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Vascular epiphyte population dynamics within human-modified landscapes of Guadalupe, Cerro Punta, Chiriquí, Panamá



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I. Abstract

Epiphytes are plants that grow on other plants non-parasitically, and globally, epiphytes compose a very large and diverse group. They are especially abundant and species-rich in the tropics- particularly, in tropical montane forest ecosystems. Human population growth in the tropics, however, has resulted in significant declines in forest cover with land being converted largely for agricultural purposes. Studies on epiphytes have traditionally been undertaken in pristine, undisturbed forest ecosystems, yet terrestrial land conversion has increased the need to understand the value of human-modified ecosystems for epiphytic populations and biodiversity conservation. This study sought to understand the relationship between human modification and epiphytic abundance and diversity. It was hypothesized that as the degree of human modification increased, the abundance and diversity of vascular epiphytes would decrease. Three study sites were selected according to their perceived level of anthropogenic modification, and 20 trees along a 100 m transect from each site were surveyed for their epiphytic composition. The diameter at breast height (DBH), tree height, and canopy cover were also measured for each tree to offer a more holistic understanding of forest ecosystem dynamics and factors shaping epiphyte communities. Results revealed a significant decline in epiphytic abundance with an increasing degree of human modification, although there was no identifiable difference in epiphytic diversity according to family-level classification. However, differences in family-level composition by abundance were present between sites, and DBH was found to be the most significant host-tree factor influencing epiphytic abundance, followed by tree height. These results provide support for the hypothesis that epiphytic abundance would show declines due to modification and are consistent with existing literature that suggests human modification may play a large role in shaping epiphyte populations. This research emphasizes the importance of conserving existing intact forest ecosystems and further exploring the relationship between landscape type and epiphyte populations, and other microclimatic factors and host-tree characteristics that may impact these relationships.

Keywords: epiphytes, human modification, tropical forests, conservation

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III. Introduction

Vascular Epiphytes and Epiphytic Families

In many pristine tropical forests, vascular epiphytes are one of the most species-rich plant groups (Quiel and Zotz, 2021). As defined by Suriyagoda et al. (2018), epiphytes are plants that grow on other plants, not parasitically but for support. They are generally restricted to humid environments, reaching their greatest diversity and abundance in wet tropical regions. Lacking root contact with the forest soil, epiphytes lack access to the most important source of nutrients for ground-rooted plants. Epiphytes do, however, have access to "canopy soil"- the buildup of decaying organic matter- and many have adaptations to acquire water and nutrients via mechanisms such as litter-trapping leaf arrangements, symbiosis with fungi and bacteria, or plant-held bodies of water called phytotelmata. It is the combination of absent forest floor contact and the diversity of nutrient and water sources in the canopy habitat, ranging from precipitation to cloud water and canopy soil, that has played a significant role in shaping the diversity of functional morphologies and nutrient- and water-acquisition mechanisms displayed by epiphytes (Suriyagoda et al., 2018). Consequently, epiphytes hold major importance for the nutrient and hydrological cycles of forest ecosystems.

In the late Cretaceous and early Cenozoic periods, the appearance of angiosperm-dominated forests had a profound effect on terrestrial ecosystems- particularly, increased global precipitation and the creation of novel niches. The heterogeneity of niche space in the angiosperm canopy was marked by stratified light intensities, degrees of humidity, and a range of substrates for growth (Nitta et al., 2020). This space was rapidly filled by a variety of epiphytic plants, and across the tropics today, epiphyte diversity can range from zero to hundreds of species per hectare, and a single tree may harbor almost 200 vascular epiphyte species (Quiel and Zotz, 2021). Globally, vascular epiphytes account for almost 10% of all vascular plants, but locally in humid montane forests, they can comprise up to 50% of vascular flora (Einzmann and Zotz, 2017).

Tropical montane forest, often referred to as cloud forest, is a type of tropical forest found at high elevations, anywhere from 800 to over 3000 meters in elevation. The term includes all forests in the humid tropics that are frequently covered in clouds or mists, thereby catching water droplets that condense on the vegetation in addition to rainfall (Bubb et al., 2004). These forests are typically characterized by an abundance of lush, evergreen vegetation, and a cool, humid atmosphere. With high levels of endemism, they are also home to many threatened species. Within this ecosystem, epiphytes capture water directly from the fogs and clouds and provide a variety of microhabitats for invertebrates, amphibians, and their predators (Bubb et al., 2004). The main families of substantial epiphytic membership include *Bromeliaceae*, *Araceae*, and *Polypodiaceae*.

