Resilient diversity, vascular epiphytes in the urban forest of Medellín, Colombia

Yudy Alejandra Gallego
Botanical Garden of Medellin
Maria Judith Carmona-Higuita
Philipps University of Marburg
Ana Maria Benavides
anamaria.benavides@jbotanico.org

Botanical Garden of Medellin

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Abstract

Urban trees serve as a habitat for vascular epiphytes, yet little is known about how these plant assemblages are structured in highly urbanized tropical cities. We conducted a systematic inventory of vascular epiphytes and nomadic lianas in the urban area of Medellín, Colombia. Epiphytes were surveyed on 600 trees across 60 sites distributed among three urban land-cover categories. In total, we recorded 9,948 individuals representing 48 species and 12 families. Bromeliaceae and Polypodiaceae dominated the assemblages, with *Tillandsia recurvata* accounting for over 70% of individuals. Vertical stratification, host tree characteristics (e.g., bark texture, tree size), and bark water retention capacity influenced epiphyte abundance and richness. The inner tree crown supported the highest species richness, and rough-barked trees retained more water and hosted more epiphytes. Dispersal mode was a key trait shaping urban assemblages: wind-dispersed species were dominant, while animal-dispersed taxa were rare. Although exotic trees like *Fraxinus uhdei* were important hosts, epiphyte-host associations were more closely linked to functional tree traits than biogeographic origin. Spatial turnover in species composition was low, reflecting ecological homogenization across the city. Our findings highlight the resilience of a subset of epiphyte species to urban conditions and suggest that urban trees function as biodiversity scaffolds. This study provides baseline data for integrating epiphyte conservation into tropical cities' urban planning and green infrastructure strategies.

Introduction

Urbanization is an accelerating global phenomenon. More than 55% of the world's population resides in urban areas, which is projected to reach 68% by 2050 (United Nations, 2024). While urban expansion poses significant challenges to biodiversity conservation, cities can still support diverse ecological communities by implementing green infrastructure. Urban trees, green corridors, parks, and vertical gardens are crucial in maintaining biodiversity, acting as ecological corridors, and providing essential ecosystem services (Tzoulas et al., 2007; Van der Walt et al., 2015). These green spaces help regulate microclimate, improve air quality, and support native flora and fauna (Balvanera et al., 2014; Ives et al., 2016).

Recognizing the need to integrate biodiversity into urban planning, Colombia has implemented the "Biodivercities" initiative, which promotes biodiversity conservation and sustainable urban development (Ministry of Environment and Sustainable Development, 2019). However, a significant challenge in assessing urban biodiversity is the lack of comprehensive inventories, particularly for sensitive and understudied groups such as vascular epiphytes. These plants, which grow non-parasitically on other plants, are susceptible to environmental changes and serve as indicators of habitat quality (Knapp et al., 2009).

Vascular epiphytes exhibit high diversity in tropical regions, including the Andean forests of Colombia, where they can constitute up to 50% of vascular plant species locally (Bernal et al., 2019; Zotz, 2016). In natural ecosystems, their richness is strongly influenced by forest structure and connectivity. However, in

urban environments, epiphyte diversity often declines due to habitat fragmentation, air pollution, and altered microclimatic conditions (Wolf, 2005; Köster et al., 2011; Higuera & Wolf, 2010). Nevertheless, some species exhibit resilience to urban conditions by tolerating drier and warmer microclimates, often forming simplified assemblages dominated by stress-tolerant taxa.

Studies in Argentina, Brazil, and Colombia have emphasized the importance of documenting epiphyte communities in urban settings (Furtado & Neto, 2015; Becker et al., 2017; Alvim et al., 2021; González & Ceballos, 2021). These inventories provide essential data for understanding how urbanization affects epiphyte assemblages and inform conservation strategies, such as integrating native species into urban planning. In Medellín, including urban and periurban areas, epiphytes exceed 311 species (Ortiz et al., 2024), yet their distribution and composition within the urban core remain poorly documented.

This study examines the diversity of vascular epiphytes in the urban area of Medellín, evaluating how land use, host tree characteristics, and site connectivity influence their composition. By identifying key ecological patterns —such as dispersal mechanisms, establishment strategies, and survival modes — this research contributes to urban biodiversity conservation. Additionally, understanding epiphyte dynamics in urban environments provides insights into environmental stressors like air pollution and urban heat island effects, reinforcing the relevance of epiphytes for sustainable urban planning.

Materials and methods

Area of Study

This study was conducted in the urban area of Medellín, located at 6°13'55"N 75°34'05"W. Medellín covers an area of 105 km² and is home to approximately 2,427,129 residents. The city has an average temperature of 24°C and sits at an elevation of 1,479 meters above sea level (DANE, 2018). Despite its high density of buildings, industries, and construction, Medellín is rich in extensive gardens and urban trees, which comprise around 830 species (Alcaldia de Medellín, 2021; Sistema de Arbol Urbano, 2019).

