

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ

Colegio de Posgrados

**What influences richness and abundance in the canopy ant community of
Cloud Forests?**

Tesis

Francisco Xavier Velásquez Espín

**Juan Manuel Guayasamín, PhD.
Director de Trabajo de Titulación**

Trabajo de titulación de posgrado presentado como requisito
para la obtención del título de Magister en Ecología Tropical y Conservación

Quito, 24 de mayo de 2023

UNIVERSIDAD SAN FRANCISCO DE QUITO USFQ
COLEGIO DE POSGRADOS

HOJA DE APROBACIÓN DE TRABAJO DE TITULACIÓN

**What influences richness and abundance in the canopy ant community of
Cloud Forests?**

Francisco Xavier Velásquez Espín

Nombre del Director del Programa: Elisa Bonaccorso
Título académico: PhD
Director del programa de: Maestría Ecología tropical y conservación

Nombre del Decano del colegio Académico: Carlos Amilcar Valle Castillo
Título académico: PhD
Decano del Colegio: Ciencias Biológicas y Ambientales

Nombre del Decano del Colegio de Posgrados: Hugo Burgos Yánez
Título académico: PhD

Quito, mayo 2023

© DERECHOS DE AUTOR

Por medio del presente documento certifico que he leído todas las Políticas y Manuales de la Universidad San Francisco de Quito USFQ, incluyendo la Política de Propiedad Intelectual USFQ, y estoy de acuerdo con su contenido, por lo que los derechos de propiedad intelectual del presente trabajo quedan sujetos a lo dispuesto en esas Políticas.

Asimismo, autorizo a la USFQ para que realice la digitalización y publicación de este trabajo en el repositorio virtual, de conformidad a lo dispuesto en la Ley Orgánica de Educación Superior del Ecuador.

Nombre del estudiante: Francisco Xavier Velásquez Espín

Código de estudiante: 00326492

C.I.: 1720483666

Lugar y fecha: Quito, 29 de mayo de año.

ACLARACIÓN PARA PUBLICACIÓN

Nota: El presente trabajo, en su totalidad o cualquiera de sus partes, no debe ser considerado como una publicación, incluso a pesar de estar disponible sin restricciones a través de un repositorio institucional. Esta declaración se alinea con las prácticas y recomendaciones presentadas por el Committee on Publication Ethics COPE descritas por Barbour et al. (2017) Discussion document on best practice for issues around theses publishing, disponible en <http://bit.ly/COPETheses>.

UNPUBLISHED DOCUMENT

Note: The following graduation project is available through Universidad San Francisco de Quito USFQ institutional repository. Nonetheless, this project – in whole or in part – should not be considered a publication. This statement follows the recommendations presented by the Committee on Publication Ethics COPE described by Barbour et al. (2017) Discussion document on best practice for issues around theses publishing available on <http://bit.ly/COPETheses>.

DEDICATORIA

A mi querida familia por siempre apoyarme, infinitas gracias por todo lo que hacen.

AGRADECIMIENTOS

A todos los que hicieron posible este estudio, gracias por su ayuda indispensable.

RESUMEN

La documentación de la biodiversidad en los ecosistemas tropicales es una piedra angular de la biología de la conservación. Este estudio describe la composición de la comunidad de hormigas en el dosel de los Andes Tropicales, uno de los puntos calientes de biodiversidad más significativos del mundo. El trabajo de campo se llevó a cabo en la Reserva Mashpi-Tayra, situada en la Biosfera Andina-Chocó a 775-1295 msnm en Ecuador. Utilizando hormigas como grupo objetivo, nos centramos en tres objetivos principales: (i) evaluar la riqueza y abundancia de Formicidae dentro de las bromelias del dosel del bosque nublado; (ii) entender qué variables abióticas explican la composición de la comunidad de hormigas; y (iii) vincular nuestros resultados a los esfuerzos de conservación. Tomamos muestras de 65 bromelias del dosel ubicadas a diferentes elevaciones sobre el nivel del suelo (17.3-35.3 m). Dentro de esas bromeliáceas, encontramos 1310 individuos de hormigas, representando 41 especies, con la mayor posibilidad de encontrar especies endémicas. El análisis de rarefacción estima que nuestro muestreo documentó el 85% de la riqueza de especies de hormigas de la zona. El género más abundante muestreado fue *Megalomyrmex* con 557 individuos, un hallazgo ecológico notable. Los Modelos Lineales Generales indican que las variables que mejor explican la abundancia de hormigas son la localización de la altura de la bromelia y la temperatura interna del depósito de agua de la bromelia. No encontramos influencia de la elevación (m sobre el nivel del mar) ni de la temperatura ambiental externa. Nuestros hallazgos son el primer intento de documentar la diversidad de hormigas de dosel en el dosel de los bosques nublados ecuatorianos. Esperamos que este estudio fundacional con la biodiversidad registrada sea utilizado como una herramienta para los intentos de conservación y los marcos legales ambientales.

