

The Effects of Altitude, Forest Type and Tree Microhabitat on Epiphytes in a Tropical Montane Cloud Forest

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Abstract

This study provides insight in the dynamics of epiphyte communities in tropical montane cloud forests (TMCF) and their sensitivity to climate change impacts and past deforestation practices. Understanding the dynamics of epiphyte communities in the TMCF's is a crucial step in ecosystem conservation and management due to their roles in nutrient cycling, microclimate regulation and biodiversity maintenance. Field surveys in Cloudbridge Nature Reserve (CNR), located in the Talamanca mountain range of Costa Rica, investigated the influence of macroclimate, forest type and tree microhabitat on epiphyte abundance and distribution. Results showed no significant relationship between altitude and epiphyte presence. Orchids were found to be more abundant in old growth forest types and on taller trees while bromeliads were more often found on trees with an increasingly bigger diameter. Epiphytes displayed significant preferences for specific tree zones (stem, inner crown, outer crown), indicating their preference of certain microclimate tree habitat. These findings highlight the sensitivity of epiphyte communities and their role in complex forest ecosystems. These findings inform broader conservation strategies for preserving biodiversity and ecosystem functions in montane cloud forests and general forest dynamics worldwide.



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1. Introduction

1.1 Forests at Risk of Climate Change

According to the United Nations International Panel on Climate Change, human-induced climate change has unequivocally caused widespread adverse impacts and related losses and damages to nature and people, beyond natural climate variability. There are already irreversible impacts as natural and human systems are pushed beyond their ability to adapt. These impacts occur across sectors and various regions worldwide (IPCC, 2023).

Across our planet, forests support the existence and prevalence of life in many ways. Since they cover about one-third of the Earth's land, forests are vitally supporting the lives of around 1.6 billion people. Forests play an important role in combatting the impacts of climate change as carbon sequestration through photosynthesis (UNEP, 2023). A top priority on the United Nations agenda is to mitigate climate change, which can be achieved through reducing deforestation rates, subsequently lowering CO₂ emissions and encouraging not only reforestation but also improved forest management practices (IPCC, 2023). However, in Costa Rica, now one of the most popular ecotourism destinations in the world, forests have not always been valued the way they are now (Delyser, 2015). The deforestation of pre-montane forests for agricultural conversion in Costa Rica began at least 1400 years ago (Anchukaitis & Horn, 2005). From 1950 to 1990, the country lost 65% of its forest cover (Evans, 1999). The primary driver for land-use change and deforestation in Costa Rica has been the conversion of forests to pastures and cash crops, such as coffee or rice (Holl, 2007). During the 1960s, the Costa Rican government implemented a policy aimed at promoting agricultural colonization, which incentivized farmers to establish their pastures in mountainous regions. Consequently, Costa Rica experienced further deforestation and witnessed extensive degradations of its steep mountain forests (Evans, 1999).

Introducing the area of interest of this research, the Cloudbridge Nature Reserve (CNR) is a privately owned nature reserve in the southern-central region of Costa Rica, that covers 280 hectares of cloud forests. CNR was founded in 2002 and it now functions as a reforestation project and education and research station. Cloudbridge aims to support the natural regeneration of previously deforested areas as well as planting old growth forest species to restore the tropical montane cloud forests to their natural mature state¹ (Delyser, 2015).

1.1 Tropical Montane Cloud Forests: Water Cycle

Tropical montane cloud forests (TMCF), often referred to as 'cloud forests', are usually defined as forests that are "frequently covered in clouds or mist" (Bruijnzeel & Veneklaas, 1998; Stadtmüller, 1987). While quantitative criteria on the definition of TMCF's are still lacking in literature, researchers commonly agree that cloud forests are recognized by the strong influence that the clouds and mist have on the forest vegetation, its ecological properties and characteristics (Bruijnzeel & Veneklaas, 1998; Stadtmüller, 1987). Typically, lower TMCF's are found at altitudes between 1500 and 2500 meters, but exceptions are possible due to local factors influencing cloud formation at lower altitudes (Bruijnzeel & Veneklaas, 1998). What makes TMCF's unique is the common presence of fog, which is not as common in other tropical rainforests. The fog presence constitutes to an extra input of water, also called horizontal precipitation, which may account for a significant hydrological influx, dependent on meteorological actors like wind speed, cloud characteristics and vegetation structure (Foster, 2001; Giambelluca & Gerold, 2011).

The occurrence of clouds and regular fog in tropical montane forests is not continuous, but rather broken into segments. This fragmentation isolates these cloud-immersed ecosystems, resulting in promotion of speciation, high endemism and, notably, an increased vulnerability to the impacts of

¹ Website Cloudbridge Nature Reserve's mission: <https://www.cloudbridge.org/the-project/conservation/>

climate change (Delyser, 2015; Foster, 2001). TMCFs do not only harbor significant biodiversity and endemism, but they also play a crucial role in providing essential ecosystem services, such as the production of water, carbon sequestration and -storage and erosion prevention (Foster, 2001; Soh et al., 2019).

As the global climate changes, the hydrological cycle will undoubtedly change with it. Since TMCFs rely on clouds to supply the majority of their moisture, they are vulnerable to climatic changes that alter weather patterns (Delyser, 2015; Foster, 2001). Due to the rapid warming of the global climate, a 1.5 °C rise is predicted by 2040. This warming trend will not only result in high temperatures globally, but also in significant alterations in the patterns of seasonal changes and extremes in both precipitation and temperature (IPCC, 2019).

Relatively small climate-driven shifts in patterns of atmospheric circulation are likely to trigger major changes in rainfall, cloud cover and humidity in tropical montane cloud forests (Giambelluca & Gerold, 2011). TMCFs, as these are characterized by lower temperatures, high humidity levels and occasional or continuous cloud cover, provide a habitat for numerous species that are especially adapted to thrive in high moisture environments (Richards, 2021). With the warming climate, cloud bases are expected to ascend, leading to a reduction in the duration of cloud cover of TMCFs (Helmer et al., 2019). In addition, forest fragmentation is expected to further increase temperatures and lower humidity levels (De Frenne et al., 2021; Richards, 2021). Considering the effects of climate change and forest fragmentation, tropical montane communities are facing exceptionally high levels of risk of extinction (Richards, 2021).

1.2 The Important Role of Epiphytes

Epiphytes are plants that grow upon other plants or objects for support, without any attachment to the ground or other nutrient sources through their roots (Petruzzello, 2020). Epiphytes can significantly change the water interception and storage capacities of forest canopies as their characteristics include the interception of atmospheric water and nutrients in tropical forests (Van Stan & Pypker, 2015). Vascular epiphytes are plants that germinate and root non-parasitically on other plants at all stages of their life, like orchids and bromeliads (Zotz, 2016). On the other hand, non-vascular epiphytes are bryophytes and lichens, notable for their considerable capacity to store water (Hembre et al., 2021).



Figure 1: The epiphyte functional groups (pictures of samples found in the field); orchid (A), peperomia (B), ferns (C), mosses and lichens (D), bromeliad (E).

Approximately 10% of all vascular plant species globally are epiphytic, which are predominantly concentrated within tropical forests. In tropical regions, epiphytes make up as much as 25% of all vascular plant species (Nieder et al., 2001). Plant species are affected by climate and climate change in multiple ways. The expected temperature rise and changes in precipitation patterns and seasonality together with the increased cloud base heights might not only affect forests as an ecosystem, but are expected to more directly have an effect on epiphyte existence (Richards, 2021). In general, scientists agree that climate change is already resulting in plant species range shifts, changes in relative abundance within species ranges and changes in microhabitat use (Delyser, 2015; Giambelluca & Gerold, 2011; Williams et al., 2008). Because epiphyte species are purely dependent on their atmospheric environment in terms of water and nutrient uptake, epiphytes might be one of the first plant species that are experiencing the direct effects of climate change (Delyser, 2015; Williams et al., 2008).

According to Richards (2021), epiphyte distributions respond to environmental factors at multiple scales (Figure 2). Within the tree's regional scale, epiphytes arrange themselves along a vertical gradient, with increasing exposure to sunlight and decreasing humidity levels, dependent on their physiological adaptations to environmental impacts (Nieder & Zotz, 1998). At the stand scale, which is a relatively homogeneous area of vegetation (henceforth referred to as 'forest type'), vascular epiphyte richness increases as trees mature.

However, the epiphyte abundance shows a negative trend with canopy openness as epiphytes on the upper part of the canopy are increasingly exposed to changing meteorological circumstances, such as higher temperatures, wind speeds and sun in the more open stands (Gradstein et al., 2008; Nieder & Zotz, 1998; Toivonen et al., 2017). At the tree scale, epiphyte roots attach to the host tree through both adhesion and interlocking mechanisms, depending on the bark characteristics. This suggests that tree diversity might also have an effect on the epiphyte diversity (Richards, 2021; Tay et al., 2023).