The city has established an ecological connectivity network encompassing parks, riverbanks, green corridors, walkways, and areas of strategic and landscape interest (Alcaldia de Medellín, 2014). This network has been used to categorize the land use of the city's urban forest into three types of coverage: 1. Green areas designated for ecological protection (ECO). 2. Green areas designated for protection associated with bodies of water (WAT, Mayor's Office of Medellín, 2021). 3. Green areas integrated with urban infrastructure, such as gardens, roundabouts, parks, and walkways (INF).

Field sampling was conducted to collect data on various classifications. In each coverage area, 20 sites were randomly selected for sampling, ensuring that the distance between the points was at least 500 meters and that the locations were evenly distributed throughout the city (Fig. 1). At each site, a census was performed on 10 contiguous trees chosen using a random method for the initial tree, focusing on trees with a diameter at breast height (DBH) of 10 cm or more. For each tree, data were collected on the abundance, growth stage, and growth form of the epiphyte individuals present.

Epiphytes are defined as true, facultative, accidental, and hemiepiphytes (Zotz, 2016). Since many epiphytic plants cluster together and may not be distinguishable to the naked eye, the term "individual" refers to each identifiable colony. Nomadic vine plants were included in the study, recognizing their distinct growth habit. Binoculars were employed to observe individuals located in the highest branches.

The location of each epiphytic plant was documented in terms of height (in meters) and position (base, trunk, inner branch, outer branch, or twigs). For nomadic vines, the position referenced was the highest point of growth. Each tree was recorded based on its distance and orientation relative to neighboring trees. Data on tree structure included the diameter at breast height (DBH), total height, and branch count, using a minimum diameter of 5 cm as a reference. The type of bark was also described and categorized as rough, fissured, smooth, exfoliating, or featuring thorns or lenticels.

Additionally, the number of pruned branches on the trees was recorded. Botanical collections were made and are housed in the Joaquín Antonio Uribe Herbarium of Medellín (JAUM). The taxonomic identification information for host trees was cross-referenced with the data available in the Urban Tree System (SAU) of Medellín and the Metropolitan Area (Sistema de Arbol Urbano, 2019). Finally, it was noted whether each species was native or exotic, according to the Catalogue of Plants of Colombia (Bernal et al., 2019).

We evaluated the significance of bark's water retention capacity to the abundance of epiphytes. We collected one to three bark samples from each tree species to conduct this assessment. Our methodology followed the approach of Einzmann et al. (2015) with a modification. Given that the bark pieces varied in size, we estimated their surface area by digitally processing images (Schneider, Rasband, and Eliceiri 2012). To determine the water retention capacity of the bark, we first measured the dry weight of each sample after drying them in an oven at 60°C for 24 hours. We then hydrated the bark samples in water for half an hour, removed excess water, and weighed them on a precision electronic scale. This process was repeated after 24 hours of hydration. The data was standardized to 1 cm^2, allowing us to calculate the water uptake in grams by taking the difference between the dry and wet weights. We evaluated the significance of bark's water retention capacity in relation to the abundance of epiphytes. We collected one to three bark samples from each tree species to conduct this assessment.

Statistical analysis

The epiphyte community structure was analyzed through a hierarchical modeling framework to assess species distribution patterns across vertical strata and host tree traits. Generalized linear mixed models (GLMMs) with Poisson distributions were applied to evaluate epiphyte abundance, incorporating fixed effects for tree zone type and relative height (normalized to 0–1 scale per tree) while accounting for nested random effects of site, tree, and canopy cover to control for spatial autocorrelation. Model significance was determined via likelihood ratio tests (χ^2) using the car package, with post hoc analysis of substrate effects derived from coefficient estimates.

Host tree characteristics were examined through two complementary approaches: a GLMM testing bark-type effects on epiphyte loads, controlling for tree size (DBH) with the site as random intercept, and a generalized additive model (GAM) with smooth terms for DBH to detect non-linear size-abundance relationships. Tree colonization rates were quantified descriptively, with mean DBH and height calculated across all sampled hosts.

Spatial patterns were characterized using geographic distance matrices (Haversine distances via geosphere), computing mean inter-tree distances within sites and inter-site distances between centroids. Community structure across vertical strata was analyzed through Pianka's niche overlap index (spaa package), visualized via heatmaps to compare species-substrate associations between trunk, middle crown, and upper crown zones.

All analyses were conducted in R (R Core Team, 2023) using vegan for diversity metrics, lme4 for mixed models, and mgcv for GAMs. Model diagnostics included AIC comparisons, residual checks for overdispersion in count data, and variance partitioning for random effects. Relative height distributions were standardized per tree to enable cross-comparisons of epiphyte positioning irrespective of absolute tree height.