The family *Bromeliaceae* (commonly known as bromeliads) contains over 50 genera and more than 3,000 species. These plants constitute one of the most morphologically distinctive, ecologically diverse, and species-rich clades of flowering plants native to the tropics and New World subtropics (Givnish et al., 2011). Bromeliads are widely distributed in the Neotropics with three main centers of diversity- the Brazilian Atlantic rainforest, the Andean slopes of Peru, Colombia, and Ecuador, and Mexico and the adjacent Central America. Many species are distributed in endangered biomes and considered endemic (Zanella et al., 2012). *Bromeliaceae* are also part of a group of plants that include bryophytes and lichens referred to as bioindicators,

used to assess the quality of the environment. Studies have found them to be highly effective in assessing air and water pollution by metals and other pollutants (Carrillo et al., 2022).

Araceae (the arum family, also known as aroids) number 140 genera and approximately 4,000 published species, and are one of the oldest members of the angiosperms. Many aroids are hemiepiphytes, germinating on a host tree but later establishing root contact with the soil (Zotz et al., 2021). Many hemiepiphyte species are considered secondary hemiepiphytes, inversely beginning their life as a terrestrial plant, then finding and climbing a tree, and later sometimes losing connection with the ground. Nevertheless, these plants differ from ordinary vines in that the stem often retains a fixed length (Croat and Ortiz, 2020). *Araceae* plants provide food and habitat for a range of animals including birds, insects, and primates, and research has also shown that they contain antimalarial, cytotoxic, antibacterial, antifungal, anti-inflammatory, and anticancer properties (Asharo et al., 2022).

Polypodiaceae (ferns) account for roughly 29% of vascular plant species in terms of epiphyte diversity (Dubuisson et al., 2009). Unlike terrestrial plants, epiphytes must contend with greater stress in the form of nutrient limitation, increased evaporative demand, drought, and extreme temperature oscillations. Epiphytic ferns possess numerous adaptations to combat these challenges, such as morphological features that minimize water loss from their leaves, vegetative desiccation tolerance, and symbiotic relationships with ants (Nitta et al., 2020). Ferns also accumulate masses of humus, or partially decayed organic matter, which provides nesting sites for many species of arboreal ants and other invertebrates.

Tropical Forests, Human Land Use, and Epiphyte Conservation

Tropical forests host over half of all global terrestrial biodiversity. However, despite this crucial role they play, tropical forest cover has been continuously decreasing as a result of human activities. At present, human population growth presents the chief threat to tropical biodiversity as this process drives an increasing need for land to provide food, living space, and other resources (Quiel and Zotz, 2021). According to Phillips et al. (2017), roughly 68,000 km² of tropical forest is lost annually, and this amount could be increasing by 3% (over 2,000 km²) each year. The most important form of land conversion is an expansion of crop and pastoral land in natural ecosystems. This raises concerns about the relationship between environmental services and biotic diversity globally, and resolving the conflict between environmental conservation and economic globalization poses a significant challenge (Phillips et al., 2017). As a result, understanding the current status of tropical biodiversity and developing effective conservation and management strategies depends on an improved understanding of non-intact forest reserves and the role of human-modified forests in conservation (Gúzman-Jacob et al., 2019).

In Central and South America, human population growth has led to massive alteration and fragmentation of native vegetation, and the conversion of forest to agricultural land endangers all components of these ecosystems. The epiphytic habitats in modified landscapes typically consist of "islands" of small natural forest fragments, secondary forests, tree plantations, and scattered isolated trees (Larrea and Werner, 2010). These landscapes tend to have reduced species richness and a modified floristic composition dominated by xerotolerant, or drought-tolerant, species. Furthermore, Larrea and Werner (2010) write that the differences between natural and managed ecosystems in species richness and composition of vascular epiphyte communities are often related to the intensity of human intervention.