Palabras clave: Bosque nublado, hormigas, dosel, diversidad, ecología de comunidad.

ABSTRACT

The documentation of biodiversity in tropical ecosystems is a cornerstone of conservation biology. This study describes the ant community composition in the canopy of the Tropical Andes, one of the most significant biodiversity hotspots in the world. Fieldwork was conducted at Mashpi-Tayra Reserve, located in the Andean-Chocó Biosphere at 775-1295 m.a.s.l in Ecuador. Using ants as our target group, we focused on three main goals: (i) to assess the richness and abundance of Formicidae inside the canopy bromeliads of the cloud forest; (ii) to understand which abiotic variables explain the composition of the ants community; and (iii) to link our results to conservation efforts. We sampled 65 canopy bromeliads located at different elevations above ground level (17.3–35.3 m). Within those bromeliads, we found 1310 ant individuals, representing 41 species, with the highest possibility of finding endemic species. Rarefaction analysis estimates that our sampling documented 85% of the ant species richness in the area. The most abundant genus sampled was *Megalomyrmex* with 557 individuals a remarkable ecological finding. General Linear Models indicate that the variables that better explain ant abundance are the location of the bromeliad's height and the internal water tank temperature of the bromeliad. We found no influence of elevation (m above sea level) and external environmental temperature. Our findings are the first attempt to document the diversity of canopy ants in the canopy of the Ecuadorian cloud forests. We expect that this foundation study with the recorded biodiversity will be used as a tool for conservation attempts and environmental legal frameworks.

Key words: Cloud Forest, ants, Canopy, diversity, community ecology.

TABLA DE CONTENIDO

Resumen	8
Abstract	9
Introducción	11
Metodología y diseño de la investigación	14
Resultados	17
Discusión.....	19
Referencias	26
Tablas	38
Figuras.....	43

INTRODUCTION

The conservation of the Andean-Chocó forests of Ecuador depends, to a large extent, on the documentation of species, evaluation of their conservation status, and endemism (Guayasamin et al., 2021; Justicia, 2007; Myers et al. 2000). In this context, because of their overall diversity and abundance, invertebrates represent an ideal group of study especially in unexplored environments and ecosystems, such as the canopy layer (Adis, Didham & Stork, 1997; Erwin, 1982). Invertebrates are the most diverse and abundant groups on Earth and recently have received particular attention due to evidence of worldwide declines (Eisenhauer, Bonn & Guerra, 2019; Sánchez-Bayo & Wyckhuys, 2019). Among terrestrial insects, ants (family: Formicidae Latreille, 1809) are one of the most diverse taxa with cosmopolitan distribution, reaching almost every microhabitat (e.g., underground, forest floor, understory, and canopy), except for some high latitude zones and oceanic islands that have no native species (Janicki et al. 2016; Bleil, Blüthgen, & Junker, 2011; Heil & McKey, 2003). Ants have been studied for centuries, and so there is a good overall understanding of their ecological roles, and they are relatively easy to sample in comparison to other taxa, making them ideal for biodiversity studies (Vergara-Torres et al. 2017; Lach et al. 2010; Andersen, 2000; Hölldobler & Wilson, 1990; Wilson, 1987; Brown & Wilson, 1959).

Since their diversification during the Cretaceous, ants have become the most abundant diverse group of eusocial terrestrial insects (King, Warren & Bradford, 2013; Moreau et al. 2006; Hölldobler & Wilson, 1998). In the Neotropics, more than 4000 ant species have been described, and Formicidae currently represents one of the best-studied invertebrate groups from a taxonomic perspective, although numerous species are still undescribed (Fernandez, Guerrero

& Sanchez-Restrepo, 2021). Recently ecological ant research in the neotropical mountains has received attention (Floren et al. 2014; Donoso & Ramón, 2006). Within tropical Andean Cloud Forests, the canopy layer remains understudied (Perillo et al. 2021; Longino & Nadkarni, 1990), and most studies concentrate sampling efforts in habitats such as the forest floor, low vegetation, and the understory layer (Basset, 2001).

