies explore the influence of climate using functional groups (e.g. tank vs atmospheric bromeliads) to detect group-specific patterns. As vascular epiphytes represent one of the most diverse plant groups in the Neotropics, a better understanding of their diversity patterns will be necessary for predicting future biodiversity changes and for prioritising conservation efforts. As shown here, abundance data can be an important building block for understanding richness patterns, and we recommend the collection of such data whenever possible.

4.6. References

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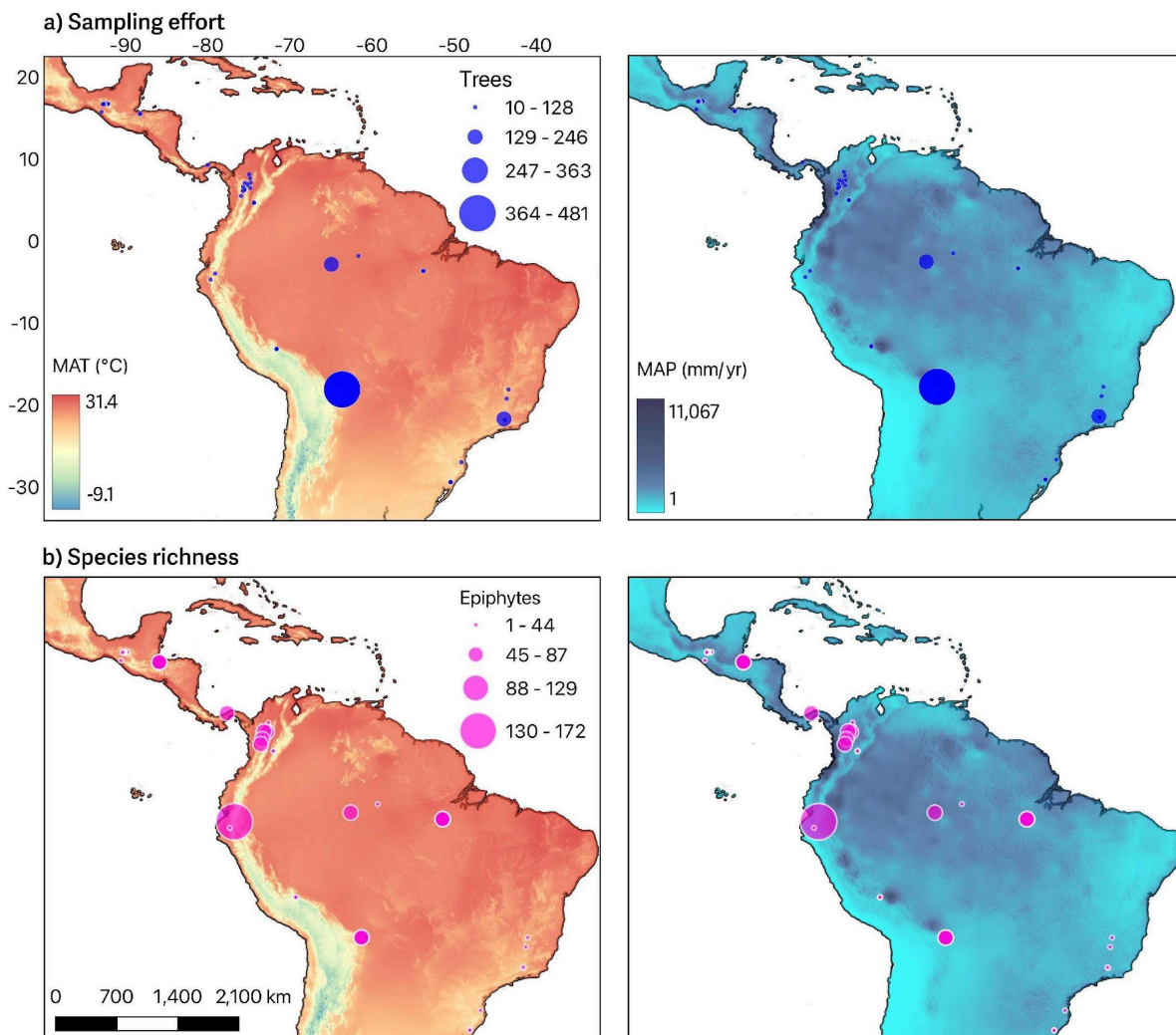


FIGURE S1: distribution of the two most significant climatic predictors (i.e. significantly associated with all epiphyte groups) in the Neotropics: Mean Annual Air Temperature (MAT - °C) and Mean Annual Precipitation Amount (MAP – mm year⁻²). Data from CHELSA V1.2 (Karger et al., 2017, available at <http://chelsa-climate.org/>). The sampling effort (a) is the number of trees sampled within the grid cells (i.e. green circles) and species richness (b) is the number of epiphyte species. Equivalent graphs showing the distribution of species richness for the most representative epiphyte groups (i.e. orchids, bromeliads and Pteridophyte) are available in Figure S2.

