Environmental Drivers for the Distribution of Epiphytic Bromeliads in a Tropical Montane Cloud Forest

Cloudbridge Nature Reserve
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Abstract

Epiphytes are a group of plants that are predominantly found in tropical ecosystems. They are distinct from other plant groups in their niche specialization, which allows them to grow on the surface of other plants and occupy all levels of the forest canopy. This adaptation enables them to play an important role in tropical forest ecosystems by providing sources of food, water, and habitat completely disconnected from the forest floor that many species rely on. Despite their ecological significance, there is relatively little information on their presence in remote regions, and foundational research on their distribution is lacking. As ecological indicators, epiphytes provide key insight to ecosystem health across forest succession stages. Cloudbridge Nature Reserve, a montane cloud forest in the Talamanca mountain range of Costa Rica, served as the study site for analyzing epiphyte abundance, diversity, and habitat preferences across three distinct forest types. Over fifteen weeks 2,298 individual occurrences were recorded, with *Tillandsia leiboldiana* being the most prevalent species. Naturally regenerated forests exhibited the highest epiphyte abundance, with old growth regions showing a higher prevalence of tank-forming epiphytes. Environmental factors, including elevation, distance to water, and moss presence were examined for their impact on epiphyte distributions with elevation having the largest influence with distance to water and moss presence having little to no impact.

Introduction

Background

Forests form the foundation for biodiversity, with over 70% of all life relying on them for survival (WWF, n.d.). Of all the forest types, tropical montane forests, or cloud forests, are particularly noteworthy for their exceptionally high levels of biodiversity relative to their land coverage (Luna-Vega et al., 2023). These forests play crucial roles in regulating regional water cycles and act as important cradles of biodiversity, supporting a large amount of endemic species that can be used as indicators of potential impacts brought upon by climate change (Still et al., 1999).

Costa Rica is on the forefront of ecosystem conservation efforts as historic trends of deforestation have moved towards a conservation/ecotourism approach due to the reality of climate change research. While conservation efforts are present throughout the country, tropical montane cloud forests (TMCF) are seen as one of the most critical ecosystems for conservation. Despite only accounting for 2.4% of total forest coverage, they contain 50% of the country's plant biodiversity, 40% of mammalian species, and 50% of bird species (Alvarado et al., 2011; Newcomer et al., 2022). TMCF are only found at elevations above 1100 meters and are characterized by their lower precipitation amounts in favor of higher humidity with frequent periods of mist (horizontal precipitation) and cooler temperatures (Helmer et al., 2019). This creates unique conditions that favor highly specialized flora and fauna, many of which are endemic to the high elevations mountain ranges. Species found here rely on stable climate conditions and are particularly susceptible to minor fluctuations in temperature and precipitation. Alterations in these conditions could create habitat that would facilitate the invasion of lower elevation species as they try to escape a warmer and drier environment (Eller et al., 2020).

The climatic conditions found in TMCF create ideal environments for supporting epiphytic species, many of which are not found in other tropical ecosystems at lower elevations. Vascular epiphytes are plants that grow non-parasitically on other plants (Benzing, 1990). The term "epiphyte" is used to describe the growth habit of plants that do not use soil and instead root and germinate in regions above the forest floor. Even with this definition, "epiphyte" is an ambiguous term with further classifications distinguishing between "obligate, accidental, and facultative" (Hoeber & Zotz, 2022). These further classifications are constantly changing, however, as a lack of information makes it difficult to apply these systems and our understanding improves (Zotz, 2013).

Temperatures and precipitation amounts have historically remained regular in the Cloudbridge region of Costa Rica, with a 10 ℃ max temperature difference (Figure 1). Ecosystems characterized by narrow temperature ranges have been shown to be more susceptible to fluctuations as species with limited temperature tolerances have a greater risk of extinction under changing climatic conditions (Beaty et al., 2023; Grinder & Wiens, 2023). Previous studies which have exposed epiphytes to conditions found at lower elevations (e.g. longer, more intense dry season conditions) saw an increase in mortality and a decrease in leaf production and efficiency (Nadkarni & Solano, 2002). Recent estimates have found that 1% of cloud forests are lost each year globally due to human activity. When combined with the impacts of climate change, recent models predict that these ecosystems are at the most risk of loss, with the potential of 60 - 80 % loss by 2050 (Evans, 2020).

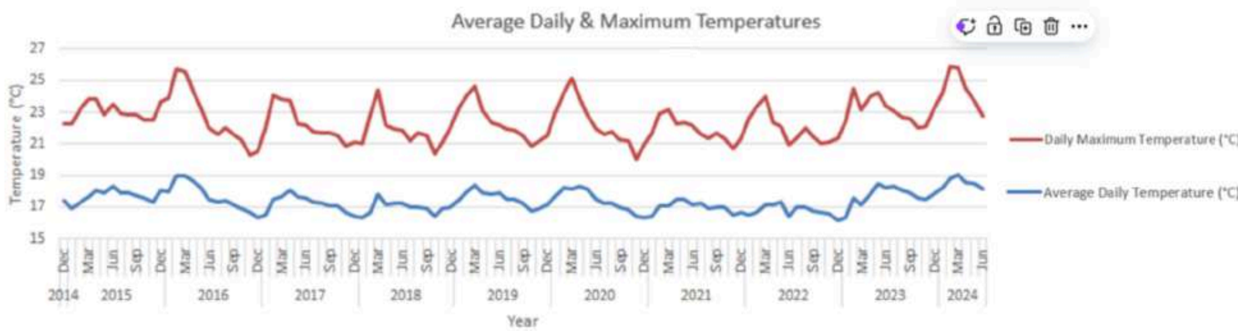


Figure 1. **Average & maximum temperatures at Cloudbridge over the past 10 years (Instituto Costarricense de Acueductos y Alcantarillados, 2024).**

Epiphytes are a unique classification of plants which accounts for around 9% of all vascular plants, and contain over 28,000 species (Zotz, 2016). The defining features of epiphytes is their growth habit, and dependence on the frequent mist coverage as a source of water as they pull atmospheric moisture from the air. This, however, does not make epiphytes more resilient to droughts even in more humid environments as it seems the mist is what provides a majority of the moisture, not just high ambient humidity (Darby et al., 2016). These plants play a vital role in the complexity and function of TMCF ecosystems, creating a population in mid-canopy levels that increases habitat complexity and providing microenvironments that support a wide range of invertebrates, amphibians, and birds (Pardow et al., 2012). Additionally, they make up more than 20% of cloud forest biomass, contributing significantly to carbon sequestration and habitat complexity (Nadkarni, 1984). As they are largely disconnected from conditions on the forest floor, they fill a unique and vital niche, converting atmospheric water into a source of available liquid for other invertebrates and animals.

Bromeliads

One of the most studied groups of epiphytes are bromeliads which are known to contain over 3,500 species spread across 80 genera (Gouda et al., 2022). These plants are endemic to the western hemisphere with the exception of *Pitcairnia feliciana* which is found in Western Africa

(Porembski, 1999). Regional variation amongst individual species has been observed such as with *Vriesea arachnoidea* being shown to grow terrestrially in most of its range, but primarily epiphytic in the Serra da Araponga region of Minas Gerais, Brazil (Gomes-da Silva, 2011). Costa Rica is among one of the more diverse countries when it comes to epiphytic diversity. Over 200 species are native to the country with a high level of endemism at 30% (Cáceres González et al., 2013).

Tank-forming bromeliads are of particular ecological significance due to their unique growth habit. These plants have evolved with a tighter arrangement of leaves that forms a basin to collect rainwater and organic material which the plant can feed off of, known as phytotelmata (Nash et al., 2021). Entire ecosystems are self-contained within these phytotelmata with new inquiline species still being discovered (Pešić et al. , 2015 ; Malfatti et al., 2020). Species such as the Yellow Heart-Tongued Frog (*Phyllodytes luteolus*) have been found to shelter, forage, and reproduce entirely in a bromeliad (Mageski, 2016). More famous is the strawberry poison-dart frog (*Oophaga pumilio*) which shares a similar life-cycle to *P. luteolus* in that mother frogs transport newly hatched tadpoles into bromeliad pools along with nonviable eggs for the developing tadpoles to feed on (Maple, 2002). Other species have also been found using bromeliad tanks such as the mosquito *Anopheles sp.*, which is a vector for malaria in humans. These insects use the standing water found in tank bromeliads as habitat for larval stages of their life-cycle. While providing food for many other animals, regions where malaria has been found have seen eradication programs of tank bromeliads in an effort to quell potential outbreaks (Britannica, 2023).