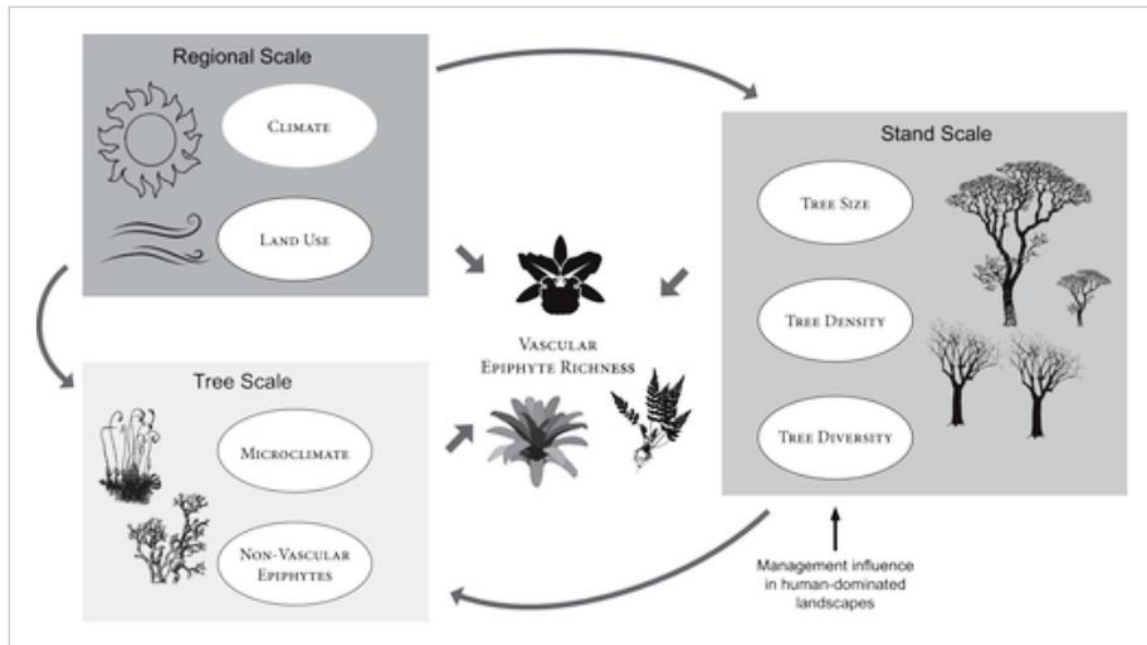


Figure 2: A general overview of the factors at regional, stand, and tree scale that influence vascular epiphyte richness (image from Richards, 2021).

As a result, at all described scales (Figure 2), the distribution patterns among epiphyte species as well as the variation in overall epiphyte richness and abundance in TMFCs underscore their high sensitivity to changes in environmental conditions. In addition, the cover, species richness and functional type of bryophytes have been closely linked to humidity, reinforcing the susceptibility of epiphytes to moisture-related variations (Benzing, 1998b; Hembre et al., 2021; Richards, 2021). Consequently, the continued existence of epiphytes faces extra potential challenges with current climate change impacts.

While scientific research has shown that epiphytes play a key role in a tropical cloud forest, the actual correlation between the effects of changing temperatures, as well as changes in forest structure due to human influence on epiphyte presence are still relatively understudied. As Richards (2021) importantly states: “preserving remaining forests offers the most promise for conserving vulnerable epiphyte species”. To gain insight in the preservation and forest management of the TMFCs of CNR, research on the current effects of climate change on the epiphytes is executed. By observing the epiphytes in terms of their abundance and composition, the effects of the changes in elevational regional scale, forest type stand scale, as well as the microhabitat on individual tree scale are addressed.

2. Research Question and Hypothesis

Considering the important role of epiphytes in the Cloudbridge Nature Reserve's TMCF, the main objective is to gain insight in the relationships between epiphyte abundance and the variables that play a role in this complex system such as elevation, forest type and tree microhabitat. Consequently, this research addresses the following question: What is the effect of 1) macroclimate (altitude), 2) forest type (planted, secondary regrowth and old growth) and 3) tree microhabitat (bole, inner crown, outer crown) on the epiphyte abundance in terms of epiphyte functional groups (mosses and lichens, bromeliads, orchids, peperomias, ferns and others)?

Hypothesis

The effect of altitude change or macroclimate on the epiphyte abundance is expected to decrease above the upper cloud line. Because epiphytes do not have access to soil water, their abundance is expected to increase with elevation up to the upper cloud line. Above the upper cloud line, the abundance of epiphytes is expected to decrease drastically due to less water availability. In between the cloud base and upper cloud line (in the clouds) the associated cooler, more humid environment, where epiphytes can obtain water through fog or dew interception and where they lose less water because of lower evaporative demand in these regions (Richards, 2021; Van Stan & Pypker, 2015). The abundance of different functional groups of epiphytes is expected to increase with higher elevation of the host tree as elevational transects have revealed abrupt shifts in biomass and species composition of epiphytic species in Colombian TMCF by the location of the host tree in terms of elevation (Benzing, 1998; Hofstede et al., 1993). Because epiphytes are purely dependent on horizontal precipitation, the species abundance is expected to increase with higher elevations, where the environmental conditions are more favorable for epiphytes with lower temperatures and higher humidity.

Forest types are expected to play a big role on the abundance of epiphytes on the host tree. The abundance of the epiphyte functional groups is expected to be the highest in the old forest type, because the trees are taller, the environment is more humid which results in more epiphyte niches and a longer establishment period for epiphytes (Gradstein et al., 2008). The secondary regrowth forest type is expected to have higher tree density, tree size and tree diversity than the planted forest type and is expected to provide more favorable conditions for epiphytes, such as higher canopy cover and humidity and lower average temperatures, resulting in the expectation that epiphyte abundance is higher in secondary regrowth than in the planted forest type.

At last, finer-scale distributions within individual tree crowns are expected to be present in trees where the stand scale is more mature, which means that tree sizes are bigger in terms of average diameter and height. As the upper crown of most trees in old growth forests are higher, the differences in microclimate within the vertical transect of one individual tree might be higher as well. From the base of the tree towards the outer crown, there is an increase in solar radiation, and fluctuations in temperature and wind circumstances. As the number of different niches on one individual tree are expected to increase with tree height, this might lead to an increase in epiphyte abundance.

3. Methodology

3.1 Study Area: Cloudbridge Nature Reserve

Cloudbridge Nature Reserve is situated in the southern-central region of Costa Rica, on the southern slopes of the Talamanca mountain range, next to Chirripó National Park, which is a UNESCO-designated World Heritage Site. Covering 700 acres, CNR encompasses a diverse TMCF ecosystem. The elevation of the nature reserve varies from 1500 to 2650 meters. While only minor portions of CNR's land consist of old cloud forest, the majority comprises areas that were formerly used as pastures. These old pasture areas are currently in various stages of secondary forest succession, with Cloudbridges goal of returning to the forests to their original 'old-growth' reference state. A QGIS map of CNR shows this distribution of forest types (Figure 3).

For this research, elevational transects were set up on two different trails called "El Jilguero" and "Montaña". On each trail, two trees were sampled every 25 meters of elevation change, based on GPS Z-coordinates. This approach ensured a continuous measurement of epiphyte abundance along the elevational gradient between 1665 and 2028 meters above sea level. El Jilguero was sampled from 1665 to 2022 meters, totaling 32 trees. At the Montaña trail, the same methodology was used, sampling two trees at every 25-meter elevational change, from 1740 to 2028 meters above sea level, resulting in 24 trees. In total, 56 trees were measured during the research period, which started at the 19th of September and ended at the 14th of December 2023.

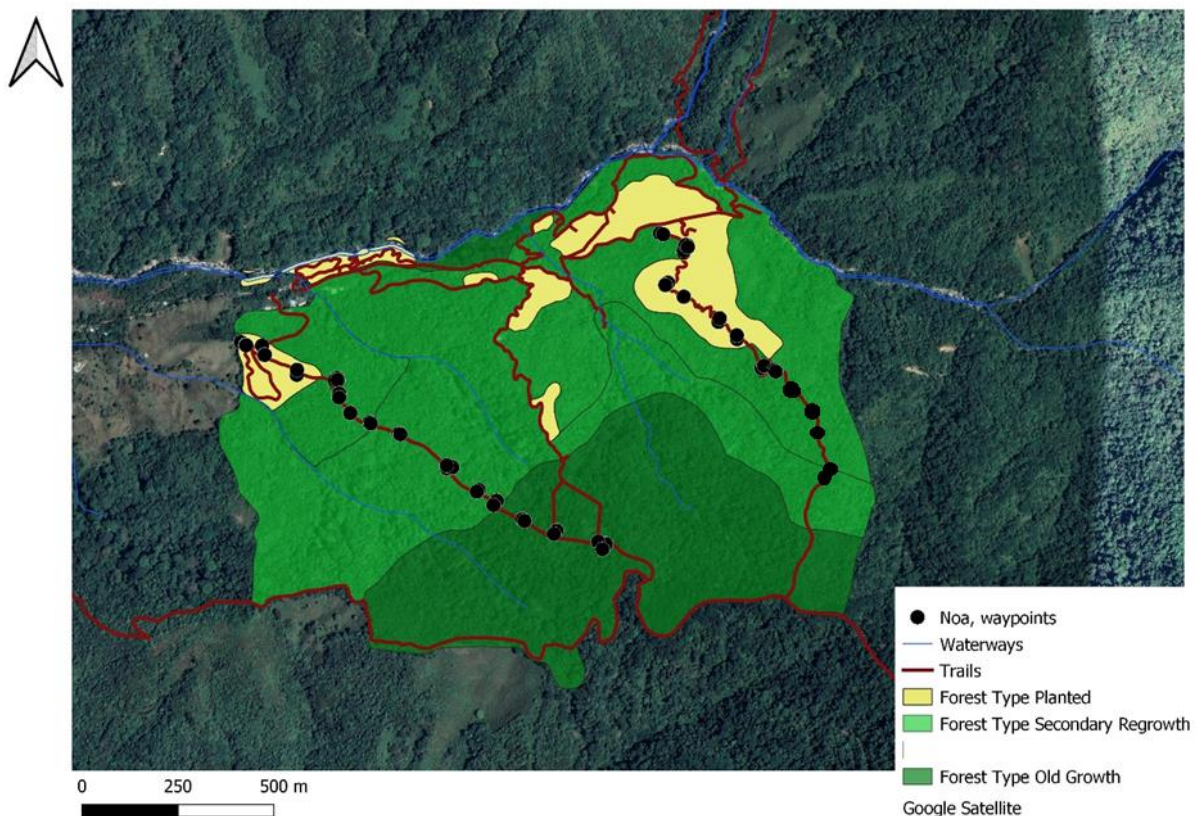


Figure 3: A satellite map of Cloudbridge Nature Reserve, with black dots representing the waypoint coordinates (black dots) of all individual measured trees on the two trails (red) Jilguero (west side) and Montaña (east side), which are crossing different forest types, indicated in yellow (planted), light green (secondary regrowth) and dark green (old growth).