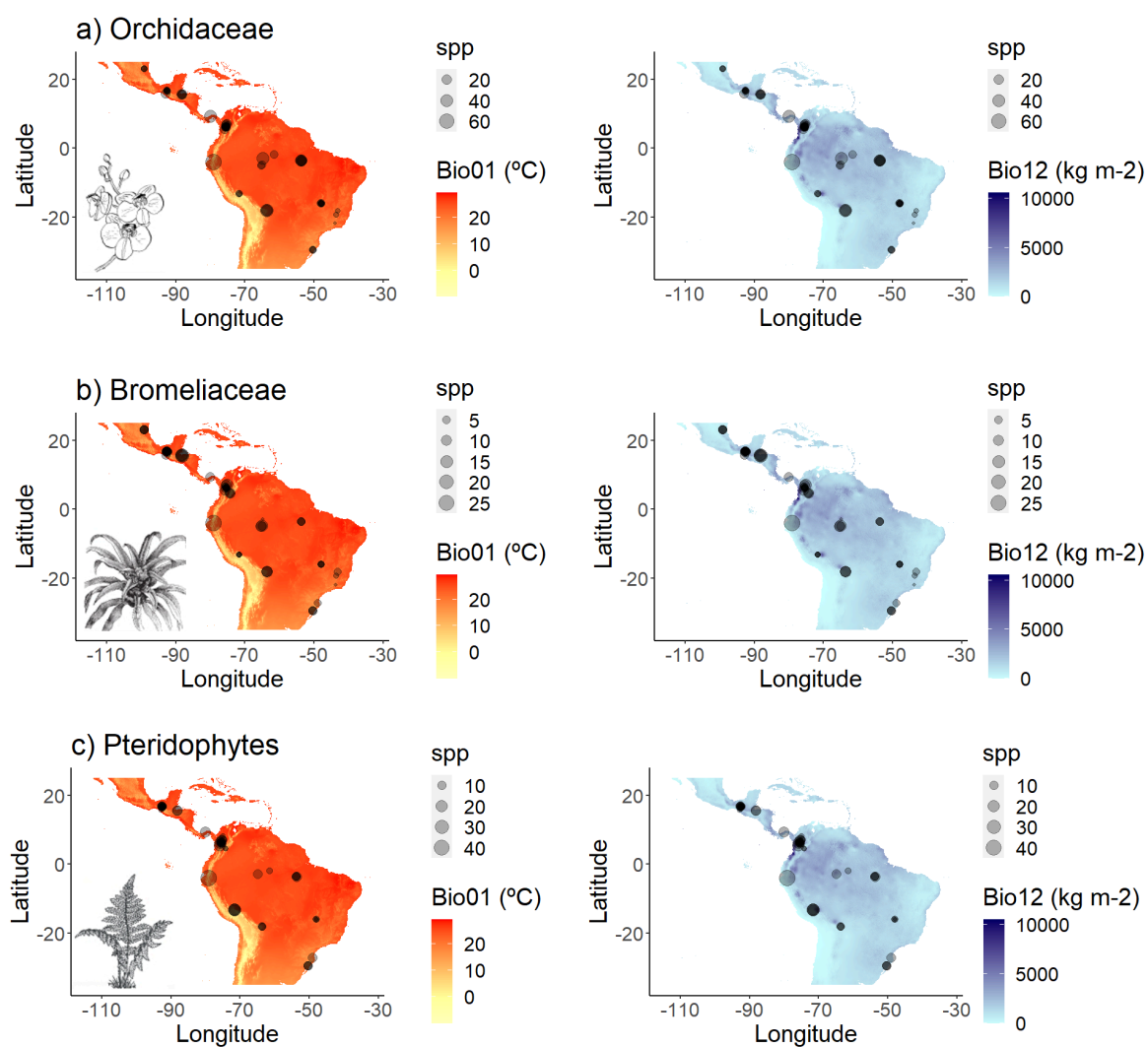


FIGURE S2: distribution of the two most representative climatic predictors (i.e. significantly associated with all epiphyte groups) in the Neotropics: Mean Annual Air Temperature (Bio01 - °C) are represented by the red scale and Annual Precipitation Amount (Bio12 - kgm⁻²) are represented by the blue scale. The species richness for each epiphyte group in grid cells with at least ten sampled trees is represented by the size of the circles for (a) Orchidaceae, (b) Bromeliaceae and (c) Pteridophytes. The sampling effort (i.e. number of trees sampled within the grid cell) is shown in Figure 1 in the main text.