Large Epiphytes

2 larger epiphytic plants were included in this study: being *Asplenium sp.* and *Anthurium salvinii*. *Asplenium sp.* is a large epiphytic fern found presently across Cloudbridge Nature Reserve (CNR) in Costa Rica. It is notable for its size and elongated leaves that are distinct from other ferns found in the area. While there is no species level identification within the current plant list, individuals appear most similar to *Asplenium serratum*. For the purposes of this project, identification was kept broad as the main focus of this study was to document distributions, and obtaining species identification was beyond our scope. These plants were chosen due to their distinct appearance and abundant presence throughout the reserve. Some individuals of *Asplenium sp.* were found to be growing terrestrially and were not recorded for this study.

Anthurium salvinii, locally known as “Tabacon” or Birds Nest Fern is a large (~1m width) facultative epiphyte that is found at 200m-1700m from Mexico to Colombia. Its name derives from its growth habit which is similar to tank bromeliads in that it consists of an arrangement of leaves that form a central basin for debris to accumulate in (Elibox, 2008). The inclusion to document *A. salvinii* in this study is due to its relative rarity compared to other epiphytic plants coupled with their potential as ecosystem indicators (Andama et al., 2003).

Figure 2. **Epiphytic plants used during this study: A. *Tillandsia leiboldiana*, an atmospheric bromeliad. B. Flowering *Tillandsia oerstediana*, a tank-forming bromeliad with organic material present. C. *Asplenium sp.* D. *Anthurium salvinii***

Gaps in Knowledge

Despite their ecological importance, research on their distributions is relatively new, and few studies focus on the abiotic factors that influence their distributions (Madison, 1977; Ding et al., 2016). Bromeliads specifically lack up-to-date information with the only comprehensive literature available being J. F. Morales' book *Bromeliaceae* (2003) which provides detailed descriptions and ranges for 17 present genera in Costa Rica and was the primary resource used for this project. While this literature does contain useful information for identifying bromeliads, it is outdated with the most recent, 2nd edition being published in 2003, and found to be incorrect in certain species' descriptions. One of the prime examples of this is found in the description of *Tillandsia oerstediana* which Morales describes as being found from 1000m - 1350m in Cordillera de Talamanca but is actually found abundantly within and around CNR (>1500m) with occurrences being found above 2091m, far above its described range. The blooming range of *T. oerstediana* was also incorrect with January to February stated, but was found in multiple stages of blooming throughout this project from July to September). Some information is also only provided in Spanish, making it difficult to use for non-Spanish speakers. Of the 195 species documented within the book, only 19 drawings are provided, with the rest of descriptions limited to highly technical text descriptions (Morales, 2003).

Another resource exists in Francisco Oliva-Esteve's "*Bromeliaceae III*" (2002) which contains 320 bromeliad species found throughout the Neotropics, but focuses specifically on species found within Venezuela. This book was not available to use during the time-frame of this project, but similar to Morales' book, the most up-to-date version was published in 2002 and is considered to be outdated.

Additionally, there is no field guide that exists for identifying bromeliads in situ, with the most available resource currently being iNaturalist. Existing resources, such as herbarium records or botanical drawings, are valuable for taxonomic reference but are impractical for fieldwork. The list of plants within Cloudbridge, while robust, is missing many species of bromeliads and has no current plants that resemble the *Asplenium sp.* that was used for this study. While this study provides some insight into the epiphytic plants found in the area, the full comprehensive species identification list is beyond the scope for a novice botanist to complete.

Research Objective

Species Occurrence Database:

The primary goal of this project was to create a species occurrence database of epiphytes found within the CNR region of the Talamanca Mountains. We sought to identify and document as many occurrences as possible including images and location data. This data can then be used in future studies to create identification tools, or study specific species' responses to climate change.

Factors that Influence Distribution:

To improve our understanding of ecosystem and epiphyte relations, we utilized GIS software and physical observations to test the impact of abiotic environmental factors on epiphyte distributions. While there is still much progress to be made in the field of identification and distributions of epiphytic plants, this project seeks to act as a foundational study that future research can build upon as available resources improve.

Elevation

Elevation is expected to have a significant impact on epiphyte distributions. Due to their reliance on atmospheric moisture, we expect to see a greater abundance of epiphytic plants at higher elevations. As horizontal precipitation begins at the cloud line and moves down the slope, higher elevation epiphytes have more access to horizontal precipitation (Marcusso et al., 2022). Temperature is also strongly influenced by elevation, which has been shown to play a crucial role in determining ecological niches (Melnick, 2002).

Forest Type

Forest type is also expected to have a significant influence on epiphyte distributions. While there are only 4 forest types on the reserve (Human Use, Planted, Natural Regrowth, Old Growth), conditions found within each type differ greatly due to topography and forest age. This creates large variation in ecological niches within each forest type that favor different epiphytic populations. If no impact were present, we would expect to see distributions of epiphytes proportional to the respective size of each type (Human Use = .22%, Planted = 7.65%, Natural Regrowth = 37.1%, Old Growth = 55%).

Distance to Water

Distance to water is not expected to have a significant impact on bromeliad distributions due to their ability to capture water from the air. If an impact is present, we expect to see a weak correlation of slightly more bromeliads occurring closer to water. The larger epiphytes may see a stronger correlation as they aren't able to store water like bromeliads, and instead absorb water more directly through their leaves (Tobón, 2011).

Moss Presence

Coexistence between epiphytes and bryophytes is a relationship that we noticed during the length of this study. Bryophytes have been shown to create microhabitats that facilitate the growth of epiphytes in more temperate environments, so we can expect a similar relationship in tropical environments as well (Spicer, 2022). We determine if an epiphyte is coexisting with a bryophyte by looking at the aerial root connection to the host and seeing if bryophytes (i.e. moss and lichen) are present. We expect to see a stronger correlation of bryophyte coexistence among smaller/atmospheric bromeliads as they have had less time to establish with their host tree.

Methods

Study Area

This study was carried out in Cloudbridge Nature Reserve (San Gerardo de Rivas, San Jose Province, Pérez Zeledón canton, Centered at 9° 28' 18.624" N, -83° 34' 40.0794" W), a 700 acre private reserve of high elevation cloud forest located within the Talamanca mountain range in Southern Costa Rica from June to October which was the rainy season (Table 1). The altitude of the reserve ranges from 1550 m.a.s.l. to 2600 m.a.s.l. and contains regions of planted, naturally regenerated, and old growth forests. Forest age between regions varies within the reserve with some regions being reforested as early as 20 years ago, with older regions containing primary old growth (>150 years). Cloudbridge Nature Reserve (CNR) sits between Chirripó National Park and San Gerardo de Rivas and acts as a buffer ecosystem for tourists entering the national park. Visitors have two ways to enter the national park from this region: the Chirripó main trail which borders CNR property, or directly through the reserve via the Montaña trail. Both methods have resulted in a significant increase in foot traffic around the reserve.

Month	T °C (min)	T °C (max)	T °C (average)	Precipitation (mm)	Humidity (%)
January	13.56	22.63	17.02	33.31	86.08
February	13.77	24.09	17.69	19.88	79.55
March	14.17	24.35	17.89	84.18	81.91
April	14.82	23.41	17.88	217.91	88.29
May	15.29	22.77	17.86	389.63	92.51
June	15.06	22.27	17.55	311.66	93.36
July	14.86	21.89	17.41	192.23	93.23
August	14.82	21.97	17.35	264.6	93.25
September	14.65	21.80	17.17	374.48	92.73
October	14.64	21.33	16.95	467.1	94.49
November	14.46	21.10	16.80	307.93	95.87
December	13.86	21.72	16.88	92.14	91.66

Table 1. Annual temperature, precipitation, and humidity in Cloudbridge (Instituto Costarricense de Acueductos y Alcantarillados, 2024)

Identification

A large portion of time during this study was devoted to bromeliad identification. There is no established database of epiphytes found within the Talamanca Mountains so available literature was used as a suitable substitute. Written descriptions found within J.F. Morales' "Orquídeas, cactus y bromelias del bosque seco Costa Rica" (2000) were helpful when coupled with the illustrations present. During the scope of this study, a large portion of bromeliads were flowering which made identification easier. While not always providing an exact species identification, this would provide a genus level I.D. which could be documented. Distinguishing between "Tank" and "Atmospheric" was done by identifying size with atmospheric being <25cm, shape, leaf structure, and presence of phytotelmata for tank bromeliads.