The canopy of the tropical cloud forest possesses unique climatic (i.e., constant humidity and rainfall) and biotic (abundance of moss and bromeliads) characteristics (Gonçalves-Souza et al., 2010; Lowman & Rinker, 2004). Many organisms use bromeliads during various stages of their life cycle (Balke et al. 2018; Gonçalves-Souza et al. 2010), and it has been shown, for instance, that ant community structures are maintained by bromeliads both in native and agroforestry systems (DaRocha et al. 2016). For instance, one of the most remarkable and fascinating ecological complex relationship known as Ants gardens (AGs) occurs between ants and epiphytes including Bromeliaceae (Morales-Linares et al. 2017; Hölldobler & Wilson, 1990). This complex interaction between plants and ants consists of the formation of a “garden” created by the ants with the deliberately selected seeds of the implemented epiphyte for the formation of carton nests. Carton nests are a fructiferous environment for plants to grow (Campbell, Kiers & Chomicki, 2022; Corbara, 2021; Dejean et al. 2018; Davidson, 1988); the material of the nest is called “Carton” and consists of a mix of organic matter (e.g.: plants, vertebrates’ poop, soil) and ant secretions; however, the specific mix can vary depending on the species of ant and the species of epiphyte interaction (Cabrera, 2021; Yu, 1994; Davidson, 1988).

In addition, the canopy is a fascinating habitat for ants; tropical lowland canopies show remarkable ecological characteristics such as high abundance, which increases when we

increase the canopy height (McCaig et al. 2020; Herz et al., 2007; Davidson & Patrell-Kim, 1996); or the presence of territorially dominant arboreal ant species documented for tropical lowlands such as the genera *Azteca*, *Crematogaster* and *Camponotus* (Dejean et al. 2018). For instance, the genus *Azteca* is characterized by its aggressive behavior linked with canopy microhabitat colonization (Philpott et al. 2018).

Furthermore, the abundance and richness of the canopy ants suggest, in tropical and temperate regions, a substantial impact on the ecosystem ecology and functionality, such as significant consumption of vegetation, channelers of energy, and soil nutrients suppliers for epiphytes (Floren et al 2014; Floren et al. 2002; Hölldobler & Wilson, 1990; Wilson, 1987). Nevertheless, Cloud Forests ecosystems such as the Andean Choco remain underrepresented in contrast to other tropical ecosystems (Floren et al. 2014; Donoso & Ramón, 2006).

This study is a first in trying to describe the diversity and abundance of the bromeliad-inhabiting ants in the canopy of a neotropical cloud forest and exploring the role that some abiotic factors play in structuring this community. It is expected, based on four major diversity hypotheses presented by Szewczyk & McCain (2016): Mid-Domain Effect, Elevational Climate Model, Area, and Thermal Energy, that the abundance and diversity will be strongly influenced by abiotic factors such as the temperature found inside (internal) and outside (external) the bromeliads, the height of the bromeliad, and the altitude of the sampling sites. The specific goals of this research are: (1) to assess the richness and abundance of the ant community inside the canopy bromeliads of a neotropical cloud forest; (2) to understand the role of some abiotic variables on the composition of the ant community; and (3) to provide a foundation study (first insight of the canopy diversity) for conservation attempts.

METHODS

Study area

The study was conducted in the Mashpi-Tayra (0.167N, 78.887W) cloud forest, managed by Fundación Futuro and Mashpi Lodge (Pichincha province, Ecuador). Located in the Andean-Chocó biogeographic region of Ecuador. This region is considered one of the 25 biodiversity hotspots in the world, making it a priority area for conservation, especially for its high endemism and anthropogenic threats, such as mining and deforestation (Fagua & Ramsey, 2019). The Mashpi-Tayra cloud forest covers 2,500 ha, with an altitudinal gradient between 500 and 1200 m.a.s.l. The average temperature for the area is 23 °C with an annual average precipitation of 2509 mm. The forest composition is cataloged as Piedmont Evergreen Forest (Sierra, 1999), and is influenced by the Andes biogeographic region (Fig.1).