3.2 Field Measurement Techniques

The sampled trees were divided into three zones: the bole, inner crown (first half from crown base to crown tip) and outer crown, following the zonation in Figure 4 that shows the zonation system created by Nieder & Zotz (1998). When a tree had lower branches, these branches were logically allocated to the zones following the argumentation on microclimate by eye. Specifically, when a branch was located close to the ground and concealed by surrounding trees or shrubs, it was classified within zone 1, with zone 2 starting at a higher point in the tree. The end of zone 2 is always defined as the region where most leaves start to occur at the top of the tree, forming the upper canopy of the sampled tree. Additional data collected for each tree included the mean diameter at breast height (DBH), where the sampled trees were required to have a DBH that is over 15 centimeters. Additionally, the mean estimated tree height is recorded based on rough estimation by eye. The location was documented with GPS coordinates and a written down description of the location in terms of forest type and orientation next to the trail for future re-visits if necessary. The distance from the trail of the sampled trees was measured using a tape measurer. The differentiation between the forest types was also addressed by taking notes on the forest type during the fieldwork for immediate determination. The genera of the sampled trees were determined by taking leaf and if possible branch samples from the trees using an extended tree cutter. Afterwards, the tree genera were determined using the books 'A Field Guide to Plants of Costa Rica' by (Gargiullo & Magnuson, 2008), 'An introduction to cloud forest trees: Monteverde, Costa Rica' (Haber et al., 2000) and the website² 'Manual de plantas de Costa Rica' (Morales, 2003). All determined tree genera were divided in self-constructed tree functional groups, based on the trees' characteristics found in literature.

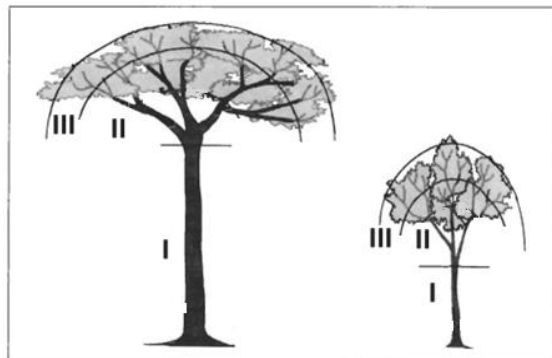


Figure 4: Zonation of tree structure, with zone I the bole, zone II inner crown and zone III outer crown, figure based on image in Nieder & Zotz (1998).

For each zone, the following measurements were taken: the percentage coverage of the host tree by epiphytic mosses and lichens and the individual count of epiphytes for each epiphytic group (e.g. bromeliads, orchids, peperomia, ferns and other epiphytes). Hemi-epiphytes were excluded from this research. When the counting measurement of the epiphyte individuals was conducted, and counting individual plant stands was not feasible, a collection of stems separated from other groups was counted as one individual when these were not further apart than five centimeters, following the approach as described by Nieder & Zotz (1998). Lastly, when a sampled tree consisted of multiple stems, the average DBH was calculated using the following formula:

$$DBH_{tree} = \sqrt{(DBH_{(STEM1)}^2 + DBH_{(STEM2)}^2 + DBH_{(STEM3)}^2)}$$

² [Website Manual de Plantas de Costa Rica](#) date accessed 24-12-2023.

3.3 Determination: Tree Functional Groups

In this section the concept of tree functional groups is further explained. The initial step involved assigning genera to the sampled trees, creating an overview to understand the variability within the sampled population. Following the genera determination, the trees were categorized into three tree functional groups based on their characteristics. The first group that was defined were the tree dominants. Characterized by their height, these trees are pivotal in shaping the overall forest structure. Additionally, their large leaves play an important role in shading and light interception, highlighting their role in the creating a certain habitat in the forest ecosystem. The second group is the understory and epiphyte hosts, encompassing shorter trees that are found in the understory of the forest. Trees within this group play an important role in shaping the vertical structure of the forest, contributing to the layered composition of the forest. The last functional group comprises the pioneer and disturbance-adapted species. This group consists of trees that are quick to colonize disturbed or previously deforested areas, actively participating in ecological succession. This group also includes trees planted through human interference, which serves as evidence of previous deforestation events. These three functional groups provide a balance between the vertical structure of the forest and the role of trees in forest succession after deforestation.

After defining the tree functional groups, the tree genera were subdivided into the three groups. This categorization is based on general characteristics of the species, as found in the catalogical manual of plants in Costa Rica², and the two books on Costa Rican plants and trees by Gargiullo & Magnuson (2008) and Haber et al. (2000). The following table provides an overview of all sampled tree genera, divided into the different tree functional groups.

Table 1: Determined sampled trees genera divided into tree functional groups: canopy dominants, understory trees and pioneer & disturbance species.

Tree Functional Group	Name (Genus)	Name (Species)
Canopy Dominants	<i>Billia</i>	<i>roseae</i>
	<i>Clethra</i>	<i>mexicana, talamanca</i>
	<i>Conceveiba</i>	unknown
	<i>Heliocarpus</i>	<i>americanus</i>
	<i>Ocotea</i>	<i>puberula</i>
	<i>Quercus</i>	<i>benthamii, salicifolia</i>
	<i>Sauriaia</i>	<i>montana</i>
Understory Trees	<i>Cestrum</i>	<i>racemosum</i>
	<i>Inga</i>	<i>punctata</i>
	<i>Lauraceae</i>	unknown
	<i>Lippia</i>	<i>cardiostegia</i>
	<i>Myrsine</i>	<i>coriarea</i>
	<i>Oreopanax</i>	unknown
Pioneer & Disturbance species	<i>Ulmus</i>	<i>mexicana</i>
	<i>Cichona</i>	<i>pubescence</i>
	<i>Cecropia</i>	<i>peltate, angustifolia, polyphlebia</i>
	<i>Erythrina</i>	<i>lanceolata, poeppigiana</i>
	<i>Sauriaia</i>	<i>montana</i>
	<i>Perrottetia</i>	<i>longistylis</i>
	<i>Acnistus</i>	<i>arborescens</i>
Unknown	-	-

Note that the categorization might prove to be more complex in real life. For example, the *Ulmus Mexicana* is categorized into the pioneer/disturbance group despite potentially being part of the upper canopy. This categorization takes into consideration factors such as small leaves, seasonally leafless periods and their predominant presence in planted areas, where they may not provide significant shade like canopy dominants would. Similarly, *Heliocarpus* is often seen as a pioneer species, but based on the characteristics and occurrence in this specific cloud forest, it is therefore categorized into canopy dominants, mainly based on the average size of these trees in the Cloudbridge Nature Reserve.

3.4 Data Analysis

To provide an initial understanding of the gathered data, simple X-Y scatter plots were generated using the program SPSS. These plots allowed the observation of linear correlations including the coefficients, indicating trends. This preliminary analysis facilitates the identification of the direction of linear relationships between epiphyte abundance and the correlated measured variables. First, a series of multiple linear regression was done to investigate the impact of elevation, tree diameter at breast height (DBH) and tree height on epiphyte abundances, including the moss cover and the number of four different epiphyte functional groups (orchids, bromeliads, ferns, peperomias and other epiphytes) and the total number of epiphytes (adding up the four groups) on the sampled trees. Backward elimination was incorporated as a variable selection technique, where non-significant predictors were iteratively removed to refine and simplify the regression calculation. The criterion for backward elimination was set at a significance level (F) of 0.05, where variables with a significance greater than 0.05 were removed (F removal set at 0.051). This model highlighted which variable(s) (elevation, DBH or tree height) had a significant effect on epiphyte abundance on individual trees.

Subsequently, three series of general linear models were used for further statistical analysis, using a Tukey post-hoc test to test for group differences. The moss cover or number of epiphytes per zone (orchids, bromeliads, ferns, peperomias, other epiphytes and all epiphytes) were used as dependent variable, with the fixed factor being the tree zone (e.g. zone 1, 2 or 3). This analysis aimed to identify significant relationships between the abundance of epiphytes in each zone. The post-hoc Tukey test then revealed the direction and strengths of these relationships between the zones.