Results

We recorded 9,948 epiphytic individuals belonging to 48 species of epiphytes and 12 families. True epiphytes dominated the assemblage (98,3%), followed by nomadic vines (0.8%) and accidental epiphytes (0.7%; Table 1). The most abundant families were Bromeliaceae (n = 7,371; 66% of all individuals) and Polypodiaceae (n = 2,131), while Araceae and Polypodiaceae were among the most species-rich (7 and 5 species, respectively). Dominant species included *Tillandsia recurvata* (n = 7,294), *Pleopeltis macrocarpa* (n = 2,053), *Asplenium theciferum* (n = 153), *Rhipsalis baccifera* (n = 93), *Campyloneurum amphostenon* (n = 71), and *T. usneoides* (n = 50). Species with wind-dispersed propagules (*e.g.*, *Tillandsia recurvata*, *T. usneoides*) accounted for the highest abundance, while animal-dispersed species (*e.g.*, *Rhipsalis baccifera*) were less frequent.

Table 1
– Summary of species, abundance, dispersal type (wind vs. animal), and growth form.

Family	Species	Abundance	Dispersal type	Growth form
Bromeliaceae	*Tillandsia recurvata*	7294	Wind	True epiphyte
Polypodiaceae	*Pleopeltis macrocarpa*	2053	Wind	True epiphyte
Aspleniaceae	*Asplenium theciferum*	153	Wind	True epiphyte
Cactaceae	*Rhipsalis baccifera*	93	Animal	True epiphyte
Polypodiaceae	*Campyloneurum amphostenon*	71	Wind	True epiphyte
Bromeliaceae	*Tillandsia usneoides*	50	Wind	True epiphyte
Araceae	*Syngonium podophyllum*	41	Animal	Nomadic vines
Commelinaceae	*Tradescantia fluminensis*	24	-	Accidental epiphyte
Araceae	*Monstera deliciosa*	23	Animal	Nomadic vines
Commelinaceae	*Callisia repens*	17	Wind	Accidental epiphyte
Bromeliaceae	*Catopsis nutans*	14	Wind	True epiphyte
Araliaceae	*Heptapleurum actinophyllum*	13	Animal	Facultative epiphyte
Orchidaceae	*Rodriguezia granadensis*	12	Wind	True epiphyte
Commelinaceae	*Tradescantia zebrina*	11	-	Accidental epiphyte
Araceae	*Philodendron erubescens*	9	Animal	Nomadic vines
Araceae	*Anthurium* aff. *salvinii*	8	Animal	True epiphyte
Aspleniaceae	*Asplenium praemorsum*	8	Wind	True epiphyte
Bromeliaceae	*Billbergia nutans*	7	Animal	True epiphyte
Polypodiaceae	*Pecluma plumula*	5	Wind	True epiphyte
Nephrolepidaceae	*Nephrolepis cordifolia*	4	Wind	True epiphyte
Araceae	*Epipremnum aureum*	3	-	Nomadic vines
Bromeliaceae	*Tillandsia juncea*	3	Wind	True epiphyte
Arecaceae	*Adonidia merrillii*	2	Animal	Accidental epiphyte
Phyllanthaceae	*Bischofia javanica*	2	Animal	Accidental epiphyte
Orchidaceae	*Comparettia falcata*	2	Wind	True epiphyte

Family	Species	Abundance	Dispersal type	Growth form
Asteraceae	*Emilia fosbergii*	2	Wind	Accidental epiphyte
Araceae	*Philodendron hederaceum*	2	Animal	Nomadic vines
Bromeliaceae	*Tillandsia* sp.	2	Wind	True epiphyte
Solanaceae	*Acnistus arborescens*	1	Animal	Accidental epiphyte
Bromeliaceae	*Aechmea* sp.	1	Animal	True epiphyte-cultivated
Rutaceae	*Citrus* sp.	1	Animal	Accidental epiphyte
Poaceae	*Cynodon dactylon*	1	Wind	Accidental epiphyte
Orchidaceae	*Dendrobium sp.*	1	Wind	True epiphyte
Poaceae	*Eleusine indica*	1	Wind	Accidental epiphyte
Moraceae	*Ficus sp.*	1	Animal	Hemiepiphyte
Araceae	*Monstera pinnatipartita*	1	Animal	Nomadic vines
Musaceae	*Musa acuminata*	1	Animal	Accidental epiphyte
Iridaceae	*Neomarica longifolia*	1	-	Accidental epiphyte
Araceae	*Philodendron bipinnatifidum*	1	Animal	Nomadic vines
Urticaceae	*Pilea* sp.	1	-	Accidental epiphyte
Fabaceae	*Pithecellobium dulce*	1	Animal	Accidental epiphyte
Polypodiaceae	*Pleopeltis bombycina*	1	Wind	True epiphyte
Myrtaceae	*Psidium guajava*	1	Animal	Accidental epiphyte
Pteridaceae	*Pteris vittata*	1	Wind	Accidental epiphyte
Cactaceae	*Selenicereus* sp.	1	Wind	True epiphyte-cultivated
Polypodiaceae	*Serpocaulon triseriale*	1	Wind	True epiphyte
Solanaceae	*Solanum nigrescens*	1	Animal	Accidental epiphyte
Bromeliaceae	*Tillandsia* aff. *fendleri*	1	Wind	True epiphyte

Epiphytes exhibited significant vertical stratification across host tree strata (GLMM: χ^2 (4) = 4.06, $p < 0.044$). The inner tree crown hosted the highest species richness (n = 33 species), while the outer crown showed the lowest (n = 7). Relative height significantly affected epiphyte counts (IRR = 1.28, z = 2.02, p <

0.044), with peak abundance at 37% of tree height. Niche overlap was highest between the trunk and the middle part of the tree crown (Pianka's index = 0.99; Fig. 2).