Canopy Sampling

This study was conducted under research permits MAATE-ARSFC-2022-2286 and MAATE-CMARG-2022-0575, issued by the Ministerio del Ambiente, Agua y Transición Ecológica of Ecuador.

Tree climbing requires specialized training to learn access and movement techniques that follow rigorous safety protocols (Jepson, 2000). The implemented methodology was proposed by McCracken and Forstner (2008), where the sampling units are composed of bromeliads ($n = 65$). Sampling was conducted in 13 trees (5 bromeliads per tree) across an elevational gradient from 775 to 1295 m a.s.l. To avoid major impacts on the epiphyte community, only trees that had more than 15 bromeliads were sampled. Additionally, we implemented a protocol to minimize structural damage when climbing (i.e., Single Rope Technique; see McCracken &

Forstner, 2008, see Figure 2.). Each collected bromeliad was photographed, and we collect the following abiotic variables: elevation (m above sea level), height (distance from ground level), external (air) temperature, internal (water) temperature, and pH of the water collected inside the bromeliads (Szewczyk & McCain, 2016). Each bromeliad was bagged and removed from the tree to the ground to collect all ants inside a tent. The ants were collected by an exhaustive search through all parts of the bromeliad, regardless of the duration time, each bromeliad was sampled in its entirety until no more ants were present. Life photos were taken for every ant morphospecies, documenting color patterns, breeds, and developmental stages, then were collected in 1L glass jars with 90% EtOH. All specimens were deposited at the Museo del Laboratorio de Zoología Terrestre, Universidad San Francisco de Quito.

Taxonomic identification

Ants were separated from other invertebrates and stored in 90% EtOH. Specimens were first sorted into morphospecies and then identified to genus level. Each morphospecies was photographed at least once using a Stereomicroscope (ZEISS SteREO Discovery.V12). Samples were identified in Laboratorio de Ecología Acuática (LEA) USFQ, using the systematics books by Fernández et al. (2019) and Bolton et al. (2006) and taxonomical ant genera keys (Baccaro et al. 2015; Schmidt & Shattuck, 2014). All bromeliads were identified to the genus level as *Guzmania* Ruiz y Pav., 1802.

Ant community characterization

To estimate the diversity of the ant assemblage (Chao & Chiu, 2016), we used Hill numbers (Chao & Chiu, 2016; Hsieh & Chao, 2016), complemented with a rarefaction curve analysis (interpolation and extrapolation) to assess the richness of each sample (Chao & Jost, 2012), using “iNEXT” package in R version 4.2 (Hsieh & Chao, 2016; Chao et al. 2014). A

Nonasymptotic Analysis (Rarefaction/Extrapolation) with ChaoRichness (Hill numbers of order $q = 0$) was conducted to generate 3 curves: the sample-size-based rarefaction and extrapolation sampling curves with 95% confidence interval; the sample completeness curve that depicts how to sample completeness (measured by sample coverage) and, a Coverage-based rarefaction (solid lines) and extrapolation (dashed lines) sampling curves with 95% confidence intervals, to assess the richness and sampling coverage. Species richness, in order $q = 0$, shows the basic data information that includes the sample coverage estimate or SC (community total probability of occurrence of the species observed in the sample).

To understand how variables drive the ant community composition in cloud forest bromeliads, a General Linear Model (GLM) with four variables: 1) Height from the ground (Hei): distance (m) from ground level to the location of the sampled bromeliad in the tree, 2) Elevation (Elev): elevation above sea level in meters, 3) Internal temperature (TI): temperature registered in the water tank, measured in Celsius, and 4) External temperature (TE): air temperature registered for the sampled bromeliad in Celsius, as correlates of the observed abundance variation in each bromeliad were generated. GLMs were built in the package ‘Lme4’ in R version 4.2 (R Core Team). Only statistically significant variables ($p < 0.05$) were retained in the final models. Model assumptions were evaluated by calculating the p-value for the fitted model by comparing it to a null model using an ANOVA; the test was selected via a “Chisq” chi-square test (Mangiafico, 2016). In addition, the overdispersion of the Poisson model was calculated with the dispersion test (Kleiber, Zeileis & Zeileis, 2020; Smith & Warren, 2019).