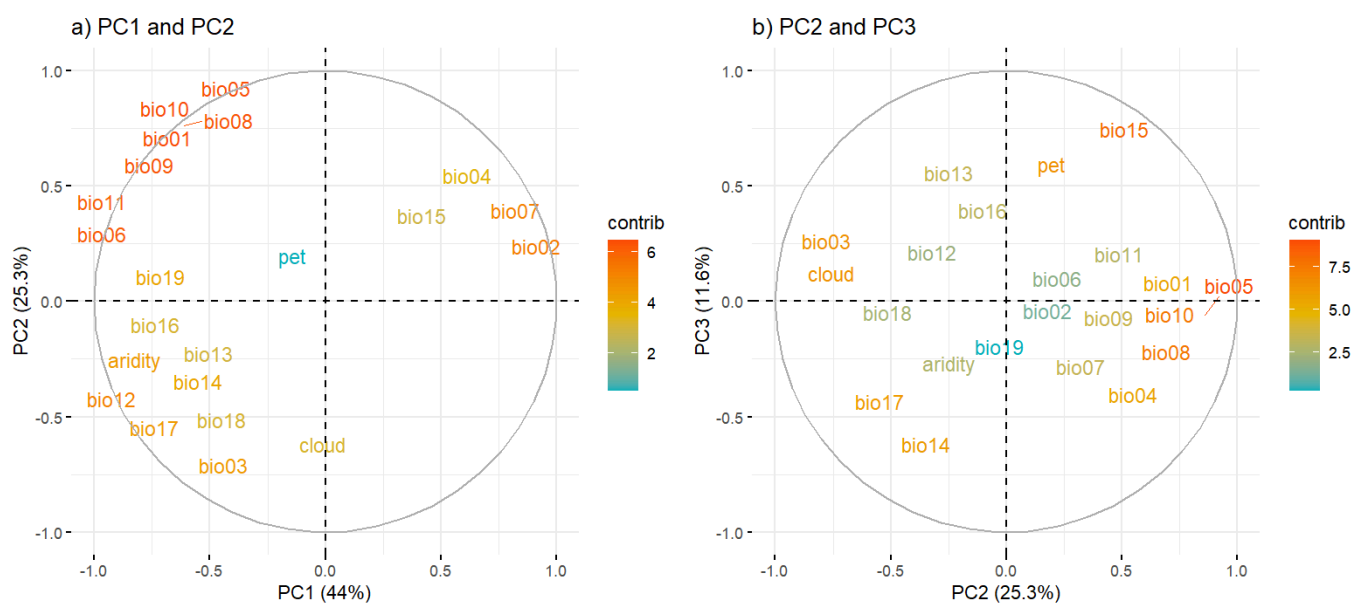


FIGURE S3: PCA plots of all climatic predictors. The axes shown (PC1, PC2, and PC3) were the axis used in the variables selection.

TABLE S1: summary of all EpiG-DB datasets (dataset code) included in the analyses. The number of trees and grid cells is the quantity of data provided and used in the analysis from each dataset. Mean annual air temperature and annual precipitation values are mean values for the grid cells. Ecoregion is the local ecoregion where the grid is included, based on WWF Terrestrial Ecoregion classification (Olson et al. 2001).