A total of 600 trees belonging to 114 species were surveyed. On average, 67.8% of trees hosted epiphytes (mean = 24.44 ± 37.22 individuals). Trees were spaced 7.68 ± 5.05 m apart, with a mean DBH of 131.99 ± 77.28 cm and height of 12.75 ± 5.27 m, and no significant difference existed between the trees of the evaluated covers (p = 0.475). Fabaceae was the most common family (27 species, 218 individuals), with 77% of its individuals acting as epiphyte hosts. Frequent hosts included *Fraxinus uhdei*, *Caesalpinia pluviosa*, *Leucaena leucocephala*, *Erythrina fusca*, and *Spathodea campanulata* (SM 1). Rough-barked trees supported more epiphytes than smooth-barked trees (p = 0.229), controlling for size and site.

No significant differences in host tree richness were found among sampling covers (F = 1.36, $p = 0.266$), averaging 5.0 ± 2.2 species per site. Although epiphyte abundance did not vary among covers (Kruskal-Wallis $\chi^2 = 0.33$, p = 0.847), species richness did ($\chi^2 = 11.60$, p = 0.003), with the highest diversity in green areas designated for protection associated with bodies of water (WAT cover, Shannon = 0.93 ± 0.41) and the lowest in green areas integrated with urban infrastructure (INF cover, Shannon = 0.40 ± 0.33; Fig. 3). A Mantel test indicated no substantial spatial turnover in epiphyte composition (r = 0.092, p = 0.032), suggesting urban homogeneity.

Bark texture significantly influenced both water retention and epiphyte abundance **(**Fig. 4**).** Rough bark, present in 50% of trees, retained more water after 30 minutes (mean = 0.127 ± 0.045) and 24 hours (0.167 ± 0.065) of immersion. Kruskal-Wallis tests revealed significant differences in water uptake at 30 minutes ($\chi^2 = 37.17$, p < 0.0001) but not at 24 hours ($\chi^2 = 17.79$, p = 0.013). Tree species with higher bark water retention hosted more epiphytes; however, this relationship was not significant in the GLM. In contrast, DBH and branch number emerged as significant predictors of epiphyte abundance, as shown in the model diagnostics (null deviance = 479.27; residual = 401.32; df = 361/358).

Discussion

Our results provide novel insights into vascular epiphytes' composition, distribution, and ecological drivers in a tropical urban context. The high dominance of wind-dispersed bromeliads and the prevalence of true epiphytes highlight both natural colonization processes and the adaptive success of specific taxa in anthropogenic environments.

Despite the rapid degradation of tropical forests, epiphytes remain largely underrepresented in urban ecological research. While studies in Panama, Brazil, and Mexico have described vascular epiphyte assemblages on isolated trees in low-density urban contexts (Einzmann et al., 2016; Izuddin & Webb, 2015), our study offers novel insights into how epiphyte communities persist and reorganize in a densely urbanized Andean valley. The results from Medellín—a city with high impervious surface cover, intense radiation, and low ambient humidity—highlight both the vulnerability and resilience of epiphyte assemblages under intense anthropogenic pressure.

Our data show a striking dominance of *Tillandsia recurvata*, which accounted for over 70% of all individuals. This species and others, such as *T. usneoides* and *Pleopeltis macrocarpa*, exemplify a functional group adapted to urban stressors: wind-dispersed, fast-growing, and desiccation-tolerant. These traits are consistent with a broader global pattern observed in tropical cities such as Mexico City, São Paulo, and Bangkok, where epiphyte communities are skewed toward a few cosmopolitans, resilient species (Zotz & Bader, 2009; Brighigna et al., 1997).

The functional traits of these species, such as CAM photosynthesis in bromeliads, enable survival under elevated temperatures, reduced water availability, and intense light conditions associated with the urban heat island effect. This supports the hypothesis that cities act as environmental filters, favoring drought-tolerant species capable of rapid colonization and independent nutrient uptake. Dispersal strategy also played a central role in structuring the community. Wind-dispersed species overwhelmingly dominated, while animal-dispersed epiphytes were rare. The lack of animal-mediated dispersal could be due to the fragmentation of urban habitats and reduced connectivity for seed vectors such as birds or bats. Thus, urban epiphyte assemblages may be functionally and phylogenetically filtered by the urban matrix.