Data Collection

Data was collected from June to September of 2024 to encompass as many different bromeliad blooming seasons as possible. Data was collected along all trails within the reserve excluding Heliconia and Private/Waterfall. The trails that were surveyed contain a gradient of elevations and different forest types, ranging from 1500m to 2400m and containing planted, naturally regenerated, and old growth sections (Figure 3). Sentinel contains regions of old growth forest, but these areas are assumed to be young relative to other old-growth regions of the reserve such as the top of Montaña (~2200m) and Skutch (~2300m). Skutch is unique in that a majority of the trail is composed of undisturbed primary forest. The differences between these trails allow us to observe epiphyte distributions across forest ages and stages of succession.

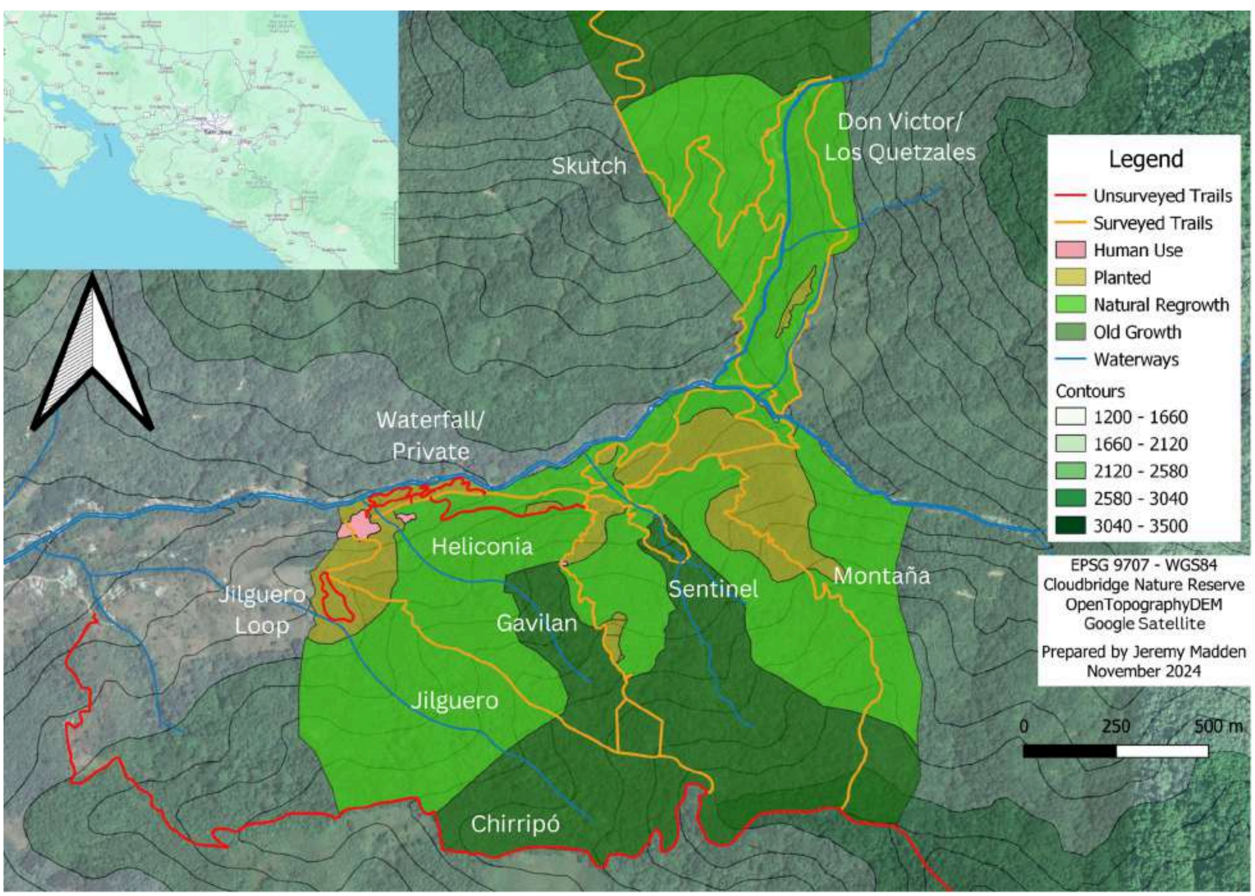


Figure 3. **Map of surveyed and unsurveyed trails within Cloudbridge Nature reserve with approximate location within Costa Rica**

For an accurate assessment of abundance across forest types, comprehensive surveys were conducted across the full length of the trail. Surveys began at the trailhead and were conducted by visual observations of epiphytic species found within <50m of either side of the trail. The height of each individual from the forest floor was not considered due to uneven terrain and difficulty assessing height of individuals further from the trail. When an epiphyte was spotted an image of the individual was taken at the closest point to ensure accurate GPS data. For locations that had large populations within a small area, each species was still counted, but limitations with GPS accuracy caused overlap of GPS points across small scale sections (>5m). This method proved useful in that with a high-quality camera, images of the canopy could be taken from the trail and later analyzed at the research station for identification and count.

Each individual epiphyte within an image was identified to at least the genus level using the aforementioned methods and compiled into an Excel spreadsheet along with the corresponding GPS location data, and bark type (Bare or Moss). This data was then imported into QGIS for further analysis. Using OpenTopography DEM, we were able to obtain elevation data of each GPS point. This method was also used to obtain the forest type for each point as attempting to do this in the field proved too difficult. Lastly, distance to water was obtained using the "Distance to nearest hub" analysis tool with the "Waterways" shapefile. This data was then exported into a spreadsheet containing: Identification, Longitude/Latitude, Trail, Elevation, Forest Type, and Moss Presence.

Data Analysis

In this study, statistical analyses were utilized to evaluate the relationships between environmental factors and epiphyte distributions. Linear regression tests were used on X-Y scatter plots from data obtained via QGIS analysis. This allowed us to test for a linear relationship between occurrences and the effects of elevation and distance to water sources. This method produced r-values to determine the strength and direction of relationships with r-values close to 1 indicating a strong positive correlation, and -1 indicating a strong negative correlation.

To test the correlation between occurrences with forest type and moss presence, Chi-square tests were used. For forest type, our null hypothesis assumes that occurrences will be distributed proportional to the respective size of each type. When compared against our expected values, a χ^2 value was obtained to determine if occurrences are distributed independent of forest type. A similar test was performed for occurrences and presence of moss with our null hypothesis predicting an equal number of occurrences on bare substrate and moss. For both linear regression and χ^2 tests we determined if a result was significant with $p < .005$, with values smaller indicating statistical significance

Results

Image Database

In total 2,154 images were captured which resulted in 2,298 individuals being cataloged. For difficult to identify plants, genus sp. was used, and unidentifiable individuals were discarded. This resulted in a final count of 2,232 individuals with a confidant identification (Appendix). A source of the present discrepancy between total images and individuals is due to multiple individuals being present in some images. Multiple individuals in the same spot were recorded to give an accurate number of the total individuals on the reserve. Additionally, some images lacked GPS data and were discarded (>20). The final database of images can be accessed via Google Drive and downloaded for future analysis.

Epiphytic Diversity

A total of 2,232 epiphytes were recorded within the reserve, with atmospheric bromeliads representing the largest group, with 58% of the total diversity. 21% of all epiphyte occurrences were a single species of atmospheric bromeliad: *Tillandsia leiboldiana.* Tank bromeliads accounted for 22% of the recorded individuals, making them the second most prevalent group (Figure 4). *Asplenium sp.* followed, consisting of 19% of occurrences. The least abundant species was *Anthurium salvinii*, which comprised only .8% of the total occurrences, with 20 individuals documented.

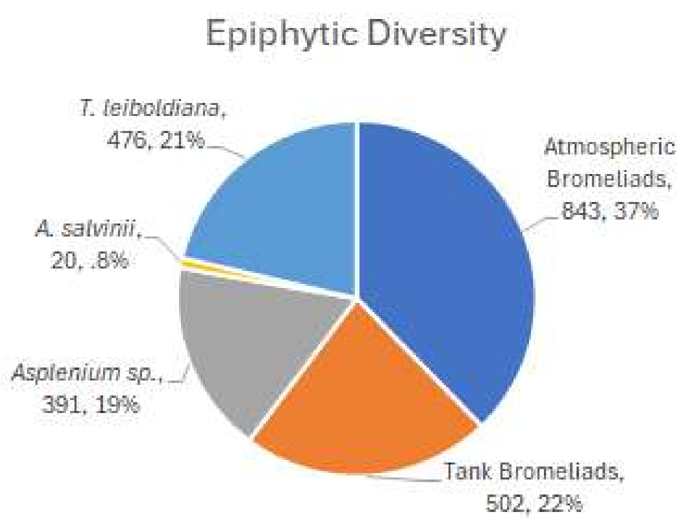


Figure 4. **Pie chart of epiphytic plant diversity within Cloudbridge. *T. leiboldiana* was categorized with atmospheric bromeliads for the purposes of this study.**

Maps

Distributions of atmospheric bromeliads saw noticeable regions of hotspots and empty regions (Figure 5). One of the most significant is found along the Montaña trail where an emergent viral disease has infected a large portion of trees (Figure 5, A). The effects of this are shown by the distinct boundaries on either side of the infected region. Further along the trail a hotspot of occurrences at the transition zone between natural regrowth and old growth is present (Figure 5, C). A large population of atmospheric bromeliads was observed along the Gavilan trail, specifically near a section containing an old growth tree (Figure 5, B). A similar concentration was observed along the Jilguero section of the trail but was evenly dispersed. The northern section of the reserve saw relatively even distributions, but again a hotspot was present along the Skutch trail at the transition zone between old growth and natural regrowth.