Database code	Number of trees	Grids cells	Mean annual air temperature (°C)	Annual precipitation (kg-m ²)	Ecoregion
ALG_db	71	1	20.4	1735.0	Serra do Mar coastal forests
AMB_antioquia_db	337	10	19.5	2990.2	Cauca Valley montane forests, Magdalena Valley montane forests, Magdalena-Urabá moist forests
AMB_arvi_db	314	10	13.8	2345.6	Northern Andean páramo, Magdalena Valley montane forests
AQ_jau_db	119	1	25.8	2252.0	Japurá-Solimoes-Negro moist forests
AQ_mamiraua_db	178	1	25.6	3656.0	Purus varzeá
CB_atlant_db	72	3	15.5	1633.0	Araucaria moist forests
CB_ducke_db	299	9	24.8	1896.5	Tapajós-Xingu moist forests
EdIRM_db	302	5	19.3	1384.2	Sierra Madre Oriental pine-oak forests
fernandezcuj	12	1	19.2	679.0	Eastern Cordillera real montane forests
fernandezman	11	5	18.9	717.2	Eastern Cordillera real montane forests
JW_biomCOL_db	183	3	14.3	1127.7	Magdalena Valley montane forests
JW_indMX_db	550	17	14.3	1494.4	Central American pine-oak forests
KW_host_spec_SL	112	1	26.3	3457.0	Isthmian-Atlantic moist forests
LM1_db	22	1	20.7	1428.0	Bahia interior forests
LM6_db	50	1	22.0	1013.0	Cerrado
LM7_db	216	1	17.6	1494.0	Bahia interior forests
MA_db	4	2	18.5	2106.5	Ucayali moist forests, Peruvian Yungas
MK_decid_db	397	1	20.2	691.0	Dry Chaco
MK_humid_db	481	1	18.8	688.0	Dry Chaco
MK_semidec_db	392	1	20.3	655.0	Dry Chaco
MMN_triunfo	41	1	16.8	2759.0	Sierra Madre de Chiapas moist forests
MVI_db	727	4	25.4	2446.25	Juruá-Purus moist forests
MW_db	75	1	18.9	1342.0	Cerrado
pillacaama	8	4	15.3	1428.5	Peruvian Yungas
RdO_db	600	8	21.4	1497.1	Cerrado
SPB_db	60	6	16.8	2326.3	Central American Atlantic moist forests
vega	205	4	12.2	1078.5	Peruvian Yungas
wernertree	83	18	16.8	1108.0	Eastern Cordillera real montane forests

TABLE S2: PCA scores of all climatic predictors and their associated axis scores (scores ≥ 0.25 marked in red). The scores are divided into the PCA result for all species and for epiphyte groups. The last three rows show the proportion of variance explained by each axis, the cumulative variance and the standard deviation. Differences between groups are due to the number of plots and distribution according to groups. PCA axis plots are available in Figure S3.

Climate predictors	PC1	PC2	PC3
Bio1 = mean annual air temperature	-0.24	0.28	0.01
Bio2 = mean diurnal air temperature range	0.27	0.13	0.02
Bio3 = isothermality	-0.16	-0.27	0.21
Bio4 = temperature seasonality	0.18	0.20	-0.30
Bio5 = mean daily maximum air temperature of the warmest month	-0.16	0.36	-0.04
Bio6 = mean daily minimum air temperature of the coldest month	-0.29	0.15	0.06
Bio7 = annual range of air temperature	0.24	0.20	-0.14
Bio8 = mean daily mean air temperatures of the wettest quarter	-0.20	0.32	-0.09
Bio9 = mean daily mean air temperatures of the driest quarter	-0.27	0.22	0.00
Bio10 = mean daily mean air temperatures of the warmest quarter	-0.20	0.33	-0.07
Bio11 = mean daily mean air temperatures of the coldest quarter	-0.27	0.20	0.08
Bio12 = annual precipitation amount	-0.25	-0.17	0.09
Bio13 = precipitation amount of the wettest month	-0.21	-0.08	0.30
Bio14 = precipitation amount of the driest month	-0.21	-0.18	-0.35
Bio15 = precipitation seasonality	0.16	0.19	0.42
Bio16 = mean monthly precipitation amount of the wettest quarter	-0.21	-0.07	0.29
Bio17 = mean monthly precipitation amount of the driest quarter	-0.22	-0.20	-0.32
Bio18 = mean monthly precipitation amount of the warmest quarter	-0.17	-0.19	0.01
Bio19 = mean monthly precipitation amount of the coldest quarter	-0.25	0.02	-0.08
Frequency of cloud cover	-0.03	-0.29	0.12
Potential evapotranspiration	-0.02	0.11	0.42
Aridity Global Index	-0.24	-0.14	-0.21
Proportion of variance	0.44	0.25	0.12
Cumulative variance	0.44	0.69	0.81
Standard deviation	3.11	2.36	1.60

TABLE S3: variables selected for the analysis and their selection criteria (PC1-PC3 refer to the first three axes of a PCA, including a total of 22 potential predictor variables).

Climate predictors	Selection criteria
Annual precipitation amount	Priority variable from PC1
Mean daily minimum air temperature of the coldest month	Non-priority from PC1
Mean annual air temperature	Priority variable from PC2
Frequency of cloud cover	Priority variable from PC2
Temperature seasonality	Priority variable from PC3
Precipitation seasonality	Priority variable from PC3
Potential evapotranspiration	Priority variable from PC3

TABLE S4: standardised path coefficients of climatic predictors significantly associated with epiphyte species richness (Spp) and abundance (Abd), for all species together and epiphyte groups. The values are piecewise SEMs coefficients and their standard deviation in parentheses, based on bootstrap confidence intervals (Fig. 2). Dashes are shown whenever there was no significant relationship between variables, and an NA is shown whenever the variable was not part of the model. Significance levels are indicated according to: $P < 0.05$ *, $P < 0.01$ ** and $P < 0.001$ ***.