We observed significant vertical stratification, with species richness highest in the inner crown and maximum abundance at approximately 37% of total tree height. This pattern is ecologically meaningful, as the inner crown offers moderate light and humidity and is potentially buffered from intense solar radiation and wind desiccation. These findings align with theories of vertical niche partitioning, where epiphytes segregate by microclimatic conditions rather than competitive exclusion *per se* (Zotz, 2007). The marked preference for external branches also suggests a mechanistic explanation related to anchorage, moisture runoff, and propagule interception. Urban environments lack the structural and thermal buffering of forest canopies, making vertical distribution a critical axis of niche differentiation.

Host trees played a key role in determining both epiphyte abundance and richness. While native species generally supported more individuals, exotic species such as *Fraxinus uhdei* and *Spathodea campanulata* emerged as important hosts, harboring the highest species richness. This highlights that epiphyte-host relationships may be more closely tied to functional traits, bark type, branching architecture, and longevity than biogeographic origin. Interestingly, despite being exotic and planted, some species have become central nodes in the urban epiphyte network. This suggests that urban biodiversity planning could benefit from a trait-based approach rather than a strict native–exotic dichotomy when selecting species for green infrastructure.

We found that bark texture significantly influenced both water retention and epiphyte load. Rough bark retained more water after immersion and supported higher epiphyte abundances, which aligns with the hypothesis that bark water retention promotes microhabitat persistence and seedling establishment. Tree size and branching complexity also correlated positively with epiphyte abundance, reaffirming their role as key structural filters in the urban canopy.

The low spatial turnover in epiphyte composition (Mantel r = 0.092) and lack of significant differences among tree cover types suggest a high degree of ecological homogeneity across Medellín. This could be

due to standardized planting schemes, uniform maintenance regimes, and the absence of large remnant forest patches. Despite this, nearly 70% of trees were colonized by epiphytes, indicating that urban trees —even when scattered and isolated—can serve as effective biodiversity scaffolds. Moreover, the high occupancy rate and low underestimation bias due to good crown visibility reinforce the view that urban trees are essential for vascular epiphytes in heavily modified environments. Our findings are consistent with previous studies in Bogotá (Gil & Díazgranados, 2005), where epiphyte richness also increased toward the upper crown.

Underestimation of diversity in epiphyte studies can occur when observing from the ground using binoculars; however, because the treetops in the city do not overlap easily and the visibility of the branches is wide, we could infer that the underestimation is very low. We had a tree occupancy percentage close to 70%, which could be considered high due to the conditions of the city, in which most trees have been planted, and microclimatic conditions (high radiation and low humidity) are predominant in the city's urban area. This, in addition, coupled with the absence of forests in the urban area, could serve as a source of propagules in the urban area. Gil and Diazgranados (2005), in a study carried out in the city of Bogotá, obtained results like those found in the present work, where the diversity of epiphytes tended to increase towards the area of the treetops. Bromeliaceae (represented mainly by *T. recurvata*) and Polypodiaceae (mainly *P. macrocarpa*) were the most abundant families. This is relevant considering that both are large cities, which, even with their development processes, can preserve some species of native epiphytes from Colombia.

Conclusions

These distribution characteristics and their relationship with the characteristics of the host may allow these species to have potential use in urban gardens since their establishment is not limited by anthropic intervention in the city. Likewise, abundant *species* such as *T. recurvata* offer other interesting ecosystem services, such as air quality biomonitors, due to their ability to intercept and collect atmospheric dust (Mejía et al., 2017).

The diversity of epiphytes in the city is dominated by wind-dispersed plants that are highly resilient to transformed environments. This study provides elements to understand the state of the city's epiphytes. It proposes management measures, such as enriching the city's tree components with native species that are not naturally dispersed, which could offer an opportunity to increase its ecological functionality.

In the last decade, Colombia has made significant progress in legally requiring the protection of epiphytes and implementing measures such as rescues, transfers, and relocations to mitigate the environmental impacts caused by the productive sector. Preliminary assessments indicate that vascular epiphytes could benefit from well-planned actions such as rescues and transfers. Although compensation actions have recently contributed to protecting vascular epiphytes, there is growing pressure to relax or eliminate legal protection frameworks. Given the prospect of abundant species

resistant to anthropic conditions, the provisions for lifting the ban in the city should be carefully evaluated to effectively direct protection actions towards species that merit it.

Declarations

The following statements must be included in your submitted manuscript under the heading 'Statements and Declarations'. This should be placed after the References section. Please note that submissions that do not include required statements will be returned as incomplete.

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Competing Interests

Authors declare they have non-financial interests to disclose.

Author Contribution

Ana María Benavides contributed to the study's conception and design. Yudy Gallego and Maria Judith Carmona-Higuita collected data. All three authors jointly wrote the first draft of the manuscript, and all authors commented on previous versions. All authors read and approved the final manuscript. Maria Judith Carmona-Higuita and Ana María Benavides performed data analyses.