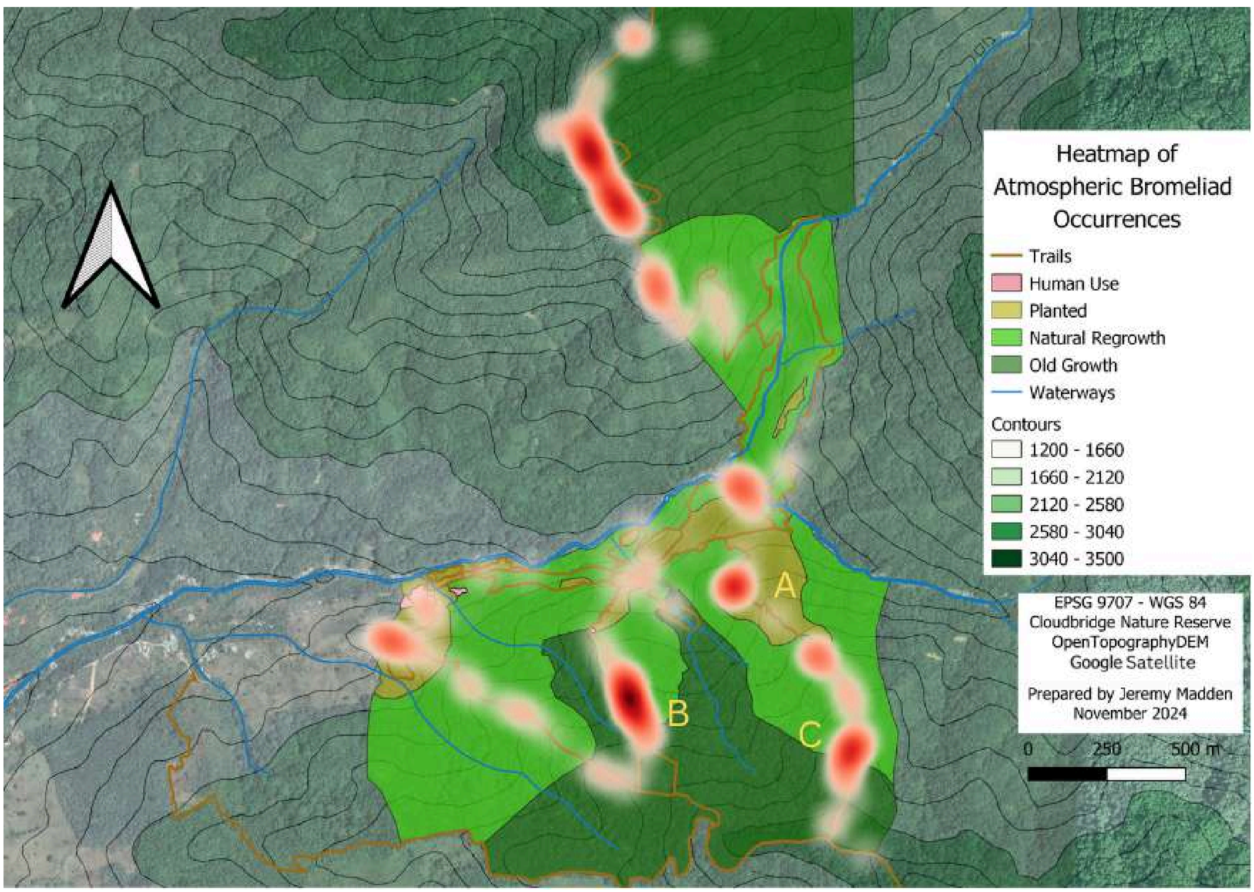


Figure 5. **Heatmap distribution of atmospheric bromeliad: A. Diseased area within the planted region of Montaña B. Hotspot of atmospheric bromeliads concentrated around old growth mother tree C. Population hotspot at transition zone between natural regrowth and old growth along Montaña.**

Tank bromeliads saw a similar pattern of hotspots in their distributions but were less widespread than their atmospheric counterparts (Figure 6). The largest concentration of tank bromeliads was found at the transition zone from natural regrowth to old growth along Skutch (Figure 6, A). Trees along this section are host to far more tank bromeliads, even when compared to old growth sections along Montaña. Continuing up Skutch, populations of tank bromeliads saw a more even distribution as forest structure shifted to primary old growth. A large concentration of occurrences was observed at the same old growth tree along Gavilan, again with individuals being dispersed from the old growth tree (Figure 6, C). The planted region of Jilguero is notable for having a small population of tank bromeliads, primarily consisting of *Tillandsia oerstediana.* This is the only location within the reserve containing this many *T. oerstediana* individuals, and represents some of the largest sections of tank bromeliads within planted regions (Figure 6, B).

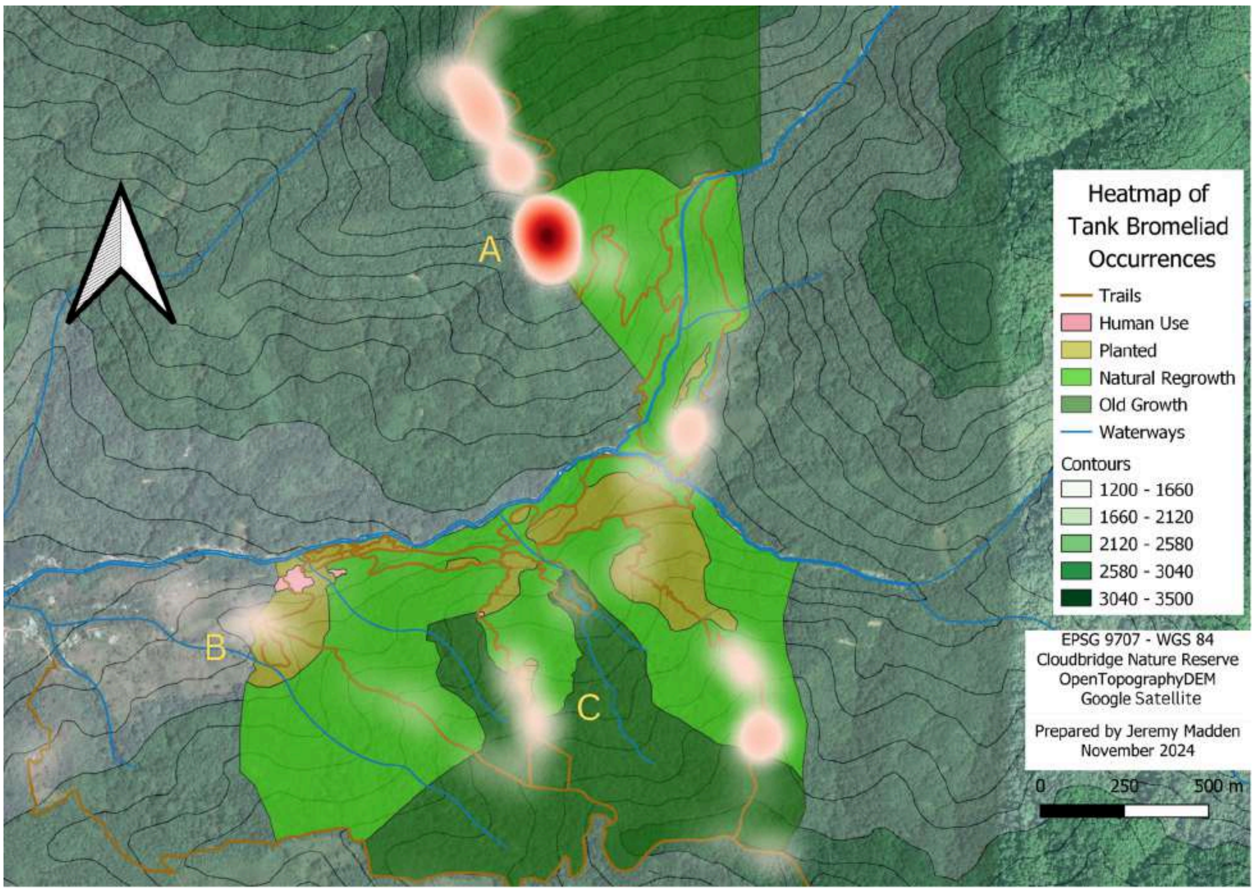


Figure 6. **Heatmap distribution of tank bromeliads: A. Population hotspot at natural regrowth / old growth transition B. Concentration of *T. oerstediana* at forest edge C. Concentration of tank bromeliads in close proximity to old growth mother tree.**