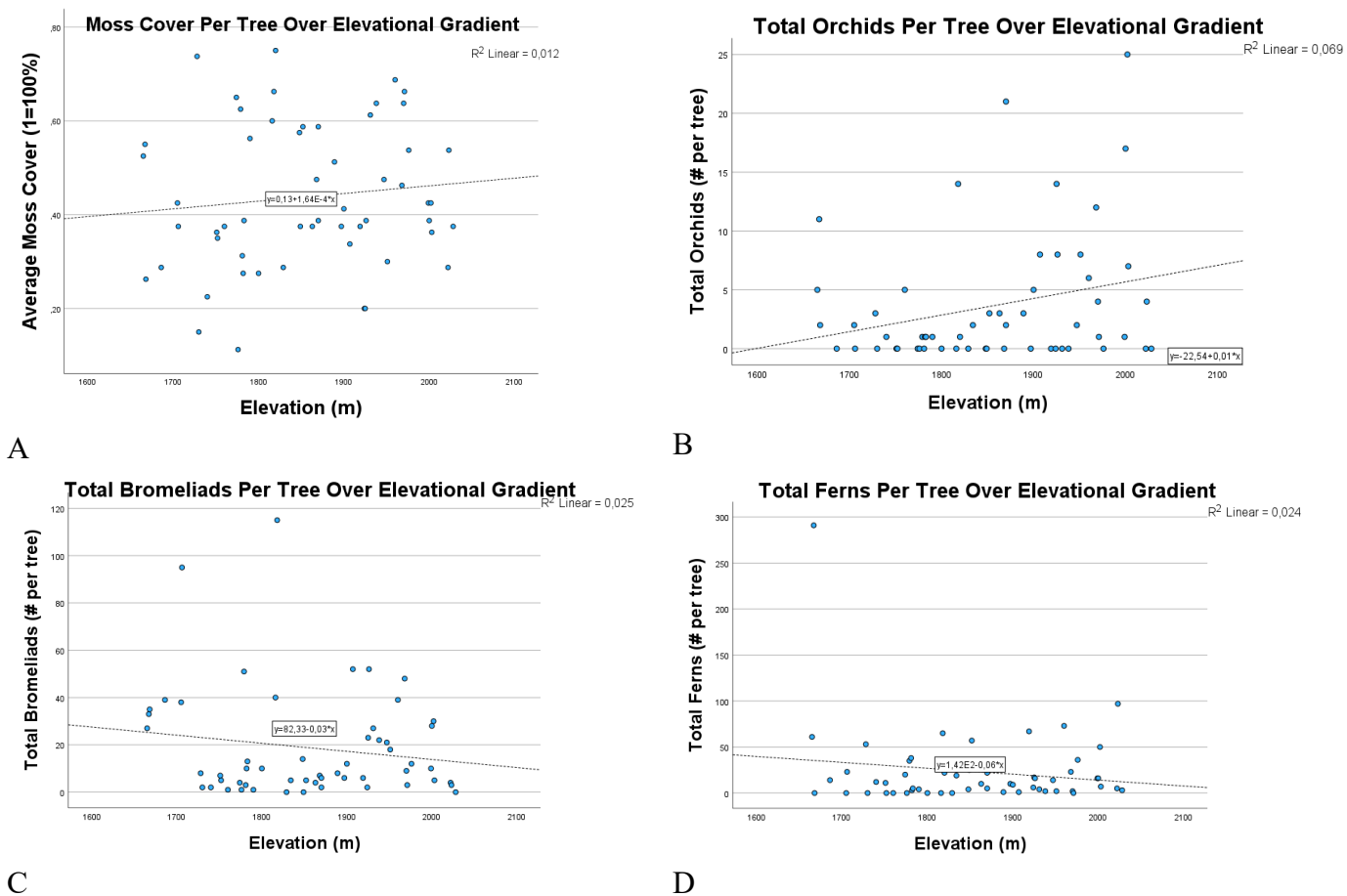
Similar general linear models were run to analyze the effects of forest type and guild on the total epiphyte abundance on individual trees. Forest type was considered as the fixed factor, with three categories (Old Growth > 30 years, Secondary Regrowth, Planted). A similar analysis was conducted with guild as the fixed factor, including the tree functional groups (Table 1).

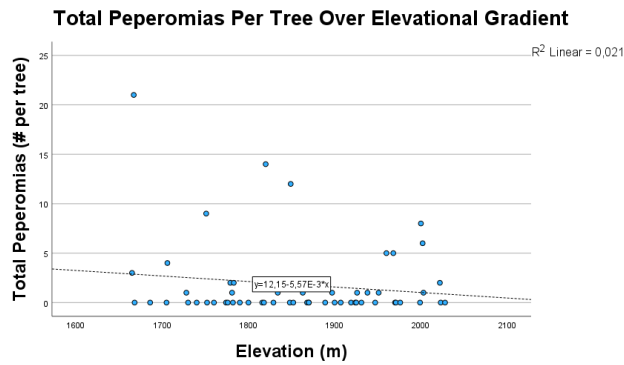
4. Results

In this chapter, the results of the field research that was executed in the Cloudbridge Nature Reserve are presented, logically following the order of the research question, “What is the effect of 1) macroclimate (altitude), 2) forest type (planted, secondary regrowth and old growth) and 3) tree microhabitat (bole, inner crown, outer crown) on the epiphyte abundance in terms of epiphyte functional groups (mosses and lichens, bromeliads, orchids, peperomias, ferns and others) and all epiphytes?”. In this chapter, the results of the analysis on the effect of altitude, forest type and microclimate on epiphyte abundance and dispersion are displayed in each sub chapter.

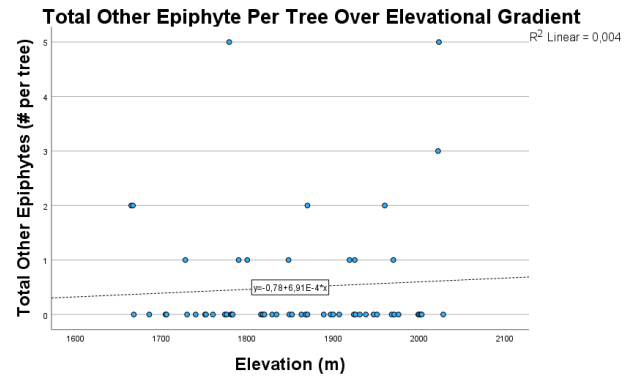
4.1 The Effects of Macroclimate Change on Epiphyte Abundance

In the first part of this chapter, normal linear relationships of epiphyte abundance are presented per category over elevational change. Figure 5 provides a first insight in potential correlations between elevation and the number of epiphytes per tree, revealing possible systematic change in abundance with increasing elevation. It is important to note, that these observations are qualitative and that statistical analysis is needed to show significance of these possible relationships.





E



F

Figure 5: Relation between epiphyte abundance on individual trees (N=56) and tree elevation (m) for moss cover (A), orchids (B), bromeliads (C), ferns (D), peperomias (E) and other epiphytes (F) with regression lines (continuous if significant, broken if non-significant).

4.2 The Effects of Forest Type on Epiphyte Abundance: Tree Genera

A total number of 56 individual host tree genera were identified, belonging to 20 different genera. The three most common found genera were *Quercus* (n=10), *Ulmus* (n=5) and *Billia* (n=4), as shown in Table 2 below (visualized in Appendix A).

Table 2: Overview of tree genera (n=20) and identified number individuals (n=56).

Tree Genus	Number of individuals
<i>Acnistus</i>	1
<i>Billia</i>	4
<i>Cecropia</i>	2
<i>Cestrum</i>	1
<i>Cinchona</i>	1
<i>Clethra</i>	1
<i>Conceveiba</i>	1
<i>Erythrina</i>	2
<i>Heliocarpus</i>	3
<i>Inga</i>	3
<i>Lauraceae</i>	1
<i>Lippia</i>	1
<i>Melastoma</i>	2
<i>Myrsine</i>	3
<i>Ocotea</i>	1
<i>Oreopanax</i>	1
<i>Perrottetia</i>	1
<i>Quercus</i>	11
<i>Sauraia</i>	1
<i>Ulmus</i>	5
<i>Unknown</i>	10
Total	56

For the tree functional groups, the most commonly identified individual trees belonged to the group of canopy dominants (n=21). The understory trees were the smallest group, consisting of 10 sampled trees (Table 3, also visualized in Appendix B).

Table 3: Overview of the tree functional groups (canopy dominants, pioneer & disturbance-adapted species, understory trees and unknowns) and number of individual trees (n=56).

Tree functional groups	Number of individuals
Canopy dominants	21
Pioneer & disturbance-adapted Species	15
Understory trees	10
Unknown	10
Total	56

4.3 The effects of Altitude and Forest Type (DBH and Tree Height) on Epiphyte Abundance

A multiple regression analysis was executed to examine the impact of elevation, DBH and tree height on the number of various categories of epiphytes (Table 4). The analysis showed that there were significant relationships for the epiphyte functional groups orchids and bromeliads. Orchid abundance significantly increases with tree height (Figure 6) and bromeliad abundance significantly increases with tree stem diameter (Figure 7). Elevation did not significantly influence any epiphyte functional group (Table 4).

Table 4: Multiple regression analysis of epiphyte abundance for all epiphytes and epiphyte functional groups (moss cover, orchids, bromeliads, ferns and other) with elevation (m), tree DBH (cm) and tree height (m). Béta coefficient, significance levels (P) and coefficient of determination (R²) are shown (P < 0,05 = *, P < 0,01 = **, P < 0,001 = ***).