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Figures

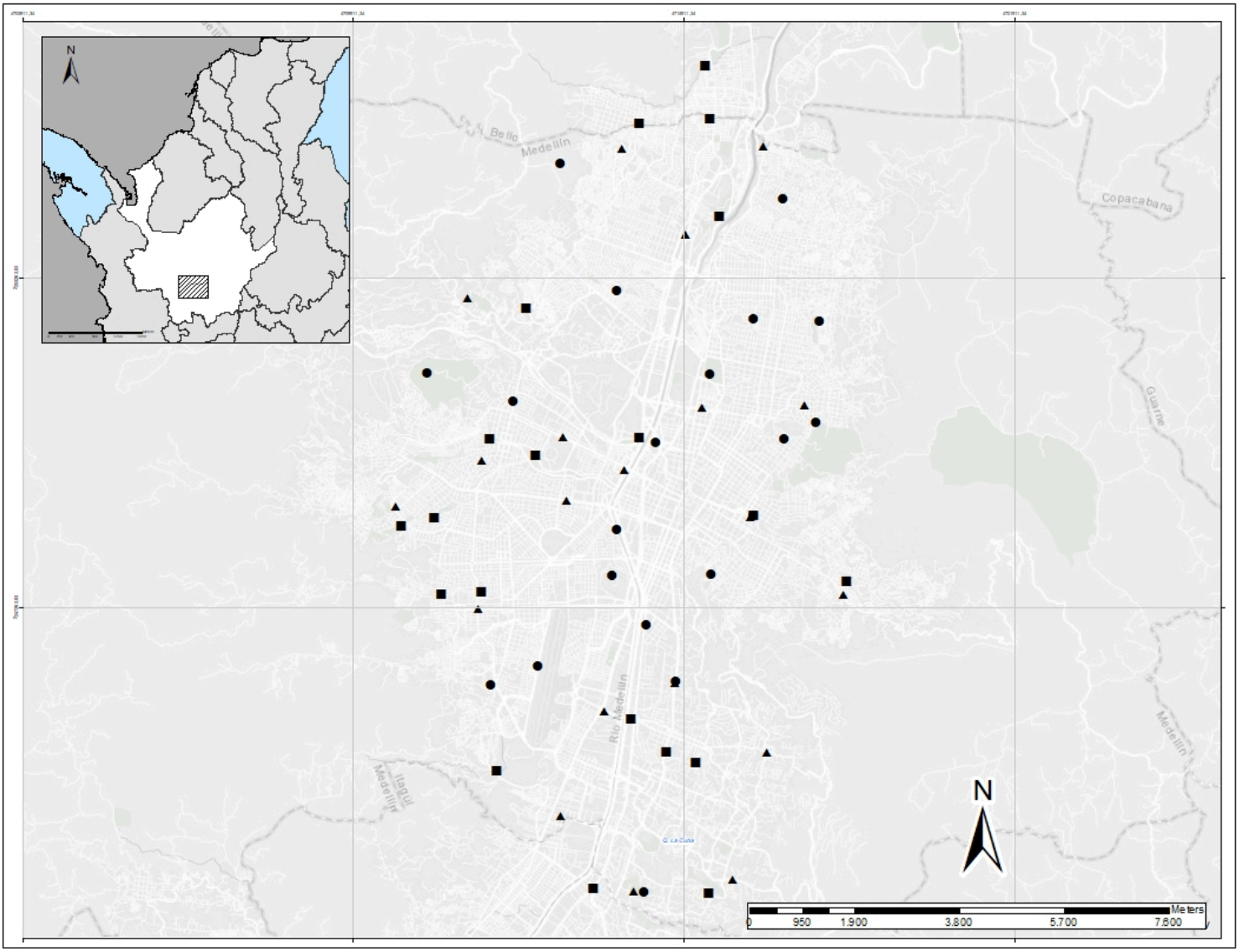

Figure 1

Sampling points of epiphytes in the urban area of Medellin, Antioquia, Colombia categorized by coverage type in the study area. Squares represent infrastructure-associated green areas (INF), diamonds indicate ecological protection areas (ECO), and triangles denote water-associated green areas (WAT).