By definition, epiphytes rely on trees for their survival. Most anthropogenic disturbances,

however, reduce the average size and diversity of host trees, which directly relate to declines in epiphyte diversity. The loss of particularly favorable host tree species and the drier, brighter conditions that result from human disturbance may also drive declines in epiphyte species diversity (Haro-Carrión, 2009). While it's likely that deforestation will affect epiphytes via regional climate changes, a more immediate impact arises via the loss of locally suitable habitat. A reduction in regional population sizes can reduce genetic variability, making local populations more vulnerable to both natural and human impacts (Poltz and Zotz, 2011). Patchy distributions also increase the risk of pollination failure as the distance between epiphytes growing on isolated trees grows too large for pollinators to cross, or since nesting opportunities are reduced in these habitats. As previously mentioned, epiphytes are excellent indicators of environmental quality due to the high vulnerability that they exhibit to changes in environmental conditions and microclimatic shifts. In addition to pollutants, they display a sensitivity to alterations in tree species and changing moisture content via logging disturbances as a result of their slow process of establishment (Larrea and Werner, 2010).

Substantial and continued human-induced loss of tropical forest cover prompts a call to protect the remaining undisturbed forests and conserve biodiversity in human-modified ecosystems. Traditionally, studies with epiphytes have been undertaken in relatively pristine forests, and to a lesser extent, in secondary forests. Thus, knowledge of the structure and dynamics of vascular epiphyte assemblages on isolated trees and disturbed ecosystems is still relatively limited (Quiel and Zotz, 2021). A better understanding of the ecology and epiphyte populations of these human-modified ecosystems is needed to support the implementation of landscape-level conservation measures.

Study Site

Cerro Punta is located in the Tierras Altas region of Panama in the province of Chiriquí at an altitude of 2,000 meters above sea level. Chiriquí is located on the Pacific side of western Panama, and Cerro Punta is the highest town in this province (Figure 1). The terrain is characterized by steep-sloping mountains cut by valleys with major rivers running through them, and with an average yearly temperature of about 15°C, the climate is relatively cool (Stanganelli 2018). The area also receives significant sunshine and rainfall, and as a result of the volcanic activity of the now inactive Volcán Barú, the soil is markedly fertile (Angher et al., 2006). Combined, these factors make Cerro Punta a highly productive agricultural town, producing 80% of the nation's vegetables and the majority of Panama's domestic food output.

Agricultural activity in Cerro Punta typically takes the form of small commercial or mixed commercial-subsistence plots found on terraced slopes (Odell 2018). The town borders both Parque Nacional Volcán Barú and Parque Internacional la Amistad, which was established as a UNESCO International Biosphere Reserve in 1982 and a World Heritage Site in 1983. As a part of the Talamanca montane forest ecoregion, these life zones are known for their rich biodiversity and high ratio of endemic species (Jones, 2006). In search of fertile soils, farmers continue to encroach upon the forest edges of these zones, though evidently, terrestrial habitat conversions can have grave implications for biodiversity and conservation initiatives. Farmers, ranchers, and loggers clear land for cultivation, livestock, or timber, creating open fields separated by or scattered with forest fragments. These areas are poorly suited for maintaining ecosystem connectivity and alter species-community interactions, leading to increased mortality, disease, competition, population extinction, and decreased species richness (Laurance, 2008). To optimize crop yields and keep up with increasing demands, farmers have resorted to chemical treatment and mechanized production practices, and road construction has increased to facilitate the transportation of food from the region (Cohen and Dannhaeuser, 2002). These practices have reduced the fertility of existing plots, forcing farmers to expand their operations inside the boundaries of protected areas. Situated in such a highly biodiverse region, Cerro Punta faces a struggle to balance the preservation of sensitive habitats with the demand for produce (Merdinger, 2015).



Figure 1. Screenshot taken from Google Earth Pro of Cerro Punta's location in western Panama.

IV. Research Question, Objectives, and Hypotheses

Research Question

What is the relationship between the degree of anthropogenic disturbance and the abundance and diversity of vascular epiphytes across three landscapes in Guadalupe, Cerro Punta?

Research Objectives

- 1. To assess the current population dynamics of vascular epiphytes in human-modified landscapes in Guadalupe, Cerro Punta, Chiriquí, Panama.
- 2. To examine the different factors associated with the growth of vascular epiphytes.

Hypotheses

As the degree of human modification increases across sites, it is hypothesized that the abundance and diversity of vascular epiphytes will decrease. Within each site, as the DBH and tree height of host trees increase, the abundance of vascular epiphytes will increase due to increased tree size and therefore greater surface area for epiphytes to establish. As canopy cover increases, however, epiphytic abundance will decrease due to decreasing light availability and dryer conditions.