Effects of Elevation

Occurrences of epiphytes were shown to have a weak positive correlation with elevation (r_{252} = .3361, p=.0003). While overall epiphytic plant occurrences increased with elevation, bromeliads were the only group to see a statistically significant positive trend. Atmospheric bromeliad occurrences were shown to have a weak, but significant, positive correlation with elevation (r_{189} = .3361, p<.0001). Tank bromeliads were shown to have a slightly stronger correlation with elevation (r_{145} = .3921, $p<.0001$), indicating that elevation may be more influential on their distribution. *Asplenium sp.* showed a slight, but significant negative correlation (r_{126}=-.1926, p=.0294). *A. salvinii* showed no statistically significant correlation with elevation (r_{18}=.0623, p=.794149)

***Figure 7*. Linear regression relationship between elevation and different Epiphytic species occurrences.**

Bromeliads

A violin-plot shows that atmospheric bromeliads have a broader distribution across elevation ranges, but share a peak concentration ~2000m with tank bromeliads. However, they appeared to show a sharper decline around 2100m with a consistent distribution of occurrences above 2150m.

The violin-plot of tank bromeliads show a more concentrated distribution. Being narrower at the lower end (2000m) and widening as elevation increases toward 2250m, suggests that while still present at these elevations, tank bromeliads are more clustered around specific elevation bands (1800m & 2000m) with a more gradual decline as elevation increases. These findings suggest that tank bromeliads may have stronger habitat preferences or limiting factors influencing their distribution at higher elevations compared to atmospheric bromeliads but this is a topic of further research. (Figure 8).

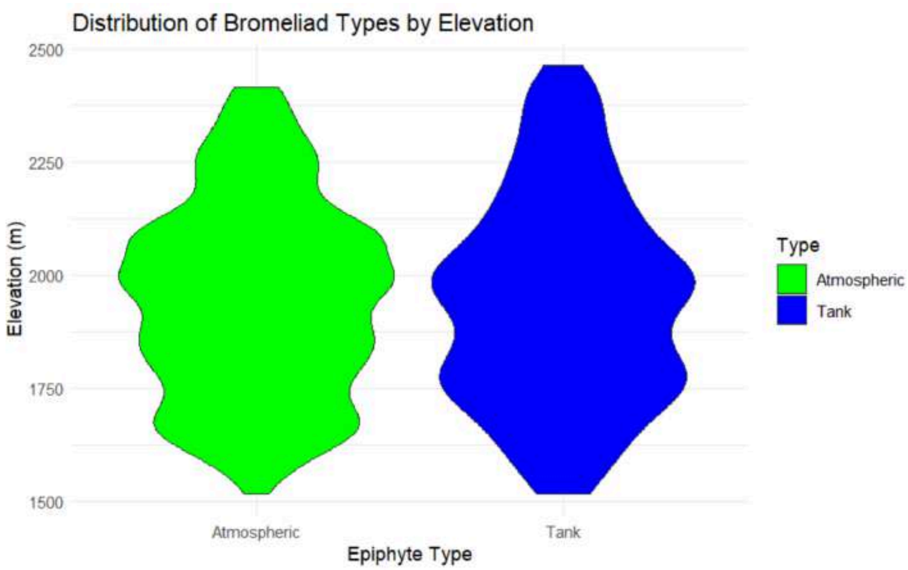


Figure 8. Violin plot of atmospheric and tank-forming bromeliad distributions by elevation.

Effects of Forest Type

Natural regrowth forest showed the highest abundance of epiphytes containing 1061 individuals. Old growth was second most abundant containing 755 with planted containing 376, and human use containing 40. These findings were deemed significant ($\chi 2=738.516$, $p < .001$) and suggest that different forest types create conditions favorable to epiphytic plants. In this case we saw that natural regrowth forest had the largest difference between observed and expected number of individuals.

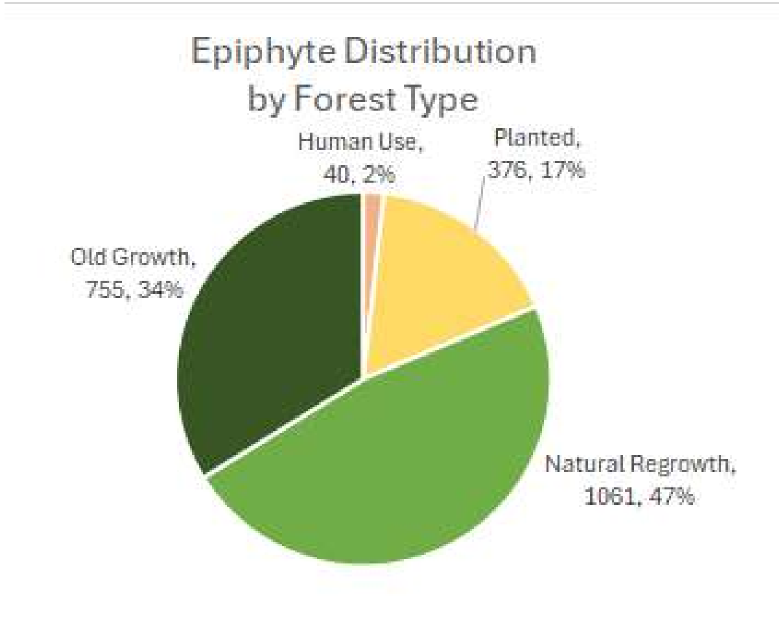
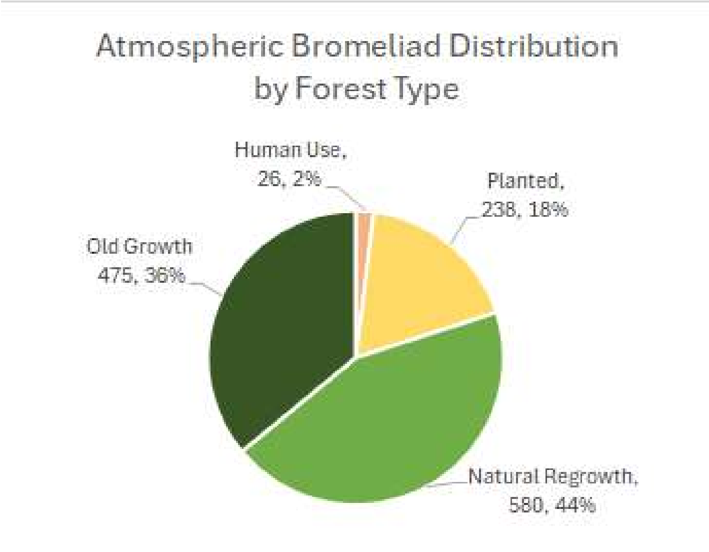


***Figure 9*. Pie chart of epiphyte distributions by forest type.**

Bromeliads

Atmospheric bromeliads showed a very similar trend to overall epiphyte distributions with most observations (44%) occurring in Natural Regrowth sections (Figure 9). In planted regions, atmospheric bromeliads showed a higher frequency over their tank counterparts (18% vs 7%). These findings were deemed to be statistically significant ($\chi 2=465.878$, $p < .0001$) indicating that conditions in planted regions may be more favorable to atmospheric bromeliads. Similarly, tank bromeliads showed a higher occurrence in old growth regions at a rate slightly higher than atmospheric (6% vs 42%). Impacts of forest type on tank bromeliad presence were also shown to be statically significant ($\chi 2=99.309$, $p < .0001$).