Data type (per tree)	Elevation GPS (m)	DBH (cm)	Height (m)	R ²
Moss Cover	-	-	-	-
	-	-	-	
Orchids	-	-	$\beta=0,325$	0,106
	-	-	P=0,015*	
Bromeliads	-	$\beta=0,283$	-	0,063
	-	P=0,035*	-	
Ferns	-	-	-	-
	-	-	-	
Peperomias	-	-	-	-
	-	-	-	
Other Epiphytes	-	-	-	-
	-	-	-	
All Epiphytes	-	-	-	-
	-	-	-	

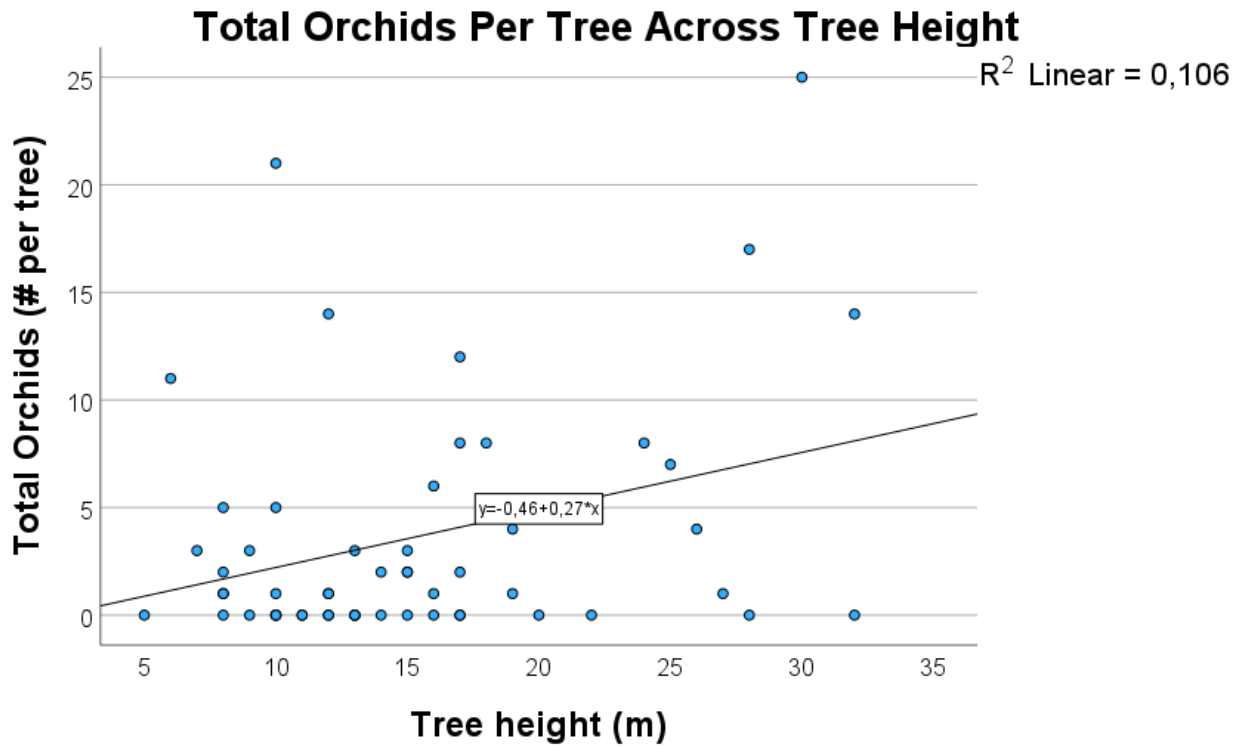


Figure 6: Significant relationship between orchid abundance (n=56) and tree height (m) with significant regression line (black) and R2 linear indicated (=0,106).

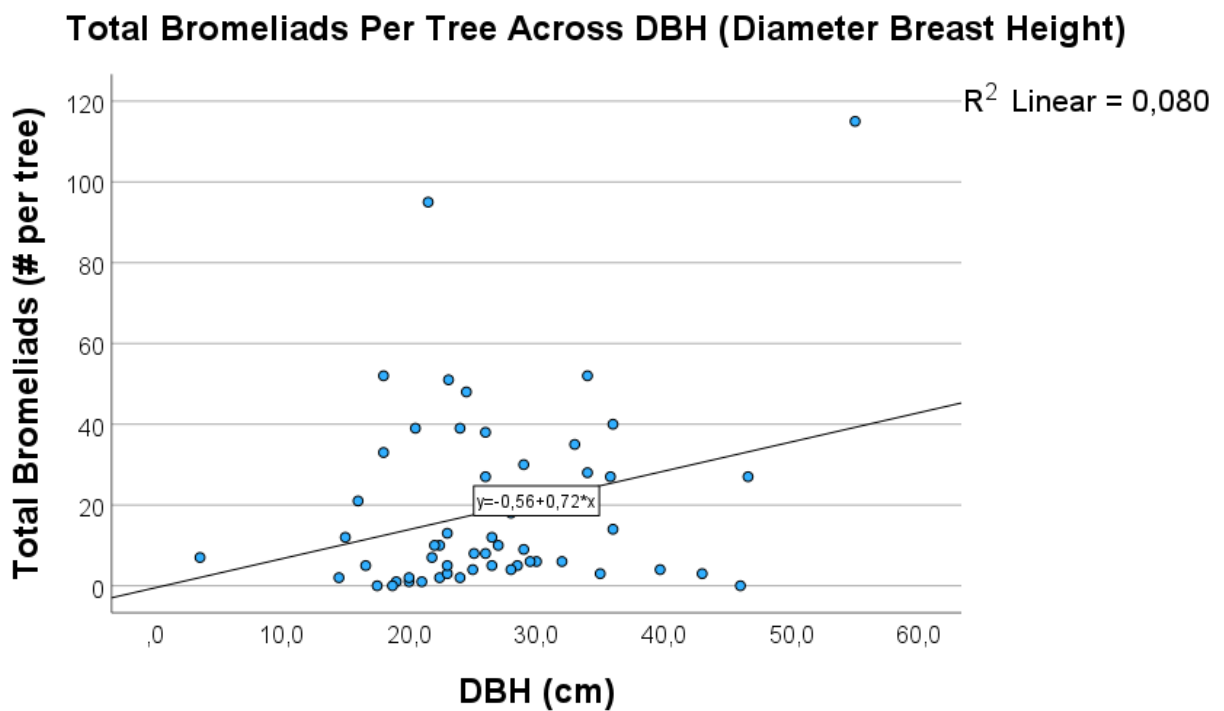


Figure 7: Significant relationship between number of bromeliads (n=56) and tree DBH (cm) with significant regression line (black) and R2 linear indicated (=0,080).

4.3 Forest Type and Guild

The relative variability in abundance of epiphytes was observed through the linear model for the forest type and guild, followed by post-hoc Tukey tests. The forest type and guild were the fixed factors, that were given a code for an easier display of the results as shown in Table 5.

Table 5: Name codes of the fixed factors used for the general linear model execution and post-hoc statistical analysis.

Forest Types		Guild (Tree Functional Groups)	
Variables	Code	Variables	Code
Planted	PL	Canopy Dominants	CD
Secondary Regrowth	SR	Understory Trees	US
Old Growth > 30 years	OG	Pioneer & Disturbance-adapted species	PI
		Unknown	UK

The dependent variables were the epiphyte functional groups (moss cover, orchids, bromeliads, ferns, peperomias, other epiphytes and all epiphytes). The general linear model run with post-hoc Tukey tests showed that there is a significant relationship between the number of orchids and the forest type, where most orchids were found in the old growth forest (OG), relative to the other two forest types (Table 6, Figure 8). For all other epiphyte functional groups and all epiphytes in total, no significant relationships were found between the forest type and epiphyte abundance. For guild, no significant relationships were found between the guild and epiphyte abundance for all epiphyte categories.

Table 6: General Linear Model results of epiphyte abundance with the relationship between forest type and guild on the number of epiphytes found for all epiphytes and epiphyte functional groups (moss cover, orchids, bromeliads, ferns, peperomias and others), with F and significance P ($P < 0,05 = *$, $P < 0,01 = **$, $P < 0,001 = ***$). Tukey post-hoc shows relative relationships between the forest type (Planted, Old Growth and Secondary Regrowth) and Guild (Canopy Dominants, Understory Trees, Pioneer & Disturbance-adapted Species and Unknown) for each epiphyte category.