V. Methods

Site Selection

Three sites in Guadalupe, Cerro Punta were selected for study according to their perceived level of anthropogenic disturbance (Merdinger, 2015). The first site was characterized by old-growth forest and bordered a farm. According to the property owners, the land has never been cleared or cut (Y. Idiola, personal communication, 2024). Dense undergrowth, an abundance of tree ferns, and four layers of canopy were present. A small walking trail had been cleared through the forest for accessibility, and the only visible sign of human influence present in addition to the trail was a water pipe running through a portion of the forest. With a very low degree of anthropogenic disturbance, this site will be referred to as LOW.

The second site possessed a higher degree of human modification and will henceforth be referred to as INTERMEDIATE. This site consisted of a forested zone with a road cut through it allowing for the passage of vehicles and human foot traffic, clearly indicating some level of forest clearing. Along with the road, a power line running parallel to the road was visible, as were other signs of human activity such as adjacent walking trails and pollution like plastic bottles and wrappers. Two layers of canopy and some undergrowth were present.

The third site will be referred to as HIGH due to its high level of human modification. This site sat at the bottom of the road leading up to the aforementioned farm that the old-growth forest of the low site borders. Like the intermediate site, a road had been constructed running through the site. However, a significantly higher number of vehicles were seen frequenting the road during the data collection period as agricultural produce and supplies were transported to and from the farm. Significantly more pollution was present on the side of the road as well. One layer of canopy and little undergrowth was present (Figure 2).



Figure 2. From left to right: sites LOW, INTERMEDIATE, and HIGH.

Data Collection

Data collection took place between April 8th and April 17th of 2024. As seen in Figure 3, a transect the length of 100 meters was established at each site using a tape measure (Flores-Palacios and García Franco, 2001). The start and end of each transect were marked with flagging tape, as was every 10 meters of transect. The beginning and end point of the transect was recorded using a Garmin GPSMAP 64s (Table 1). For every 10-meter segment of transect at each site, two epiphyte-hosting trees were sampled. This amounted to 20 trees per site and 60 trees total.

To remove sampling bias, each tree present within every 10-meter segment was assigned a number beginning with 1. Using a random number generator, a number representing the tree to be sampled was selected (Acharya et al., 2013). Trees eligible for sampling were those that either bordered the walking trail of the LOW site or the road present in the INTERMEDIATE or HIGH sites. Due to the density of vegetation and uneven topography in the LOW site, only trees that could be safely accessed were considered for sampling. At the high-modification site, trees were primarily sampled from one side of the transect as trees and surrounding vegetation on the other side were largely cleared.

For each tree surveyed, the diameter at breast height (DBH), tree height, and canopy cover were measured. DBH was measured in centimeters using a diameter tape and refers to the diameter of the tree measured at 1.35 meters above the ground at the tree's base (Wang et al., 2016). A handheld range-finder (Nikon PROSTAFF 1000) was used to record the height of each tree in meters, and the final tree height was calculated by adding the observer's height to the measurement recorded by the range-finder. A spherical densiometer was used to find the percentage of canopy cover under each tree (Paletto and Vittorio, 2009). The abundance of epiphytes was found using visual inspection with surveys taken from the ground using binoculars (Poltz and Zotz, 2011). Epiphytes were counted and grouped by family (Figure 4), and family identification was made using a digital field guide of epiphytes of Panama (Laube et al., 2008).

Table 1. O The coordinates of each transeet's beginning and endpoints.				
Site	Level of Modification	Transect Start	Transect End	
		17P 329288.00 m E	17P 0329328.00 m E	
I Low	980840.00 m N	0980892.00 N		
•	T , 1 ,	17P 328890.00 m E	17P 328970.00 m E	
2	Intermediate	981220.00 m N	981289.00 m N	
2	XX' 1	17P 328859.00 m E	17P 328995.00 m E	
3	High	981131.00 m N	981174.00 m N	

Table 1. UTM coordinates of each transect's beginning and endpoints



Figure 3. Screenshot taken from Google Earth Pro and edited in Canva with pins and paths of the relative transect locations.



Figure 4. From left to right: an epiphytic Bromeliaceae, Araceae, and Polypodiaceae.