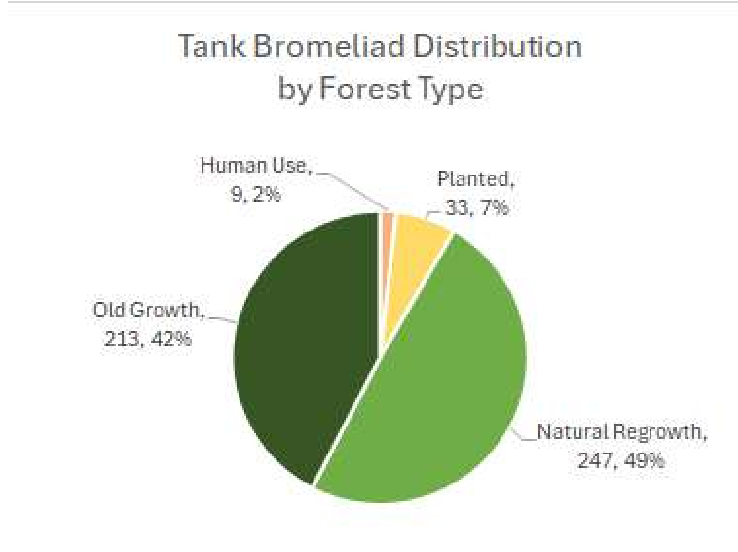


Figure 10. **Distribution of Atmospheric & Tank-forming bromeliads by forest type**

Large Epiphytes

Asplenium sp.

Asplenium sp. was an outlier compared to other plant groups for forest type. Similar to the bromeliads, the highest level of occurrences were present in natural regrowth regions (Figure 11). Unlike the other plants, however, the second most populous forest type was planted, containing over 25% of occurrences. Similarly, these plants were the only group to have old growth as their least populous forest type. These results were deemed statistically significant ($\chi2=351.730$, $p < .0001$), and suggest that environmental conditions found in planted / natural regrowth are more favorable to supporting *Asplenium sp.*

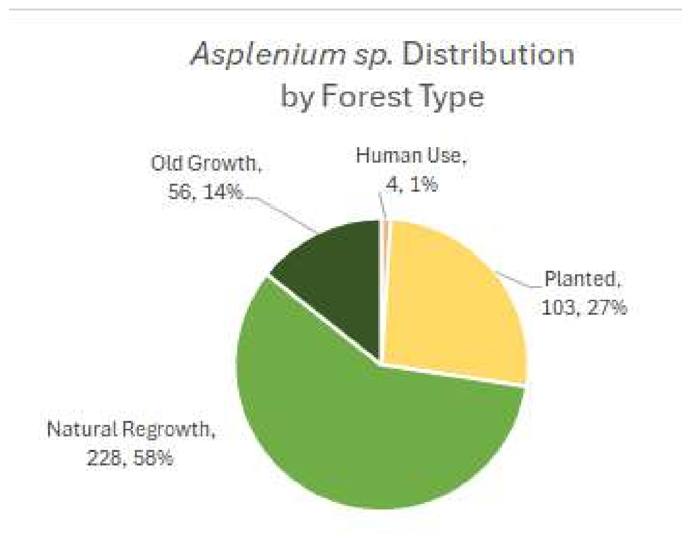


Figure 11. **Distribution of *Asplenium sp.* by forest type**

A. salvinii

While a majority of *A. salvinii* occurrences were in old growth regions, we are unable to make any claims about forest type preference as there were too few individuals recorded to be considered statistically significant ($\chi 2$=.243, p =.97039).

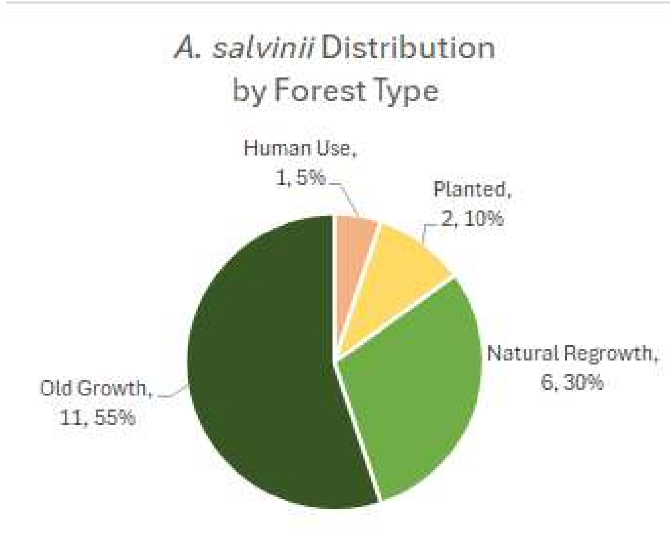


Figure 12. **Distribution of *A. salvinii* by forest type**

Effects of Water Distance

Distance to water appeared to have an impact on tank bromeliad, and *asplenium sp.* distributions, with no significant impact present on atmospheric bromeliads or *A. salvinii*. For atmospheric bromeliads, the trendline shows a near zero positive correlation, but these results were found to not be statistically significant (r_{250} = .0555, p=.38031). Therefore, we must assume that there is no relationship between the two, and atmospheric bromeliads are indiscriminate with their distributions in relation to distance to water sources.

Tank bromeliads, however, did see a moderate positive correlation with more individuals being present at further distances from water (r_{209} = .5771, p<.0001). These results were found to be statistically significant and may suggest that tank bromeliads are less reliant on proximity to water sources than their atmospheric counterparts.

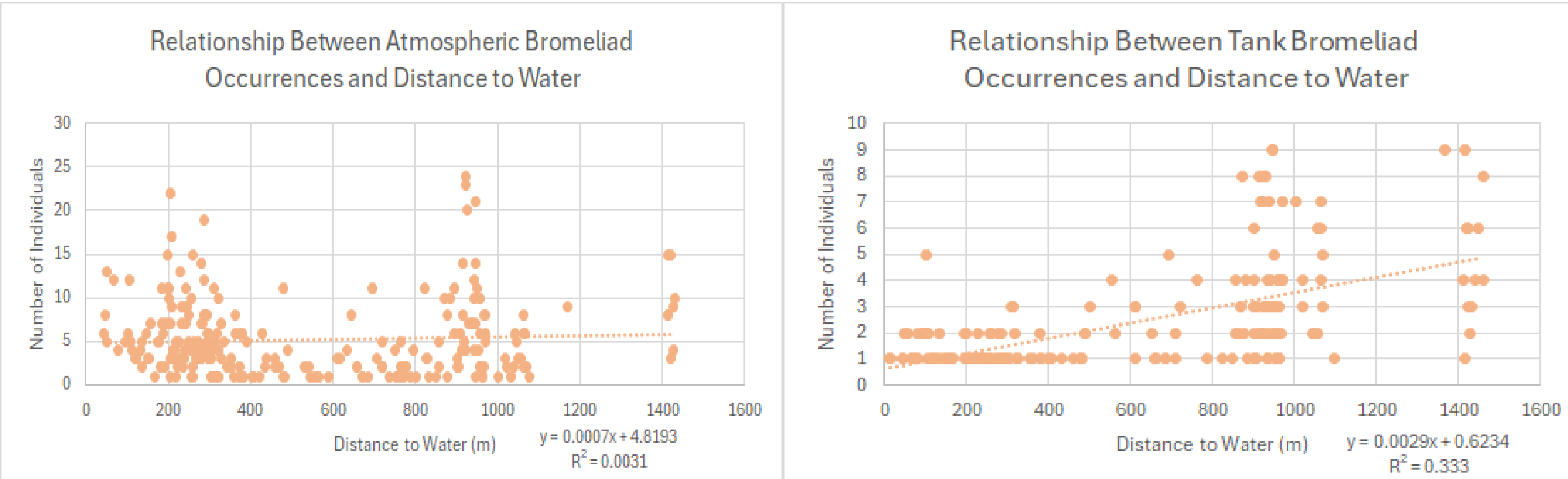


Figure 13. **Linear regression relationship between distance to water and atmospheric / tank bromeliad occurrences.**

Large Epiphytes

Asplenium sp. showed a statistically significant weak positive correlation with distance to water (r_{210}= .2506, p=.000228). While weaker than tank bromeliads, the trend suggests that they are slightly indiscriminate with their occurrences in relation to proximity to water sources.

While there was a slight negative trend for *A. salvinii* presence and distance to water, there were too few individuals to have a statistically significant correlation (r_{14} = -.1902, p=.48046).