RESULTS

Ant community composition

The ant bromeliad survey resulted in a total of 1310 individuals from 41 morphospecies, 6 subfamilies (Ectatomminae, Formicinae, Heteroponerinae, Myrmicinae, and Ponerinae, and 23 genera. The Dolichoderinae subfamily is represented by 3 genera: *Azteca* (2 morphospecies), *Dolichoderus* (1), and *Tapinoma* (3). The subfamily Ectatomminae presents only 1 genus, *Holcaponera*, and 1 morph. Formicinae is represented by 3 genera: *Brachymyrmex* (1 morphospecies), *Camponotus* (5 morphospecies), and *Nylanderia* (3 morphospecies). Heteroponerinae is confirmed by 1 genus and 1 morphospecies, *Acanthoponera*. The subfamily Myrmicinae is the most represented of all the 7 subfamilies with 8 genera: *Acromyrmex* (1 morphospecies), *Apterostigma* (2 morphospecies), *Crematogaster* (2 morphospecies), *Cyphomyrmex* (2 morphospecies), *Megalomyrmex* (1 morphospecies), *Pheidole* (5 morphospecies), *Solenopsis* (2 morphospecies), *Wasmannia* (1 morphospecies). Finally, the subfamily Ponerinae presented 7 genera: *Anochetus* (1 morphospecies), *Hypoconera* (1 morphospecies), *Mayaponera* (1 morphospecies), *Neoponera* (2 morphospecies), *Odontomachus* (1 morphospecies), *Pachycondyla* (1 morphospecies), and *Rasopone* (1 morphospecies). (See Fig.3, Fig.4, and Table.1).

Interpolation and extrapolation for species diversity

The function iNEXT (iNtrapolation and EXTrapolation) from R generates the rarefaction curves and sampling coverage. Based on the obtained results, with an observed richness (sample size) of 41 (Quartile Deviation Lower Control Limit (LCL) 34.09 and Quartile Deviation Upper

Control Limit (UCL) 47.90), we have an overall Sampling Coverage (SC) of 0.85 (LCL 0.79 and UCL 0.91). The double sample size extrapolation reaches an SC of 0.94 (LCL 0.88 and UCL 1) (Fig.3). Formicidae canopy community presents a species richness observed value of 41 and an estimator of 61 (Standard Error (S.E.) 15.13, 91-41). For the Shannon diversity or Shannon entropy, we have an observed value of 28 with an estimator of 37 (S.E. 3.81, 44.13-29.17). The Simpson diversity or inverse Simpson Concentration presents an observed value of 18 with an estimator of 21 (S.E. 3.479, 28.29-14.66). (See Table 4, Table 5, and Table 6).

Shannon, Simpson, Evenness and, Density

Four diversity indices (Shannon, Simpson, Evenness, and Density) were calculated with the R package “Vegan: Ecological diversity” (n = 65) in order to estimate the biodiversity of the cloud forest canopy, see summary Table 7.

Environmental drivers of ant diversity in canopy bromeliads

The estimated results obtained by the GLM model are presented in Table 8. The variable Height (*Hei*) and Internal Temperature (*TI*) are significantly correlated with the abundance values. The correlations are positive (an increase in *Hei* and *TI* produces increases in abundance). The other variables, Elevation (*Elev*) and, External Temperature (*TE*), do not significantly affect the abundance. To test the influence of abiotic variables on the community composition, we constructed a General Linear Model (GLM), as follows:

GLM

Full model

$$Ab \sim Elev + Hei + TI + TE$$

Mathematical notation of the model

$$Ab_i \sim \text{Poisson}(\mu_i)$$

$$E(Ab_i) = \mu_i \text{ and } \text{var}(Ab_i) = \mu_i$$

$$\log(\mu_i) = \eta_i$$

$$\eta_i = \beta_1 + \beta_2 \times Elev_i + \beta_3 \times Hei_i + \beta_4 \times TI_i + \beta_5 \times TE_i$$

Call of the formula: *Ab* Abundance is the dependent variable, and *Elev* Elevation, *Hei* Height, *TI* Internal temperature, and *TE* External temperature are the independent variables. *The overdispersion of the model was: $z = 2.3964$, $p\text{-value} = 0.008279$ and dispersion 60.32102.

Analysis of Deviance (ANOVA)

The p-value obtained for the fitted model, by comparing it to a null model with the ANOVA function, was significant statistically $2.2e-16$ (<0.05) (See Table. 9).