Data Analysis

All data was analyzed and graphs were produced using Microsoft Excel. One-way analysis of variance, or ANOVA, tests were used to determine if there was a significant difference in the abundance of epiphytes between sites, and in the host tree characteristics of DBH, height, and canopy cover (Melnick, 2022). Fisher's least significant difference (LSD) procedure was performed post hoc to compare the differences between the LOW, INTERMEDIATE, and HIGH groups (Meier, 2006). Bar charts depicting the total abundance of epiphytes per site, the abundance of families across all three sites, and the relative abundance of each family per site were generated, with error bars representing one plus or minus standard deviation to indicate variability within the data. Shannon-Wiener diversity and evenness indices were calculated to indicate the level of diversity and family evenness per site (Dotson, 2019). Scatter plots graphing increasing DBH, tree height, canopy cover and the abundance of epiphytes per tree were created and analyzed with a linear regression model (Melnick, 2022).

VI. Ethics

This project was reviewed and approved by the SIT Institutional Review Board. The Institutional Review Board is primarily concerned with research involving human subjects for either life or social sciences. No interviews were conducted during this study and no human subjects were involved. To ensure minimal ecosystem disturbance, transects were established in areas where paths were already established for human use, and the equipment used was small and light. Transportation within the study period was limited to walking and public transportation to reduce carbon emissions. During data collection, epiphytes were solely observed from the ground. No plants were detached from their host or collected from the trees, nor was undergrowth vegetation removed. Care was taken to respect the local ecosystems and community of Guadalupe.

VII. Results

Vascular Epiphyte Abundance and Diversity

From the 60 trees sampled, a total of 547 epiphytes were observed. Epiphyte abundance was greatest at the LOW site with a total of 284 epiphytes, comprising a majority of the total vascular epiphytes observed. 165 epiphytes were observed in the INTERMEDIATE site, and 98 epiphytes were observed in the HIGH site (Figure 5).



Figure 5. Abundance of vascular epiphytes observed at each site

Bromeliaceae comprised the greatest number of epiphytes across the three sites, with a total of 232 plants observed belonging to the family *Bromeliaceae*. *Polypodiaceae* comprised the second largest population with a total of 170 individuals, and the least observed were *Araceae* with a total of 145 epiphytic individuals (Figure 6).



Figure 6. Abundance of vascular epiphytes by family from all study sites.

Bromeliaceae dominated the LOW site yet were the least common family found in the INTERMEDIATE site. *Polypodiaceae* made up the largest portion of vascular epiphytes in the INTERMEDIATE site while *Bromeliaceae* and *Polypodiaceae* were relatively equal in abundance in the HIGH site. *Araceae* were the second most abundant vascular epiphyte family in the LOW and INTERMEDIATE sites, and the least abundant in the HIGH site (Figure 7).



Figure 7. Abundance of vascular epiphytes by family at each study site.

A one-way analysis of variance (ANOVA) test was performed in Excel to determine the significance of the difference between the abundance of epiphytes per site. With a p-value of 0.000006 (<0.05), results revealed a statistically significant difference in the number of vascular epiphytes by site (Table 2). Post-hoc, Fisher's least significant difference (LSD) procedure using two-tailed t-tests assuming equal variance revealed that the most statistically significant difference between sites was found between the LOW and HIGH site, followed by the LOW and INTERMEDIATE site (Table 3).

Source of Variation	Sum of Squares	df	Mean Square	F	P-value	F crit
Between Groups	887.43	2	443.72	14.94	6.07E-06	3.16
Within Groups	1692.75	57	29.70			
Total	2580.18	59				

Table 2. One-way ANOVA test with three groups (LOW, INTERMEDIATE, and HIGH), measuring variance between the number of observed vascular epiphytes.

Table 3. P-values generated by Fisher's least significant difference post-hoc test, comparing epiphytic abundance in each site to one another.

	LOW vs.	LOW vs.	INTERMEDIATE vs.	
	HIGH	INTERMEDIATE	HIGH	
P(T<=t) two-tail	1.57E-05	0.004	0.01	

The Shannon-Diversity Index (H) and Shannon Evenness (E) values were calculated for each site using the three families identified. Values ranged from 0.93 to 1.05 for Shannon Diversity and 0.843 to 0.956 for Shannon Evenness, with the LOW site possessing the lowest Shannon Diversity and Evenness and HIGH site the highest (Table 4).