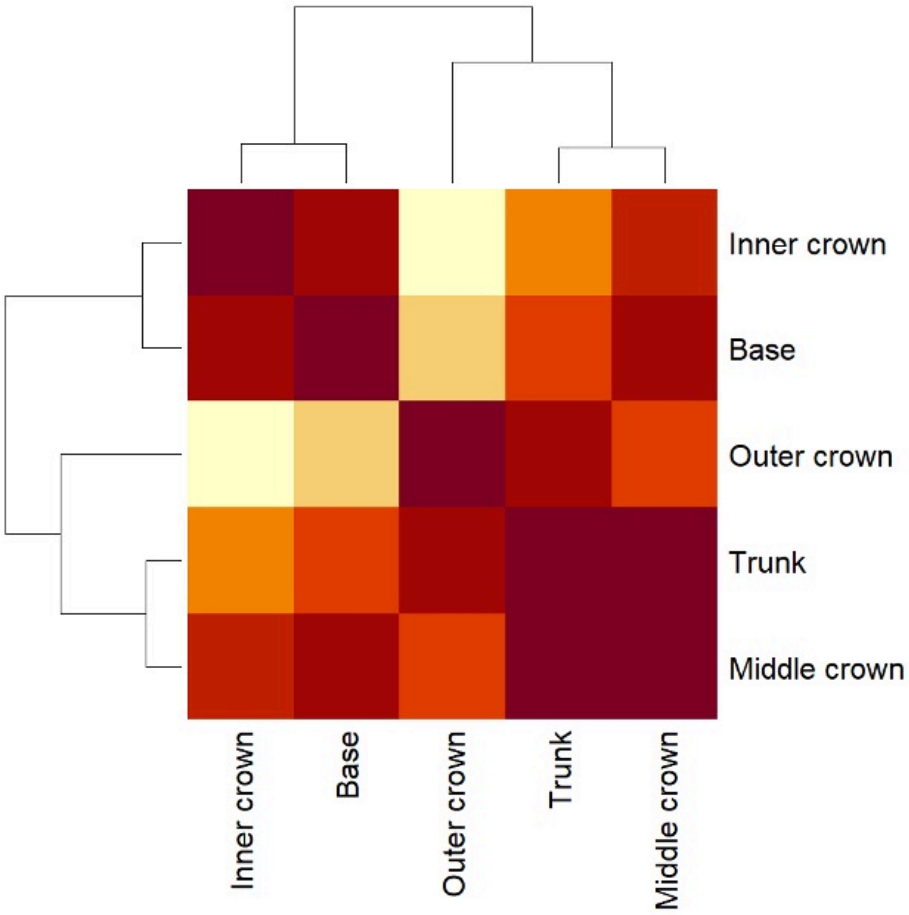

Figure 2

Niche overlap matrix or Pianka's index heatmap by tree strata.