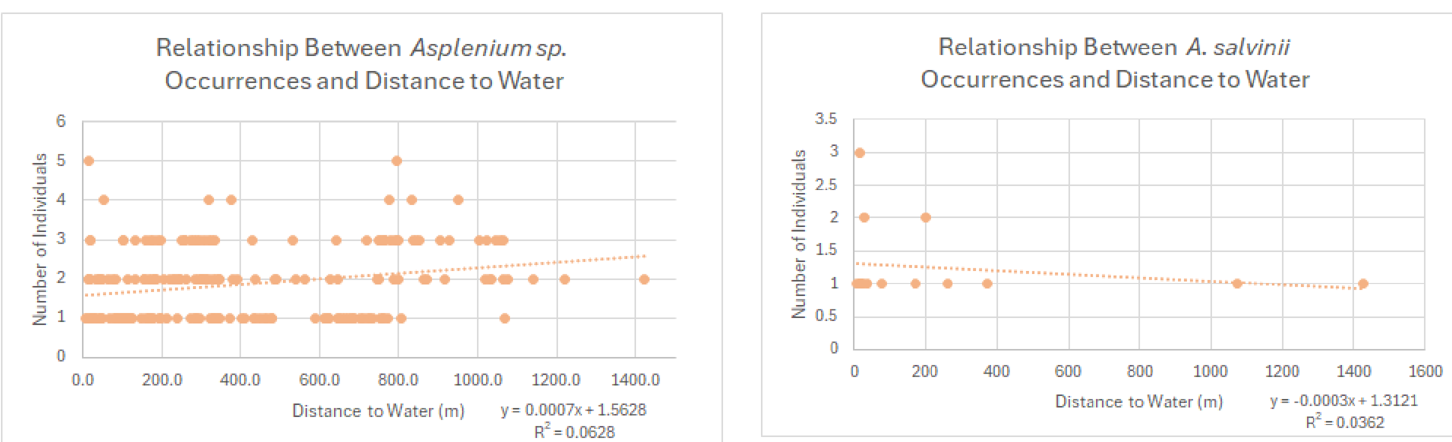


Figure 14. **Linear regression relationship between large epiphyte distribution and distance to water**

Effects of Moss Presence

Across planted, naturally regrowth, and old growth sections, there was a greater proportion of epiphytes coexisting with a bryophyte (lichen, moss) than existing on bare bark. 1,406 individuals were recorded coexisting with bryophytes while 826 were recorded on bare bark (Figure 15, $\chi2$=150.717, $p < .0001$). Of the epiphytes that were recorded, tank bromeliads and *A. salvinii* showed little to no correlation with moss presence.

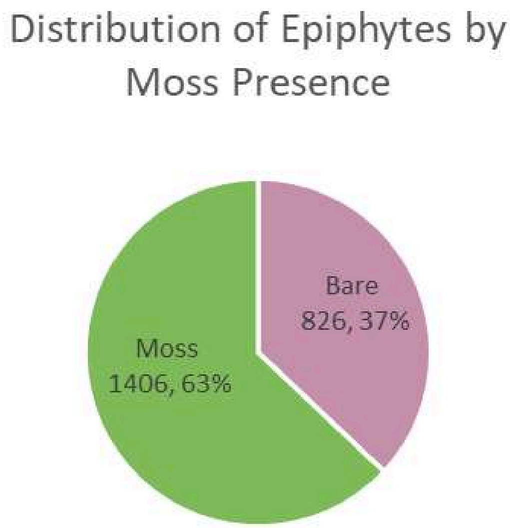


Figure 15. **Pie-chart of epiphyte occurrences and their correlation with moss presence**

Bromeliads

The presence of moss was shown to have a more significant impact on atmospheric bromeliads, with 64% being shown to occur with bryophytes (Figure 16, $\chi2$=106.615, $p < .0001$).

Tank bromeliads showed a lower correlation with moss presence with 59% found to be coexisting with bryophytes (Figure 16, $\chi2$=16.135 $p = .00006$).

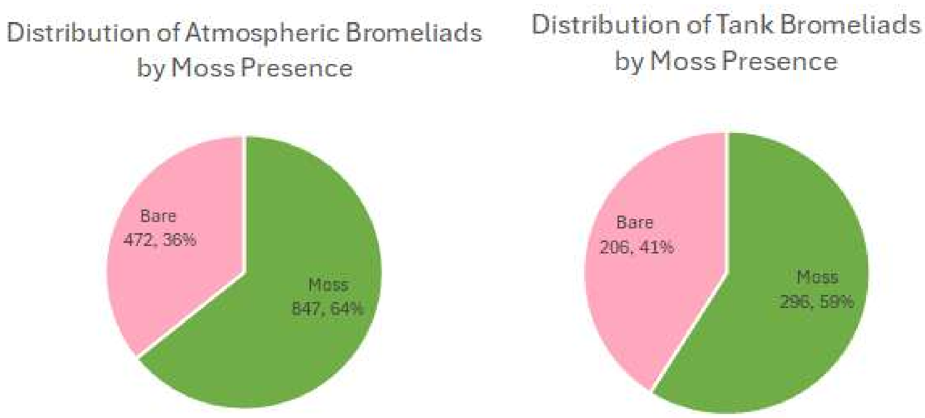
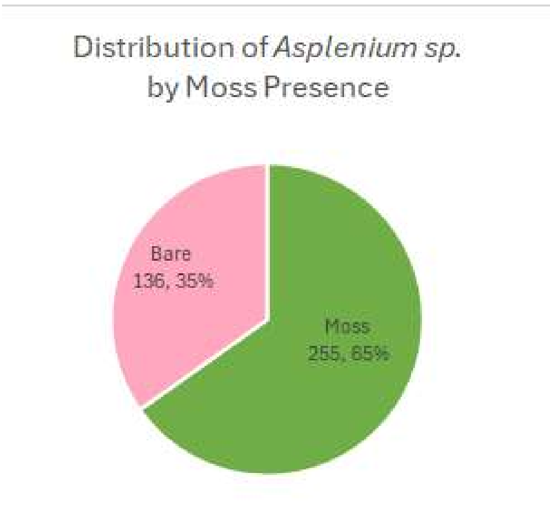


Figure 16. **Pie-chart of bromeliad occurrences and their correlation with moss presence**

Large Epiphytes

The only statistically significant result we obtained for large epiphytes was with *Asplenium sp.* We saw a slight preference for coexistence with moss, with 65% found to be coexisting with bryophytes. (Figure 17, $\chi2=36.217$, $p < .0001$).

We observed that *A. salvinii* occurred more often on bare bark but results were not statistically significant (Figure 17, $\chi2=.8$, $p = .37109$).



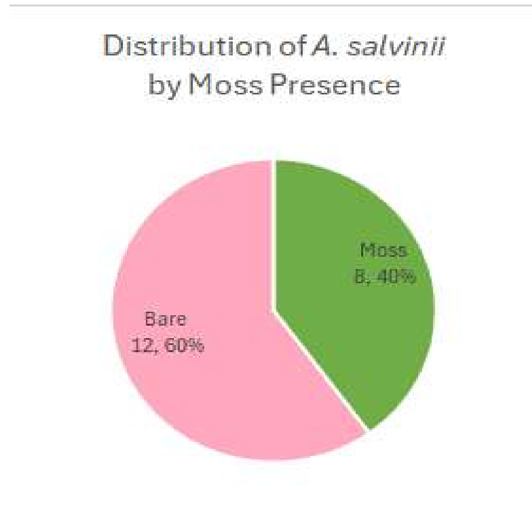


Figure 17. **Pie-chart of large epiphyte occurrences and their correlation with moss presence**

Discussion

Image Database

We were able to obtain over 2,000 images of epiphytic bromeliads and large epiphytic plants over a four month period. During this time, over 200 different flowering species were documented. While we were unable to I.D. most species, expert taxonomists may be able to provide proper identification and utilize our data. Image identification can lead to further research such as species niche modeling to monitor individual species response to climate change. Access to the image database can be obtained through Google Drive. Additionally, further analysis can be performed on the environmental data obtained to test potential influences as technology improves.

Epiphytic Distributions

Atmospheric bromeliads were the most abundant vascular epiphyte found in the reserve accounting for 58% of recorded species. We do not know if this number is standard for similar ecosystems as no baseline currently exists to define a healthy distribution of epiphytic plants within Costa Rica. However, comparative studies in other ecosystems can offer insight. One study conducted in humid montane forest (1430 m.a.s.l.) in Mexico estimated the total biomass of vascular epiphytes at 255 g/m^2 with bromeliads accounting for 92% of this biomass (Heitz, 1997). The authors of this study state the difficulty of extrapolating this value to an entire forest, but acknowledge that this is the only value available for describing epiphytic distribution patterns.

In this study, tank bromeliads were the second most abundant group and although many individuals lack species level identification, they still fall under the broad categorization of "tank-forming" due to their size or presence of phytotelmata. Additionally, tank-forming bromeliads contained the highest number of unique individuals with single occurrences. These isolated occurrences were often represented by unique species found exclusively but in very localized areas (<10m) showing the potential for overlooked diversity within microhabitats. Additionally, the lack of flowers in many of these unique individuals made identification too difficult. This suggests that true epiphytic diversity within CNR may be underestimated, especially for less common species or those restricted to limited microhabitats. We recommend further monitoring of epiphytic diversity over longer periods to encompass more flowering seasons, with a focus on unique individuals as they are potentially more at risk to disturbance.