Table 4. Shannon-Diversity	/ Index (H	I) and Shannon Evenness ((E)) for each site.
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	LOW	INTERMEDIATE	HIGH
Shannon Diversity Index (H)	0.93	0.95	1.05
Shannon Evenness (E)	0.84	0.86	0.96

DBH, Tree Height, and Canopy Cover

Scatterplots were made using Excel to compare the DBH (cm), height (m), and percent canopy cover of each tree to the number of vascular epiphytes present per tree in each site. In Site 1, LOW, there was an upward trend of an increasing number of vascular epiphytes as the DBH and tree height increased, with an R² value of 0.43 (Figure 8) and 0.45 (Figure 9) respectively. With an R² value of 0.003, canopy cover and epiphyte abundance demonstrated an insignificant relationship (Figure 10).

Site 1: LOW



Figure 8: Diameter at breast height (cm) vs. the number of vascular epiphytes per tree that were observed in Site 1, LOW, with a linear trendline and R² value.



Figure 9: Tree height (m) vs. the number of vascular epiphytes per tree that were observed in Site 1, LOW, with a linear trendline and R² value.



Figure 10: Percent canopy cover vs. the number of vascular epiphytes per tree that were observed in Site 1, LOW, with a linear trendline and R^2 value.

In Site 2, INTERMEDIATE, the upward trend of an increasing number of vascular epiphytes per tree as the DBH and tree height increased persisted, with an R² value of 0.36 for DBH (Figure 11) and 0.21 for tree height (Figure 12). There was a very small downward trend for vascular epiphyte abundance to canopy height, with an R² value of 0.046 (Figure 13).

Site 2: INTERMEDIATE



Figure 11: Diameter at breast height (cm) vs. the number of vascular epiphytes per tree that were observed in Site 2, INTERMEDIATE, with a linear trendline and R² value.



Figure 12: Tree height (m) vs. the number of vascular epiphytes per tree that were observed in Site 2, INTERMEDIATE, with a linear trendline and R² value.



Figure 13: Percent canopy cover vs. the number of vascular epiphytes per tree that were observed in Site 2, INTERMEDIATE, with a linear trendline and R² value.

In Site 3, HIGH, the upward trend of an increasing number of vascular epiphytes per tree as the DBH increased was demonstrated with an R² value of 0.34 (Figure 14), while there was a weak relationship between tree height and the number of epiphytes with an R² value of 0.23 (Figure 15). Canopy cover and the number of vascular epiphytes demonstrated a downward trend with epiphytes decreasing as canopy cover decreased, generating an R² value of 0.22 (Figure 16).





Figure 14: Diameter at breast height (cm) vs. the number of vascular epiphytes per tree that were observed in Site 3, HIGH, with a linear trendline and R^2 value.



Figure 15: Tree height (m) vs. the number of vascular epiphytes per tree that were observed in Site 3, HIGH, with a linear trendline and R² value.



Figure 16: Percent canopy cover vs. the number of vascular epiphytes per tree that were observed in Site 3, HIGH, with a linear trendline and R^2 value.

For each site, the average DBH, height, and canopy cover of all trees sampled was calculated, and a one-way ANOVA test was performed in Excel to determine if there was a significant difference in these factors across sites. With each growth factor producing an ANOVA p-value of less than 0.05, the test confirmed there was a statistically significant difference in DBH, height, and canopy cover across the three sites (Table 5). Fisher's post-hoc LSD test revealed that there was no significant difference in DBH or tree height between the HIGH and INTERMEDIATE sites, yet DBH, tree height, and canopy cover were significantly different, with the percent canopy cover between the LOW and HIGH sites having the lowest p-value (Table 6).

Table 5. Average DBH, height, and canopy cover per site, and the p-value resulting from a
one-way ANOVA test with three groups (LOW, INTERMEDIATE, and HIGH), measuring
variance between DBH, height, and canopy cover.

	DBH (cm)	Height (m)	% Canopy Cover
Average LOW	34.33	21.40	73.69
Average INTERMEDIATE	25.01	13.60	63.08
AVERAGE HIGH	25.085	15.24	36.92
ANOVA P-Value	0.026	1.81E-07	3.54E-17

Table 6. P-values generated by F	isher's least significant difference post-hoc test,
comparing DBH, tree height, and	percent canopy cover in each site to one another.