Dependent Variable (per tree)	Forest Type	Tukey post-hoc	GUILD	Tukey post-hoc
Average Moss Cover	F = 0,880	PL = OG = SR	F = 0,806	UK = US = PI = CD
	P = 0,421		P = 0,496	
Number of Orchids	F = 6,186	(PL = SR) < OG	F = 0,377	UK = US = CD = PI
	P = 0,004*		P = 0,770	
Number of Bromeliads	F = 1,146	PL = OG = SR	F = 1,346	US = CD = UK = PI
	P = 0,326		P = 0,270	
Number of Ferns	F = 0,893	SR = OG = PL	F = 2,056	CD = UK = US = PI
	P = 0,415		P = 0,117	
Number of Peperomias	F = 0,260	OG = PL = SR	F = 0,790	UK = CD = US = PI
	P = 0,772		P = 0,505	
Number of Other Epiphytes	F = 0,042	PL = SR = OG	F = 1,415	PI = CD = US = UK
	P = 0,959		P = 0,249	
Total of All Epiphytes	F = 0,040	SR = OG = PL	F = 2,241	UK = CD = US = PI
	P = 0,961		P = 0,094	

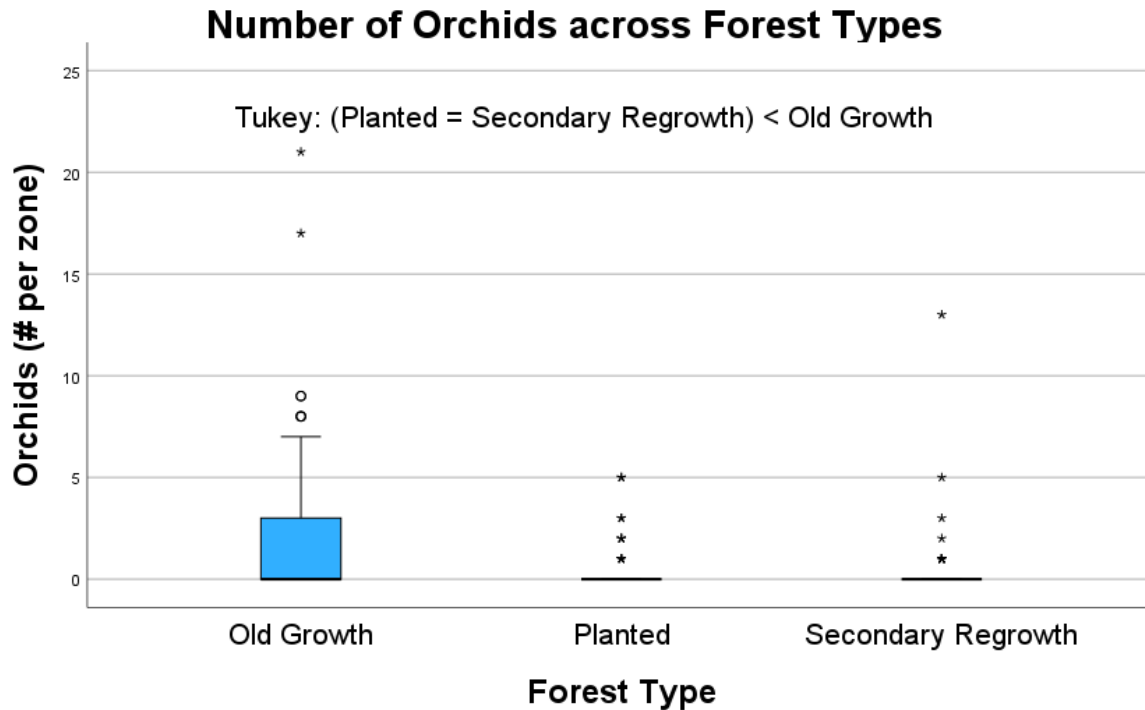


Figure 8: Box-plot graph showing the results of the general linear model on orchid abundance relative to forest type (Old Growth, Planted, Secondary Regrowth). Blue boxes represent 50% confidence interval, with whiskers indicating outer 25% confidence interval. Dots represent outliers. Tukey-post hoc results shown in text box, indicating significant relationship between the abundance of orchids and the forest type.

4.4 The Effects of Microclimate on Epiphyte Abundance

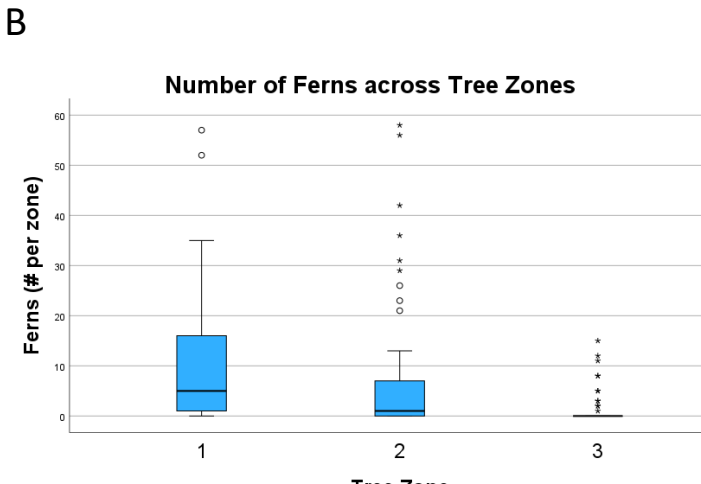
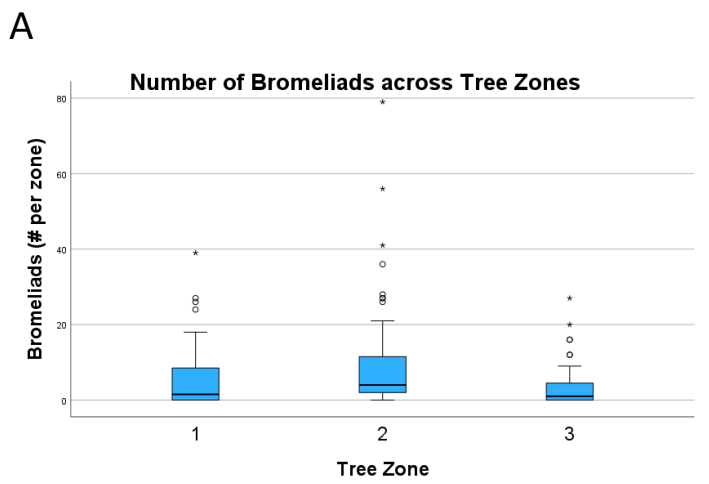
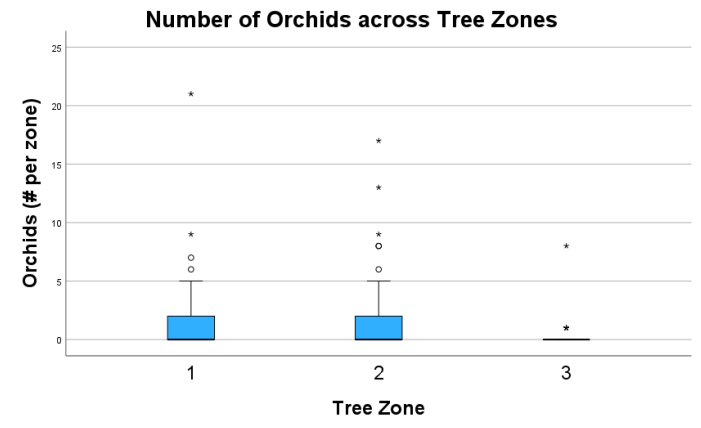
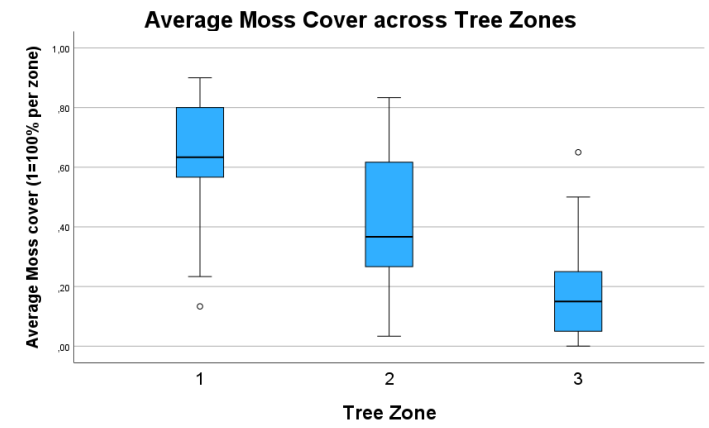
The effects of microclimate on epiphyte abundance have been observed through a general linear model, where the epiphyte abundance and distribution was analyzed for the tree zones (1 bole, 2 inner crown, 3 outer crown) of epiphytes were the input data per tree zone. Afterwards, a Tukey post-hoc test showed the relative relationships between the different tree zones.

The relative variability in abundance of epiphytes was observed through the linear model for the different tree zones. The abundance of all epiphyte functional groups varied significantly for the three tree zones (Table 7). In short, the moss cover is generally highest in zone 1 (bole) and is decreasingly lower in zone 2 (inner crown), followed by zone 3 (outer crown). Orchids were most often found equally in zone 1 and 2, relative to zone 3. Bromeliads were most often found in zone 2, but similarly often in zone 1 and 3. The abundance of peperomias and ferns was generally highest in zone 1, but equally lower in zone 2 and 3. In general, the most number of epiphytes have been found in zone 1 and 2, relative to zone 3 (Table 7).