DISCUSSION

Estimating species richness is a challenging task, especially in the canopy. Our sampling effort proved to be adequate to estimate the number of species in our study, the bromeliad microhabitat from the canopy layer of the Andean-Choco Cloud Forest of Mashpi-Tayra. Rarefaction analyses estimated that we documented approximately 85% of the Formicidae species from the Mashpi-Tayra canopy bromeliad microhabitat. This is an extraordinary result given that sampling the canopy is a challenging endeavor, to say the least (McCracken & Forstner, 2008); then, we can conclude that the analyses presented below, rely on a representative measure of species richness, which is the most fundamental unit of biodiversity. To exemplify the efficiency of the sampling, if we had doubled the number of surveyed

bromeliads ($n = 130$), we would have documented 93% of the species (Fig.4), in other words, just an additional 8% of what we found.

Our findings (41 morphospecies and 23 genera in 65 bromeliads) indicate the remarkable diversity of ants in the cloud forest (Table 1 and Figure 2). For instance, another canopy montane ecosystem studied in Costa Rica found a total diversity of 27 species inside 13 genera from 14 trees across three different habitats and degraded ecosystems (Schonberg et al. 2004). In addition, a canopy ant research study conducted in Panama found a diversity of 23 ant species with the major dominance of the genus *Azteca*, also found in this study but with non-major dominance (Ribeiro et al. 2013). Thus, our findings may reflect the biodiversity hotspot and possible high-endemism linked to the Andean-Chocó region (Fagua & Ramsey, 2019; Sarkar et al. 2006). In addition, the following results are just one token of the biodiversity puzzle from the canopy layer of Mashpi-Tayra cloud forest since only the microhabitat provided by bromeliads was sampled. It is strongly recommended that to understand the ants of the cloud forest an exhaustive sampling including more canopy microhabitats must be performed (e.g.: under tree bark, in holes, within specialized tree structures, other epiphyte species, etc.) (Hölldobler & Wilson, 1990).

There is also the caveat that our interpretation of ant species richness, due to hyper-diverse groups, relies heavily on external morphology (Schär et al. 2022; van Elst et al. 2021; Wilson, 2003). Therefore, a pending study should approach species identity from a multivariate and integrative perspective to solve the true ant diversity identity (De Queiroz, 2007; Vieites et al. 2009; Padial et al. 2010). Besides, elevational gradients present a strong congruence in patterns which affects long-term macroevolutionary processes (Longino, Branstetter & Ward, 2019).

Thus, expanding the elevational range studied may indicate insights into elevational influence in the ant canopy community.

The three-dimensional structure of the canopy, and the abundance of bromeliads and other epiphytic plants, provide a diversity of microhabitats that benefit the evolution of specialization and ecological interactions (Scheffers & Williams, 2018; Petruzzellis et al. 2017; Basset et al. 2015; Lowman & Rinker, 2004). For instance, ants can shape and mediate the communities found inside the bromeliads of their gardens (Talaga et al. 2015; Céréghino et al. 2010; Frank & Lounibos, 2009). Additionally, these complex mutualistic associations shape the microhabitat as well. Bromeliads obtain part of their nutrients by interacting with microorganisms such as ants and enhancing their reproductive allocation (Leroy et al. 2016).

In parallel, bromeliads might function as islands of stability for invertebrate communities, protecting them from extreme variations in wind, temperature, humidity, and light (Richardson et al. 2015; Parker, 1995; Geiger, 1965). For example, ants use non-water-holding axils of bromeliads as shelter, these plant species are known as “myrmecophytes” for their association and specialization (Frank & Lounibos, 2009; Frank et al. 2004). Thus, interestingly, bromeliads can be considered as a source of heterogeneity (a very different microhabitat when compared to other microhabitats in the forest) but also a place of stability (relatively similar conditions among different bromeliads); spatial heterogeneity promotes the diversification of species (Stein et al. 2014) (see Table 2 and Table 3 for heterogeneity and ants bromeliads occurrence).

Furthermore, the Ecuadorian Andean-Chocó is known for its biodiversity (Fagua & Ramsey, 2019), and in this sense, ants fit the perfect role as a focal taxon (Fernandez, Guerrero & Sanchez-Restrepo, 2021). The most abundant genus was *Megalomyrmex* Forel, a distinct taxon

from the Neotropics with 557 individuals of one morphospecies (Longino, 2010; Brandão, 1990). This genus is characterized by its diversity in form and behavior (Boudinot, Sumnicht & Adams, 2013). For instance, some species tend sternorrhynchans, while others have lestopibiotic (thieves) behaviors stealing from fungi-growing ants (Attini tribe) or even xenobiotic (guest ant) behaviors (Adams et al. 2012; Adams, 2008; Brandão 1990). In addition, the *Megalomyrmex* was the most present genus in the canopy reaching an occupancy of 21 out of 65 sampled bromeliads (See Table 3). It is strongly recommended to focus attention on these findings due to the abundance and presence of this genus.