Climate predictors	All species		Orchidaceae		Bromeliaceae		Pteridophytes	
	Spp	Abd	Spp	Abd	Spp	Abd	Spp	Abd
Annual precipitation	0.35*** (±0.06)	0.56*** (±0.01)		0.14** (±0.05)		0.47*** (±0.02)		0.47*** (±0.03)
Cloud cover frequency		-0.19*** (±0.02)		0.62*** (±0.07)		0.11*** (±0.03)		-1.46*** (±0.05)
Precipitation seasonality	-0.25* (±0.12)	0.26*** (±0.02)	-0.63*** (±0.19)	-0.23* (±0.11)	-0.48* (±0.19)	0.08* (±0.04)		2.50*** (±0.09)
Mean annual air temperature	-1.69* (±0.67)	-4.71*** (±0.16)		-10.91*** (±1.09)	1.65* (±0.65)	-0.44* (±0.22)		-2.04*** (±0.44)
Temperature seasonality				13.11*** (±1.28)	-0.61* (±0.30)	-3.39*** (±0.53)		
Mean min. air temp. of the coldest month	1.89* (±0.88)	5.79*** (±0.22)		13.06*** (±1.38)	-1.82* (±0.73)			3.43*** (±0.61)
Potential evapotranspiration		-1.23*** (±0.03)						-2.80*** (±0.09)

5 FINAL CONSIDERATIONS

The presented thesis elucidates the intricate relationships between land cover change, climate, and epiphyte diversity in the Neotropics, offering crucial insights into ecological and conservation dynamics. The vulnerability of epiphyte species richness to land cover change, especially in pastures, is underscored, with the negative impacts on diversity mitigated by maintaining scattered trees. Structural complexity emerges as a key factor fostering similarity between forest and pasture epiphyte assemblages, advocating for conservation efforts that involve preserving or planting trees in pastures to enhance habitat suitability for epiphytes. By delving into the intricate relationship between climate, abundance, and species richness of vascular epiphytes, this thesis provides nuanced insights across different taxonomic groups. The direct relationship between climate and species richness challenges the more-individuals hypothesis (MiH), necessitating a nuanced understanding of the drivers shaping large-scale patterns of epiphyte diversity amid climate change. Another study explores factors influencing the similarity of epiphyte assemblages between forests and pastures, revealing structural and microclimatic dependence as key drivers. Specific tree zones play a crucial role in determining epiphyte composition, suggesting practical conservation recommendations. The advocacy for maintaining and planting scattered trees in pastures to enhance structural complexity underscores the importance of preserving regional vascular epiphyte diversity. The findings from this research contribute significantly to our understanding of the ecology and conservation of plants, particularly epiphytes, in the Neotropics. The study also addresses the crucial need to unravel the mechanisms underlying spatial patterns of biodiversity, especially in the context of climate change and landscape

modification. The exploration of climatic drivers of vascular epiphyte diversity in the Neotropics reveals intriguing patterns. The structural equation models employed shed light on the complex relationships between climatic predictors, species richness, and abundance. Notably, the analysis distinguishes between different taxonomic groups, including orchids, bromeliads, and Pteridophytes. In conclusion, these studies significantly contribute to our understanding of the complex interactions shaping epiphyte communities in the Neotropics. The findings have practical implications for conservation, emphasizing the pivotal role of land cover, climate, and habitat structure in safeguarding the unique and diverse flora thriving in the canopy ecosystems of this ecologically vital region.

As expected, the integration of human pressures with environmental aspects across different scales provided crucial understanding about the general state of art of epiphyte distribution in one of most diverse subcontinents worldwide: the Neotropics. From smaller scales (i.e., tree host scale) to larger ones (i.e., landscape scale), degradation is significantly altering epiphyte species richness, abundance, and composition. However, the expected negative effects of degradation were sometimes overshadowed by a few positive or neutral effects, emphasizing how responses to degradation are remarkably diverse, even among sensitive species groups such as epiphytes. Despite the inconsistency in the impact of degradation, the dependence on a climatically stable habitat with high water availability and mild temperatures was evident when exploring climate effects. However, while consistent, we found temperature to be more determinant than water availability, suggesting that subcontinental patterns are slightly dissimilar from those found in relatively smaller spatial scales.

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