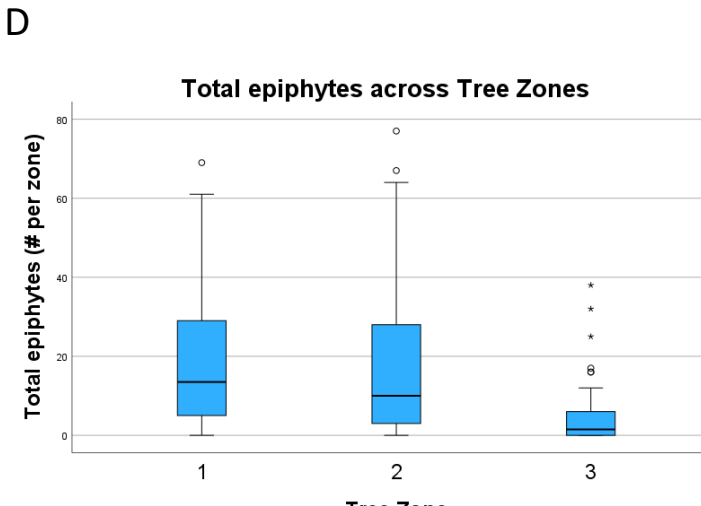
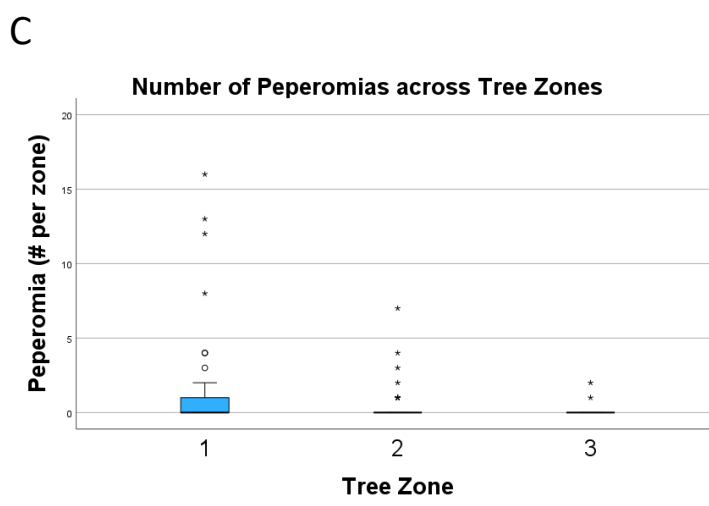
Table 7: General Linear Model results of epiphyte abundance with the relationship between tree zone on the number of epiphytes found for all epiphytes and the epiphyte functional groups (moss cover, orchids, bromeliads, ferns, peperomias and others), with F and significance P ($P < 0,05 = *$, $P < 0,01 = **$, $P < 0,001 = ***$). Tukey post-hoc shows relative relationships between the tree zones (1 bole, 2 inner crown, 3 outer crown) for each epiphyte category.

Dependent Variable (per zone)	Zone	Tukey post-hoc
Average Moss Cover	F = 86,550	3 < 2 < 1
	P < 0,001***	
Number of Orchids	F = 5,049	3 < (1 = 2)
	P = 0,007**	
Number of Bromeliads	F = 6,490	(3 = 1) < 2
	P = 0,002**	
Number of Ferns	F = 5,184	(3 = 2) < 1
	P = 0,007**	
Number of Peperomias	F = 6,444	(3 = 2) < 2
	P = 0,002**	
Number of Other Epiphytes	F = 3,007	(3 = 2) < 1
	P = 0,052	
Total of All Epiphytes	F = 7,2	3 < (2 = 1)
	P = 0,001**	

The results of the general linear model for all epiphyte functional groups and epiphytes in total are presented in Figure 9 below. Table 7 and Figure 9 both show that all epiphyte types follow a spatial distribution, where the prevalence of most epiphytes is generally higher in the lower zones (1, 2) of the tree.



For viewing purposes one data point is excluded from the graph.



Note: two far outliers have been deleted for viewing purposes

Figure 9: Box-plot graphs showing the results of the general linear model on epiphyte abundance for all epiphytes and epiphyte functional groups; moss (A), orchids (B), bromeliads (C), ferns (D), peperomias (E), excluded: other) relative to tree zones stem (1), inner bole (2) and outer bole (3). Blue boxes represent 50% confidence interval, with whiskers indicating outer 25% confidence interval. Dots represent outliers.

5. Discussion

For this research, the following research question was introduced: “What is the effect of 1) macroclimate (altitude), 2) forest type (planted, secondary regrowth and old growth) and 3) tree microhabitat (bole, inner crown, outer crown) on the epiphyte abundance in terms of epiphyte functional groups (mosses and lichens, bromeliads, orchids, peperomias, ferns and others)?”. Results showed no significant relationship between altitude and epiphyte abundance. Orchids were significantly more abundant in the old growth forest type, while taller and larger diameter trees harbored more epiphytes overall, particularly orchids and bromeliads. This research has shown that all epiphytes are significantly preferring a certain allocation in certain tree zones, indicating microclimate habitat preferences by mosses and lichens, ferns, orchids, peperomias and bromeliads.

Reading Guide

This discussion will address:

1. The influence of macroclimate on epiphyte abundance
2. The impact of forest type on epiphyte abundance
3. The relationship between tree microhabitat and epiphyte abundance
4. Strengths, limitations and implications for management
5. Practical implications

5.1 Macroclimate

The hypothesis that epiphyte abundance would increase with higher elevation, where environmental conditions are more favorable for epiphytes, was not supported by the results of this study in CNR. While previous studies by Benzing (1998) and Hofstede et al. (1993) suggest that epiphyte abundance increases with elevation, the lack of a significant relationship between elevation and epiphyte abundance in this research may be attributed to the relatively small temperature differentials over the few hundred meters elevation change where the epiphytes were counted (Chapter 4.1). A study by Yulia et al. (2011) on orchid diversity at different altitudes showed that the orchid species diversity was highest at the altitude of 1922 meters above sea level and the highest number of individuals counted was significantly highest at an altitude of 1796 meters above sea level. This suggests that epiphytic species-specific characteristics might have a more pronounced impact on the diversity of epiphyte communities in the CNR, something this study did not cover specifically. Nevertheless, the threat of climate change to cloud forest ecosystems remains a pressing concern. The results of this study did not show a relation with epiphyte abundance and temperature change, but the whole of CNR is still located in the cloud zone. With the expected shifting of the cloud zones due to climate change (Helmer et al., 2019), the future cloud forests in the CNR are at risk.

5.2 Forest Type

The hypothesis of this study was that epiphyte abundance is strongly related to forest types. The results partially support this expectation as a significant relationship was found between the old growth forest type and orchid abundance, with the highest orchid abundance observed in this forest type. However, no significant relationships were found between forest types and other epiphyte functional groups or all epiphytes in general. Consistent with the hypothesis, host tree characteristics, particularly height and bole diameter, showed significant correlations with the abundance of epiphytes. Orchid abundance increased significantly with tree height, while bromeliad abundance was increasing significantly with DBH. Guild, however, did not seem to play a significant role in the abundance of epiphytes.

The findings suggest that taller trees and those with larger stem diameters, which is often an indicator of tree age (e.g. older growth forests), provide more suitable habitats for certain epiphyte

species. This may be attributed to the increased surface area available on larger trees or to an increase in microhabitats availability for epiphyte colonization, but this remains unsure due to the complexity of the spatial distribution patterns among habitats, as described by Cascante-Marín et al. (2006) and Woods et al., (2015). Research by Yulia et al. (2011) underlines that forest type and host tree density and richness plays an important role in the abundance of epiphytes. For example, Yulia et al. (2011) found that the highest number of orchid individuals was recorded at their research area with the highest host tree density and richness, which could be considered an 'old growth' forest type. Although it is agreed upon that old growth forests are important habitats for orchids, the influence of other forest types or host tree species-specific characteristics, as well as the effect of microhabitat heterogeneity remains less clear (Cascante-Marín et al., 2006; Woods et al., 2015). In conclusion, the results of this study in CNR suggest the complex interplay between forest types, individual host tree characteristics and epiphyte abundance.

5.3 Tree Microhabitat

The hypothesis was that finer-scale distributions within individual trees are expected, mostly in older tree stands. This was based on the practical theory that the higher the tree, the bigger the microclimate habitat differences within one host tree (Nieder et al., 2001; Nieder & Zotz, 1998). The results of this research in the CNR support the hypothesis, revealing significant variations in epiphyte abundances across the tree zones (stem, inner bole, outer bole). The epiphytic functional groups; mosses and lichens, orchids, bromeliads, ferns and peperomias displayed distinct preferences for different tree zones, suggesting a strong relationship between microclimate and epiphyte distribution on stand scale. These findings align with previous studies by for example Woods et al. (2015), where similar spatial distributions were observed in a Costa Rican tropical wet forest. Species-specific preferences in terms of availability of solar radiation, adhesion to the host tree bark and sensitivity to climatic conditions are proposed as reasons for the epiphyte microhabitat allocation.

The data analysis for this study did not combine data on forest type, epiphyte species-specific characteristics and microhabitat preference of epiphytes, while there might be a strong relationship between these factors as suggested by Woods et al. (2015). However, the increase in microhabitat heterogeneity as trees grow, underlines the importance of microhabitat diversity in structuring tropical epiphyte communities.

5.4 Strengths, Limitations, Future Research and Implications

While this study provides valuable insights into the factors and the relationships between these factors influencing epiphyte abundance, limitations such as limited spatial scale and limited time and means for field surveying and data analysis should be acknowledged. Future research could further explore the effects of altitude or temperature change on the abundance of epiphytes, as now the elevation range where the fieldwork was executed was only a few hundred meters, still within the cloud cover zone. Additional factors could be taken into account, such as species-specific characteristics like epiphytic growth stages and death rates as suggested by Hietz et al., (2006). Measuring growth factors such as humidity, substrate availability or solar radiation and canopy cover could also be taken into consideration. In this data analysis, some factors influencing epiphyte abundance were now analyzed separately, while these might be strongly correlated, such as forest type and epiphyte abundance and allocation in the tree zones. For example, research by Hietz et al., (2006) showed that the epiphyte density was three times higher in a disturbed plot compared to a similar undisturbed plot, while the analysis of this research did not cover the direct relationship between epiphyte allocation and forest type.