The *Megalomyrmex* genus is more related to predation and being social parasites rather than herbivorous (Adams et al. 2000; Brandão, 1990). Moreover, this genus is known for its low abundance (Longino, 2010). This insight should be followed to understand the true ecological dynamics of the Formicidae taxa in the canopy. If the canopy layer is being assessed, a deeper focus on the ecology of the group is needed.

The second most abundant taxa sampled in the canopy was the genus *Pheidole* Westwood, 1839 with 5 species. The genus *Pheidole* is the most common in the family Formicidae making it a hyper-diverse genus, especially in the neotropics (Fernandez, Guerrero & Sanchez-Restrepo, 2021; Sarnat et al. 2015). *Pheidole* and *Megalomyrmex* belong to the most abundant and diverse subfamily Myrmicinae. In addition, our study has found 3 different genera which belong to the Attini tribe: *Acromyrmex*, *Apterostigma*, and *Cyphomyrmex*. The last two genera were documented for the first time inside the canopy by our study (Greer & Moreau, 2021). Many species of this tribe have developed specialized skills such as fungus farming (Schultz et al. 2015; Ward et al. 2015). Further studies focused on interspecific relationships to understand the dynamics of the community are needed.

The presence of the genera: *Rasopone*, *Mayaponera*, *Odontomachus*, *Anochetus*, *Neoponera*, *Pachycondyla*, and *Hypoponera* which belongs to the subfamily Ponerinae, suggests a strong prevalence of predation in the canopy due to their almost exclusive predatory behavior (Fiorentino et al. 2023). The presence of these predators has been used as an insight for understanding the abundance of ants in tropical lowlands (Davidson et al. 2003). Thus, focusing on the ant predators found inside the Andean-Choco Cloud Forest of Ecuador will help to understand the ecological relationships between ants. However, our study serves as a baseline for further taxonomical and ecological characterizations. Finally, the richness assessment presents a sample coverage of 85% with 41 different species found inside 65 bromeliads.

Despite the high diversity of tropical arboreal ants, perhaps the most remarkable aspect of them is their abundance (biomass) (Davidson & Patrell-Kim, 1996). The main hypotheses that have been proposed to explain ant diversity, size, and spatial location are (i) thermal energy (TE), (ii) mid-domain effect (MDE), (iii) area (A), and (iv) the elevational climate model (ECM) (Szewczyk & McCain 2016). TE (i) is supported as a driver of diversity in Formicidae because warmer temperatures could lead to longer foraging periods and more energy is available for a variety of ecological functions. MDE (ii) If species ranges are randomly distributed within a bounded domain, they will overlap closer to the center of the domain than at the edges, thus decreasing species richness from the center toward the edges. However, this distribution, geometric in nature, can be found elsewhere in the curve. A (iii) based on the species-area relationship, predicts that as the area in a determined elevational increase, diversity in that elevation should increase. Finally, ECM (iv) states that precipitation and temperature drive diversity due to the impact on productivity. (Szewczyk & McCain 2016).

Our study provides several insights for understanding what drives ant abundance. The abundance model, including the four variables (Elev, Hei, TI, TE), is the only model that reaches statistical support (Fox et al. 2015). Additionally, two variables reach a satisfactory p-value, the height from the ground (Hei), and the internal temperature (TI). Both variables, when compared against the dependent variable of abundance, present an "arch" pattern (Fig. 6), which seems to support the Mid Domain Effect hypothesis. Figure 6 suggests that the geometric restriction is in the middle section c.a. 25 meters. This big-scale pattern presented in groups like birds (Jetz & Rahbek, 2001) seems to act on a local scale for ants. The model shows that when we increase Hei by 1, we expect that the abundance increases by 0.13. By increasing one unit of TI, a rise of 0.17 in abundance is expected. However, this increase is up to a point, then passing the height of 25-30 m the abundance starts to decrease (Fig 6.). Furthermore, our results indicate that the temperature inside the bromeliad presents no significant variance or increase when we reach higher canopy heights and further studies need to address the suggested geometric behavior presented in this study.