	DBH (cm)	Height (m)	% Canopy Cover
LOW vs. INTERMEDIATE	0.032	3.32E-06	0.00077
LOW vs. HIGH	0.042	0.00012	3.24E-15
INTERMEDIATE vs. HIGH	0.98	0.074	7.21E-10

VIII. Discussion

Vascular Epiphyte Abundance and Diversity

This study sought to analyze the relationship between epiphytic abundance and diversity and the degree to which the landscape they are found has been anthropogenically modified. Across three sites of low, intermediate, and high modification, 547 vascular epiphyte individuals were found from 60 sampled trees. In a study conducted in a tropical montane forest region in Tanzania on species composition, diversity, and distribution of vascular epiphytes, 59 host trees were sampled and 476 epiphytes were recorded in the area (Mangosango and Griffiths, 2019). The total number of epiphytes found across nearly the same number of host trees in a likewise tropical montane forest, then, can be considered substantially sufficient to conduct statistical analysis.

Recorded vascular epiphytes were limited to three main families chiefly found in tropical montane forests, those being *Bromeliaceae, Araceae,* and *Polypodiaceae.* A one-way ANOVA test comparing the abundance of epiphytes at each site confirmed that the difference between epiphytic abundance per site was statistically significant (Table 2). These differences were also statistically significant when each site was compared with one another in post-hoc t-tests, and with a p-value of 0.000016, the LOW and HIGH sites had the greatest difference in epiphytic abundance, followed by the LOW and INTERMEDIATE sites (Table 3). Pairing these results with the finding that as the degree of human modification increased, the abundance of vascular epiphytes significantly decreased (Figure 5), these results provide support for the hypothesis that the abundance of vascular epiphytes will decrease with an increasing degree of human modification.

In regards to the relative abundance of each epiphytic family surveyed in this study, *Bromeliaceae* accounted for 60.91% of the epiphytic population in the LOW site, with *Araceae* holding the second largest population (Figure 6). However, *Polypodiaceae* were most abundant in the INTERMEDIATE site, accounting for 54.54%, and in the HIGH site, *Bromeliaceae* and *Polypodiaceae* each made up approximately 40% of the epiphytic population. The difference in the relative abundance of epiphytic families could indicate a compositional change in epiphytic populations with increasing levels of modification. Nevertheless, Shannon-Wiener diversity and evenness indices calculated for each site were remarkably similar (Table 4). The greatest Shannon diversity recorded was 1.05, with the highest evenness being 0.96; the lowest Shannon diversity and evenness, 0.84. Surprisingly, the HIGH site rather than LOW had the highest diversity and evenness, contradicting the hypothesis. The abundance of *Bromeliaceae* in the LOW site may have been responsible for the slightly lower Shannon diversity given that the Shannon diversity index considers both species richness and evenness.

A limitation of this particular study was that the specific form of human modification- for instance, an agroforestry system, timber plantation, or other- was unable to be accounted for. Human modification was more broadly categorized and evaluated by the observed level of disturbance and frequency of land use, with community conversation confirming that the LOW site was for the most part untouched. However, the previously mentioned forms of human modification have generally been shown to reduce epiphytic abundance, species richness, and diversity. For example, in montane forests in Venezuela (Barthlott et al., 2001) and Ecuador (Benitez et al., 2015), the abundance and diversity of vascular epiphytes was lower in secondary forests than in adjacent primary forests. Moreover, there was a compositional change, with fewer

ferns and more bromeliads in secondary forests. Similar results were found in the Dominican Republic, Slovakia, and Ecuador, with life-form diversity and abundance of epiphytes higher in old-growth or primary forests than secondary (Nadkarni, 2023). The results found in this study are therefore consistent with previous studies that indicate human modification reduces epiphytic abundance and may cause compositional changes in community makeup, though no significant results were found pertaining to diversity.

The lack of significant results for changes in epiphytic diversity with respect to human modification could be explained by another limitation of this study, which was that observations of the vascular epiphytes were made from the ground using binoculars. The inability to physically access the forest canopy made species-level identification not possible for this study, resulting in family-level classifications. Numerous studies, however, have found decreases in species richness and diversity amongst epiphyte populations in human-modified areas in comparison to old-growth or primary forest zones. In Mexican cacao plantations, epiphytic orchid diversity was higher in rainforest areas than in cacao plantations, with only seven species in common (Morales-Linares et al., 2020), and in the aforementioned research by Barthlott (2001) and Benitez et al. (2015) on montane forests of Venezuela and Ecuador, species diversity was also lower in secondary forests than primary forest. According to visual observations during the study period, many of the epiphytes demonstrated unique characteristics in form, size, and color. Should species diversity calculations have been possible for this study, there is a likely possibility that greater differences in Shannon diversity and evenness would have been observed.