5.5 Practical Implications

Several practical limitations should be considered in the interpretation of the findings in this report. Firstly, the diversity of epiphyte species poses a challenge. This study did not account for species-specific preferences, as it was already challenging to identify the species. Certain species of the same genus may demonstrate heightened sensitivity to environmental changes, which could be overlooked in this research. Furthermore, the variations in tree characteristics, such as bark texture and canopy cover at the sampled trees, may impact epiphyte abundance, which are factors that are now not included in the analysis. The time constraint in this research posed a significant limitation. The extensive time required for data collection limited the number of trees sampled within the four-month research period. Consequently, the absence of any historical records of changes in epiphyte abundance impedes the ability to assess trends in epiphyte abundance within the TMCF of CNR. This means that potential insights into the forest's state of regrowth succession or the potential climate change impacts on the epiphyte communities are not being considered.

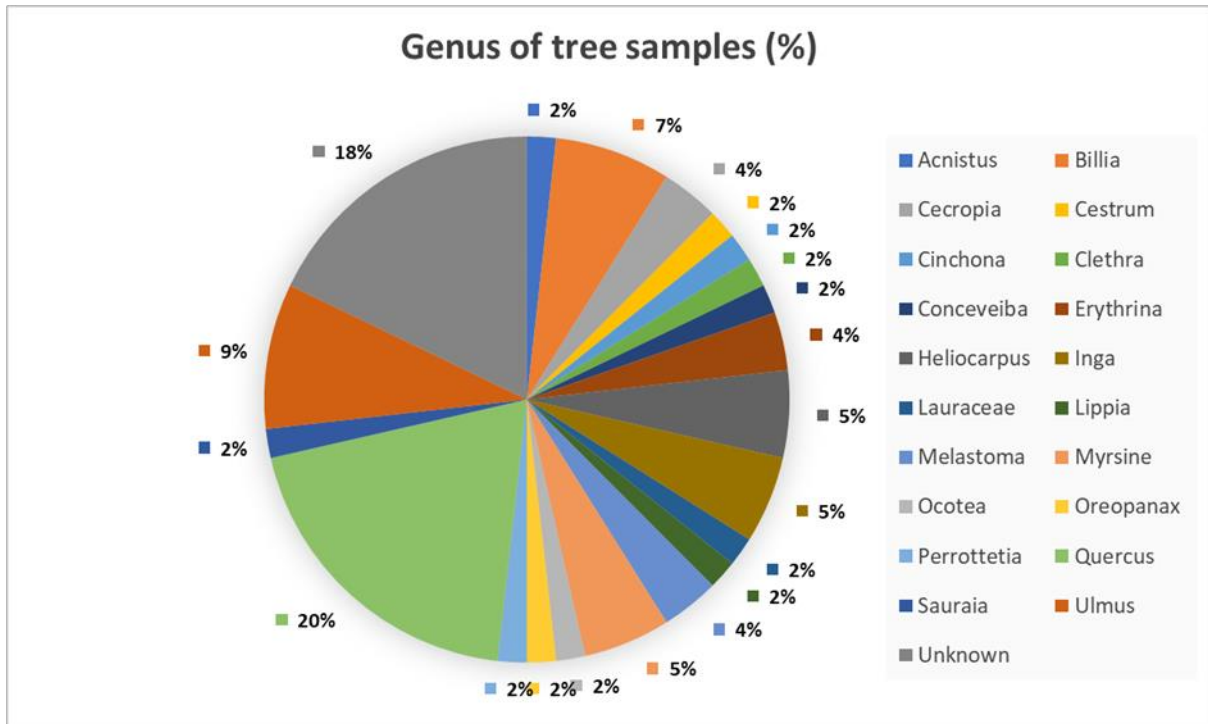
The sampling approach used in this research focused solely on trees that were located next to the trail, which may introduce a bias in exposure to climatic factors such as wind, temperature changes and sunlight availability, as the trail openness might have an impact on the trees microclimate. The selection of trees observed in this research may not be fully representative of the overall epiphyte abundance in the densely tree populated cloud forest. Measurements were taken at two different trails, each in different areas of the reserve where there might have been different successional patterns of forest (re-)growth, which adds complexity to the interpretation of the results. The varying stages of secondary growth might affect epiphyte abundance in a different manner, resulting in additional limitations of the data as forest type categories might have been overly simplified. In addition, the categorization of guilds poses another challenge. The determination of tree species is prone to errors and grouping them introduces further potential errors, as the tree functional groups were roughly divided into groups based on literature (Gargiullo & Magnuson, 2008; Haber et al., 2000; Morales, 2003).

6. Conclusion

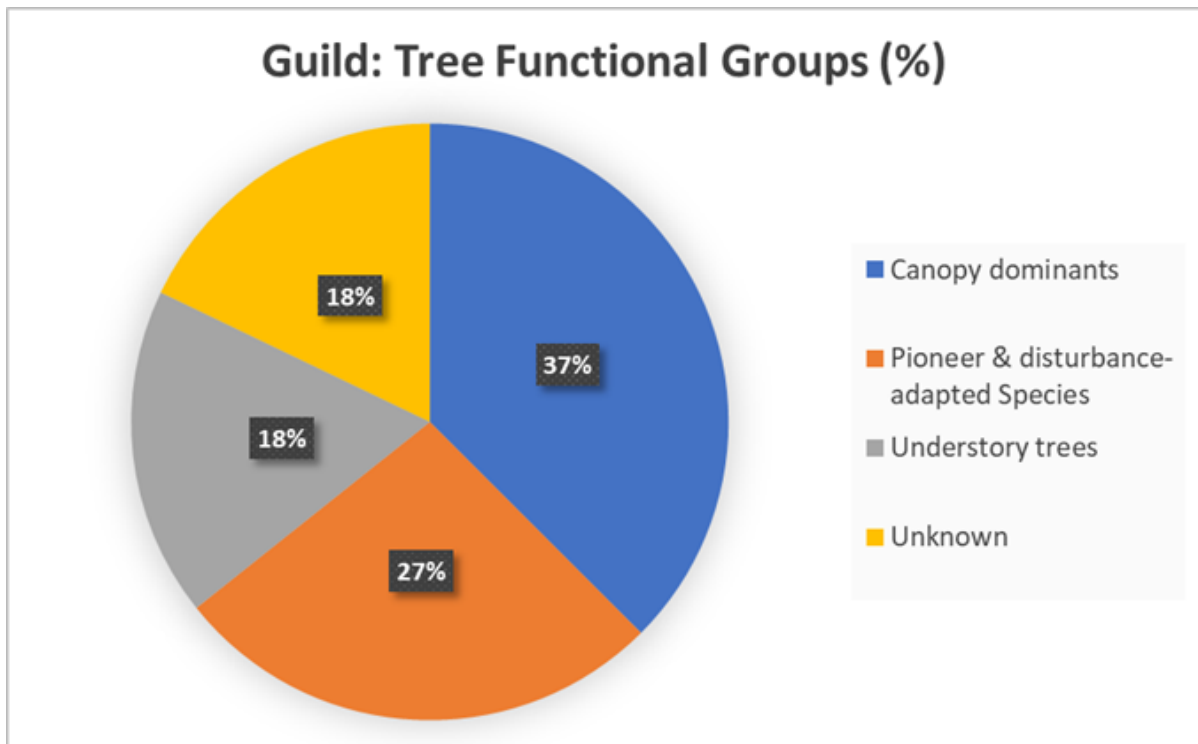
In conclusion, the main question for this research was: “What is the effect of 1) macroclimate (altitude), 2) forest type (planted, secondary regrowth and old growth) and 3) tree microhabitat (bole, inner crown, outer crown) on the epiphyte abundance in terms of epiphyte functional groups (mosses and lichens, bromeliads, orchids, peperomias, ferns and others)?”. Despite the hypothesis that elevation would correlate with epiphyte abundance, this research found no significant relationship between altitude and epiphyte presence. However, orchids were notably more abundant in old growth forests, indicating that epiphyte communities might be more abundant or diverse when the age and structure of a forest are like an old growth forest type. Additionally, taller and larger diameter trees harbored more orchids and bromeliads, emphasizing the importance of forest conservation of old growth forests and bigger trees. Consequently, the importance of tree microhabitat is clearly underlined in this research. Most epiphyte functional groups showed a significant preference in tree zone, indicating preferred allocation zones for epiphyte functional groups.

This study provided insight into the complex interactions between macroclimate, forest type, tree microhabitat and epiphyte abundance. Understanding the dynamics of the epiphyte communities in the TMCF in CNR does not only increase scientific knowledge on the important role of epiphytes in dynamic cloud forest ecosystems, but could also inform conservation strategies in TMCF's and beyond by improving forest management techniques. This could be improved by planting more specific host tree species and managing canopy cover in favor of the epiphyte communities and the forests as an ecosystem. By recognizing the important role of tree microclimate and individual host tree characteristics, one might be able to better manage and preserve these unique and diverse ecosystems for future generations.

Appendix A: Pie Chart Tree Genera



Appendix B: Pie Chart Tree Functional Groups



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