Atmospheric Bromeliads

Elevation and forest type were shown to be the environmental factors with the biggest influence on atmospheric bromeliad distributions. A weak positive trend was identified for atmospheric bromeliad occurrences and elevation, indicating that conditions found at higher elevations support larger populations. This finding coincides with our expectations and could be explained by our theory of the top-down movement of horizontal precipitation across elevation gradients. We believe that this trend is linear with an upper-limit, however, with previous studies showing populations drop-off significantly above the tree-line into high elevation páramo (Cristóbal-Pérez, 2023). We are unable to prove this, however, as the elevation where this transition occurs (2,900m - 3,100m) is outside the bounds of CNR. The violin-plot of occurrences indicate that atmospheric bromeliads are not strongly concentrated at any specific elevation but are instead well-represented throughout the elevation gradient.

We found that atmospheric bromeliads showed a slight preference for naturally regenerated forests, containing 8% more than the next most abundant region, old growth. These findings align with our expectations and may suggest that certain conditions in planted or secondary forests—such as increased light availability due to younger canopy structures—may favor atmospheric bromeliads which have been shown to be more sun-tolerant than other epiphytic species (Quevedo-Rojas et al., 2024). The presence of atmospheric bromeliads in these disturbed or secondary areas may also suggest a degree of resilience to ecological disturbance, as they can thrive in environments with less stable microclimatic conditions and regardless of soil quality and (Takahashi, 2024). These findings suggest that while both bromeliad types are present across all forest types, atmospheric bromeliads have a slight preference to planted regions over tank bromeliads which prefer old growth.

We found that distance to water sources did not influence the distribution of atmospheric bromeliads, a result that aligns with our expectations. Atmospheric bromeliads primarily rely on atmospheric moisture found in the form of mist, rather than liquid water for survival (Zotz & Heitz, 2001). This independence from liquid water allows for distributions in areas that see high water availability fluctuations.

Moss presence was found to have some influence on atmospheric bromeliad presence with 64% found to be coexisting with bryophytes. Of the individuals found coexisting, natural regrowth and old growth contained the highest abundance which supports our hypothesis. While we cannot claim causation, the field of substrate ecology and bryophyte relationships is one that we suggest be explored further as this relationship could be important in determining their distributions.

Tank Bromeliads

Elevation and forest type were shown to be the most influential factors determining tank bromeliad distributions. Similar to their atmospheric counterparts, tank bromeliads saw a correlation with more individuals being found at higher elevations. This relationship was found to be slightly weaker than atmospheric bromeliads but may be explained by less individuals being recorded in the canopy leading to a bias towards easy to identify, low elevation individuals. Further research can perform species counts within the canopy of high elevation forests with new technology such as drones, which have been shown to be an effective tool for surveying inaccessible ecosystems (Kim et al., 2023).

As we expected, tank bromeliads were found more abundantly in old growth forests, occurring at a rate 6% higher than their atmospheric counterparts. This finding aligns with prior research which found that mature, primary forests provide optimal conditions for tank bromeliads and while not a focus of this study, also saw the highest species richness of arboreal frogs inhabiting these bromeliads (Galindo-Leal et al., 2003). These undisturbed areas have more stable microenvironments, and the increased canopy cover allows for more opportunities to collect falling organic material within the phytotelmata (Benzing, 2000 ; Zotz, 2005). Other old growth regions on the reserve such as Sentinel and Montaña showed slightly lower concentrations likely due to forest age and canopy structure. One interesting finding during the course of this study was the large concentration of tank bromeliads surrounding an old growth tree along the Gavilan trail. Surrounded by natural regrowth, a single old growth tree (*Ulmus mexicana*) still stands, hosting a surprising amount of biodiversity evident on both heatmaps. This could indicate that tank bromeliad dispersal from its mother tree may be fairly localized, but this is a point of further research.

Our findings showed that tank bromeliads were more often found at further distances from water sources. The trend aligns with our predictions and can possibly be explained by tank bromeliads having a reduced dependence on ambient humidity, and liquid water. Unlike atmospheric bromeliads, the presence of a phytotelmata tank allows these larger bromeliads to store water for extended periods of time. It is important to note, however, that due to the topography of CNR, distances further away from water tend to be higher elevations, where tank bromeliads have been shown to correlate with. Additionally, higher elevations of the reserve are less likely to have been previously farmed making old growth sections more common. While a correlation was evident, we believe that it is not a causation, and is more-so an example of tank bromeliad independence and a by-product of the effects of elevation.

Moss presence appeared to have no impact on tank bromeliad presence with a majority of individuals found to be growing on bare surfaces. This relationship appears to be less impactful for tank bromeliad presence. A possible explanation for this could be that mature tank bromeliads have grown to outcompete any mosses while their larger size reduces their reliance on moss as an intermediary substrate (Males et al., 2023). This relationship should be investigated further as it could provide insight into factors that determine young tank bromeliad survival.

Asplenium sp.

Asplenium sp. distributions were unique in that of all the epiphytic plants recorded, it was the only group to see a negative correlation with elevation. Additionally, while they showed the highest percentage for occurrences in natural regrowth, they were also the only plant group to have over 25% occurrence in planted regions. While no prior literature establishes this connection, we believe that these results suggest that *Asplenium sp.* fills a different ecological niche than bromeliads, with a preference for lower elevation regions of younger forests.

Distance to water was shown to only have a slight impact on *Asplenium sp.* distributions, with a very weak positive correlation observed. Unlike *A. salvinii*, these plants may be less reliant on available liquid water. Similar to bromeliads, these plants capture water from the air and absorb it directly into the leaf, with an increased leaf surface area and similar growth form to tank bromeliads to collect water (Chen et al., 2023).

While we saw a correlation between moss presence and *Asplenium sp.* distributions, this plant group was the only one with a significant number of individuals growing terrestrially. We did not include these individuals in this project but the ability for these epiphytes to grow in both conditions is noteworthy and a potential point of future research.

A. salvinii

Due to its rarity, only 20 individuals were recorded throughout the course of this study, making statistical analysis and claims difficult. Despite this, the large abundance found on Sentinel is noteworthy as 90% of occurrences were found along 1 section of the old growth region of the trail. The other 3 individuals are also unique because they are found in ecosystems vastly different than what the majority occur in. One individual was recorded in the human use region at the entrance to the reserve. One individual was recorded at the top of the Jilguero / Gavilan trail, and one individual was recorded in the dead zone of the planted region along Montaña. Further monitoring of these plants is recommended as their rarity and limited distribution make them particularly susceptible to disturbances.

T. leiboldiana **Dominance**

One interesting discovery made during this project was the widespread distribution of *Tillandsia leiboldiana. T. leiboldiana* accounted for 38% of atmospheric bromeliads, and 21% of all epiphytic species recorded. It is evident that this species performs particularly well in the conditions present at CNR with individuals being found in all forest types, and throughout the elevation gradient. One potential explanation for the widespread distribution is their ability to perform a specialized form of photosynthesis known as Crassulacean Acid Metabolism, more efficiently than similar plants (Crego et al., 2024). This adaptation allows *T. leiboldiana* to survive in especially harsh conditions that other plants cannot. Despite its widespread distribution, there could be a concern that the population could become susceptible to an emergent viral infection (Ladino et al., 2019). Regardless, this species should be further monitored for its resilience and proliferation.

Further Research

These findings show some of the impacts environmental factors have on epiphyte distributions, but they do not paint the full picture. Environmental factors such as solar radiation and horizontal precipitation amounts are known to play crucial roles in determining species niches, but were unable to be recorded. While monitoring solar radiation throughout the reserve is difficult, we suggest installing tools to measure horizontal precipitation such as the low cost method to create fog harps outlined by Virginia Tech (Kennedy et al., 2022). This would allow us to track one of the most important variables affecting vascular epiphyte distributions while also providing key insight into a phenomena that could see large impacts brought upon by climate change.

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Appendix - Species List of Epiphytic Plants Recorded

Atmospheric Bromeliads

Catopsis sp.
- *nutans*
- *sessiliflora*
- *wangerinii*

Tillandsia sp.
- *complanata*
- *excelsa*
- *leiboldiana*
- *oerstediana*
- *punctulata*
- *utriculata*

Racinaea sp.
- *adpressa*
- *spiculosa*

Tank Bromeliads

Aechmea sp.

Guzmania sp.
- *Lingulata*

Mezobromelia sp.
- *pleiosticha*

Vriesea sp.
- *Monstrum*

Werauhia sp.
- *acuminata*
- *ampla*
- *gladioliflora*
- *graminifolia* (endemic)
- *werckleana*

Large Epiphytes

Anthurium sp.
salvinii

Asplenium sp.