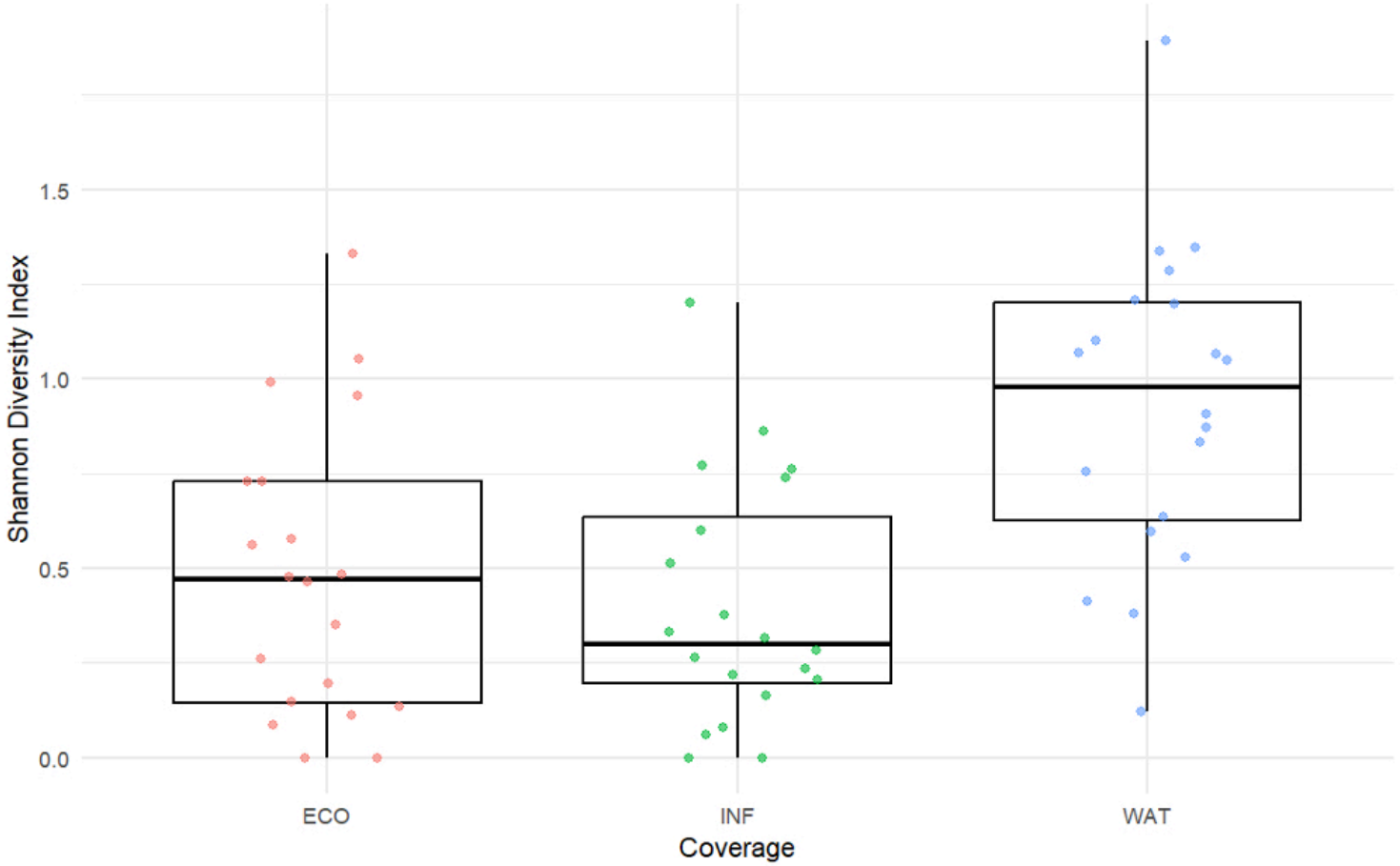

Figure 3

Boxplots – Diversity index comparisons between city covers: green areas designated for ecological protection (ECO), green areas designated for protection associated with bodies of water (WAT), green areas integrated with urban infrastructure (INF).

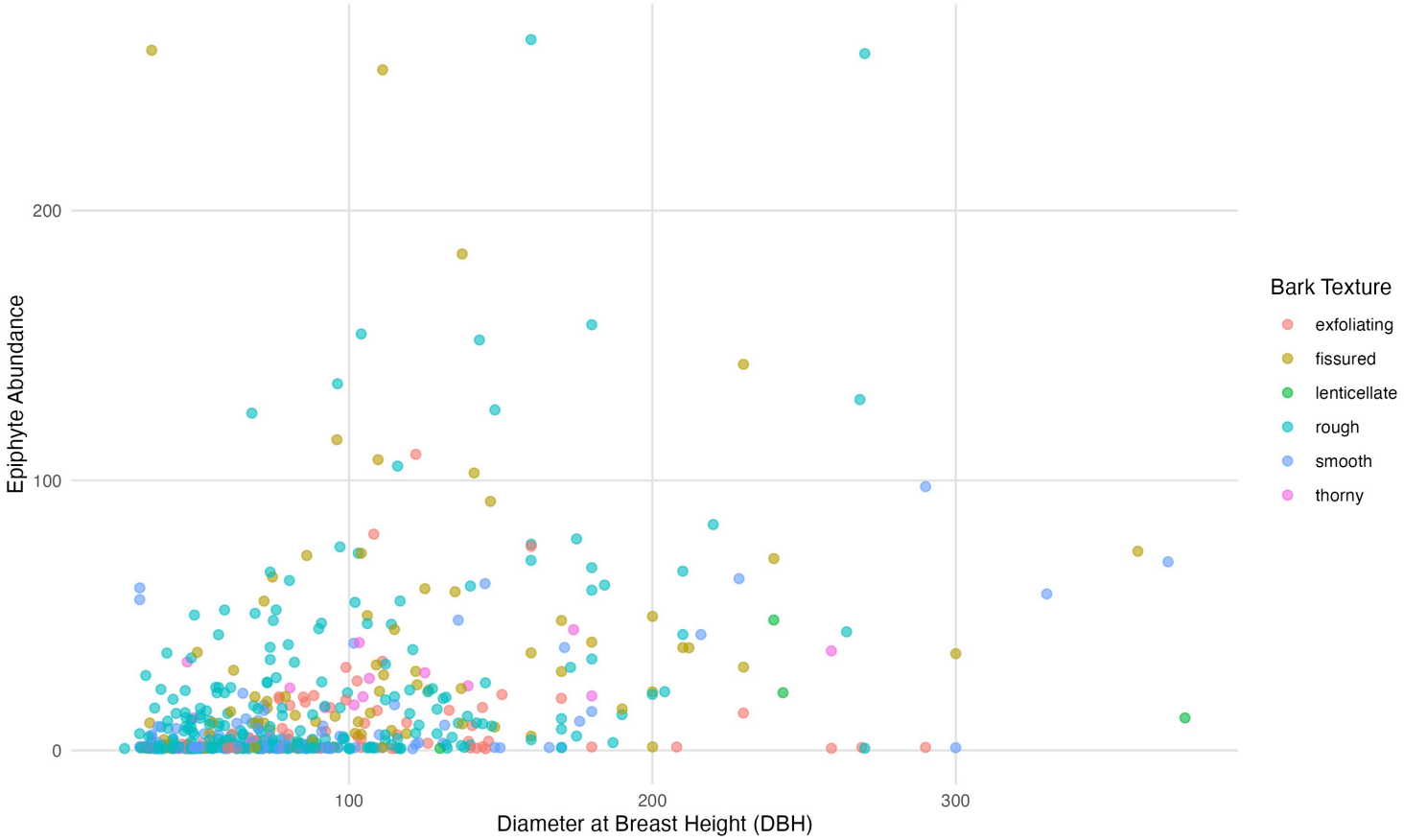

Figure 4

Relationships between DBH and epiphyte abundance with bark type.

Supplementary Files

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- SupplementaryInformation.docx