Host Tree Characteristics and Epiphyte Communities

In addition to statistically significant differences in the abundance of vascular epiphytes per site, there were also statistically significant differences in the DBH, tree height, and canopy cover between the three sites (Table 5). On average, site LOW had the greatest tree DBH, height, and canopy cover. DBH and tree height were most statistically different between the LOW and INTERMEDIATE sites, while canopy cover was most statistically different between the LOW and HIGH sites (Table 6). Tree growth relies on several different factors such as climate, plant-plant interactions, genetics, age, and biotic disturbance (Garfi and Garfi, 2023). Disturbance, both human-induced and natural, also plays a crucial role in shaping the dynamics of forest systems by influencing composition, structure, and functional processes (Glasby and Russell, 2019). In each of the sites, there was a strong positive relationship between DBH and epiphyte abundance (Figures 8, 11, and 14). A study conducted in the lowlands of Panama found similar results, where there was a positive correlation between epiphyte abundance and host DBH, which supports the general notion that large and old trees are of disproportionate importance for epiphytes (Quiel and Zotz, 2021). Another study conducted on epiphyte assemblages in a lowland tropical forest in Southeast Asia likewise found that about half of all epiphyte species recorded in their study were observed on trees with a DBH greater than 60 cm, emphasizing the importance of tree size on epiphyte populations (Gogoi and Sahoo, 2018).

Tree height had some relationship with epiphytic abundance but to a lesser degree than DBH, demonstrating a slight positive relationship in the LOW and INTERMEDIATE sites (Figures 9 and 13), while canopy cover only demonstrated a slight negative relationship in the HIGH site (Figure 16). As trees grow, their morphological and physiological characteristics, including tree architecture, bark roughness, and canopy soil chemistry often influence epiphyte community development. While this study does not offer strong support for an association

between epiphytes and tree height, other studies have shown that epiphytes are associated with crown height and the orientation of host trees in relation to variability in microclimatic conditions (Wang et al., 2016). Vertical environment heterogeneity in humidity, temperature, the accumulation of organic matter, and solar irradiance, for example, have been found responsible for epiphyte distribution with respect to tree crown height (Woods et al., 2015).

Human disturbance in this study was shown to significantly impact host tree characteristics, and in turn, characteristics of host trees influence epiphytic populations. DBH was revealed to be the most significant growth factor influencing epiphytic abundance within these study sites. Future research in this region may take interest in analyzing additional host tree characteristics and microclimatic conditions that could influence epiphyte community development, and how these many variables including DBH, tree height, and canopy cover interact. Understanding the relationship between human modification, microclimatic conditions, and forest composition, then- particularly, how ecosystems in this area respond to disturbancemay paint a broader picture of the interplay between host trees and epiphytic communities in human-modified landscapes.

IX. Conclusion

Epiphytes are tremendously important to the structure and function of tropical montane forests, playing invaluable roles in the natural processes within these ecosystems and serving as major contributors to the high diversity of insects and other animals. Vascular epiphytes themselves are also a highly diverse group, making it possible to play such diverse ecological roles. Nevertheless, this group is threatened by human interference as populations grow and increasingly large areas of land are converted from forest for human use. Without host trees, epiphytes cannot survive, making the issue of tropical forest conservation of great significance for epiphyte conservation.

It was hypothesized that human modification would significantly shape epiphytic abundance and diversity in this study, though only epiphytic abundance varied significantly between sites, with the site of lowest modification possessing the highest abundance and the highest modification, the lowest. Results also supported the hypotheses that DBH and tree height would demonstrate a positive relationship with epiphytic abundance, although increasing canopy cover did not generate a decline in epiphyte abundance. Consequently, the research objectives of assessing epiphytic communities in Cerro Punta and disentangling a piece of the puzzle that is epiphytes and their host tree preferences were achieved during this study.

This study and existing literature on epiphytes in human-modified landscapes highlight the importance of protecting intact forest reserves where epiphytes thrive. However, it is clear that other types of forested zones and human-modified landscapes will play a role in the future in supporting epiphytic populations given that they may be the only available landscapes for epiphyte survival in some regions. A compelling avenue forward is presented for future research on the many factors that influence epiphytic growth within human-modified ecosystems and the types of conservation strategies that may be developed to support epiphytic communities.

X. References

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