The configuration of the canopy layer is different from the ground even if they are in the same forest; for instance, the canopy is drier and hotter than the ground (Davidson et al. 2003). In this sense, more abiotic variables, such as rainfall should be addressed to understand what other variables can shape the community inside the bromeliads. Furthermore, most studies are focused on lowlands. Thus, the abiotic variables chosen need to fit with the adequate conditions of the selected elevation range.

Finally, is important to mention that this study serves as a foundation study for documenting the biodiversity found inside the canopy layer of the endangered ecosystem of the Ecuadorian Andean-Choco Cloud Forest. As it is shown, during the last ten years, mining concessions in

the Andes have proliferated, even within protected areas (Fagua & Ramsey, 2019; Roy et al. 2018; Myers et al. 2000). Thus, our study despite showing the new insights of ant ecology and how abiotic variables shapes the communities, it is the first to show the ant diversity in the canopies of Ecuadorian cloud forests; many of the 41 identified morphospecies likely correspond to geographic endemics or, even, new species. For instance, this could serve as a potential scientific source for creating legal frameworks for promoting the rights of nature as it was the local case of “Los Cedros” in Ecuador where the documentation of biodiversity and endemic species was used as a tool for legal conservation efforts against mining (Prieto, 2021; Guayasamin et al, 2021).

ACKNOWLEDGEMENTS

We thank for the value support and help from: USFQ (Elisa Bonaccorso, Gabriela Gavilanes, Karla Barragan), Mashpi Lodge Reserve (Mateo Roldan, Anderson Medina, dragon fly staff and kitchen staff), TAMUCC (Rebecca Davis), TMA (Jerry Toth), Fundacion Futuro (Felipe Andrade, Gustavo Pazmiño and park rangers), volunteers (Stephen Connelly, Daniel Connelly, Salome Herrera and Juan Diego Chavez), field assistants (Jose Vieira and Amanda Quezada).

REFERENCES OR LITTERATURE CITED

- Adams, R. M., Mueller, U. G., Schultz, T. R., & Norden, B. (2000). Agro-predation: usurpation of attine fungus gardens by *Megalomyrmex* ants. *Naturwissenschaften*, 87, 549-554.
- Adams, R., & Antonov, L. D. (2012). Fitness consequences of nest infiltration by the mutualist-exploiter *Megalomyrmex adamsae*. *Ecol Entomol. Ecological Entomology*, 37, 453-462.
- Adams, R.M.M. (2008) *Unraveling the Origins of Social Parasitism in Megalomyrmex Ants*. The University of Texas, Austin, 1–114 pp.
- Adis, J., Didham, R. K., & Stork, N. E. (1997). *Canopy arthropods* (Eds). Chapman & Hall.
- Andersen, A. N. (2000). Global ecology of rainforest ants: functional groups in relation to environmental stress and disturbance.
- Baccaro, F. B., Feitosa, R. M., Fernández, F., Fernandes, I. O., Izzo, T. J., Souza, J. D., & Solar, R. (2015). Guia para os gêneros de formigas do Brasil. *Manaus: Editora INPA*, 388.
- Balke, M., Gómez-Zurita, J., Ribera, I., Vilorio, A., Zillikens, A., Steiner, J., ... & Vogler, A. P. (2008). Ancient associations of aquatic beetles and tank bromeliads in the Neotropical forest canopy. *Proceedings of the National Academy of Sciences*, 105(17), 6356-6361.
- Basset, Y. (2001). Invertebrates in the canopy of tropical rain forests How much do we really know?. *Plant Ecology*, 153(1), 87-107.

- Basset, Y., Cizek, L., Cuénoud, P., Didham, R. K., Novotny, V., Ødegaard, F., ... & Leponce, M. (2015). Arthropod distribution in a tropical rainforest: tackling a four dimensional puzzle. *PloS one*, 10(12), e0144110.
- Bleil, R., Blüthgen, N., & Junker, R. R. (2011). Ant-Plant Mutualism in Hawaii ‘i? Invasive Ants Reduce Flower Parasitism but also Exploit Floral Nectar of the Endemic Shrub *Vaccinium reticulatum* (Ericaceae) 1. *Pacific Science*, 65(3), 291-300.
- Bolton, B., Alpert, G., Ward, P. S., & Naskrecki, P. (2006). *Bolton's catalogue of ants of the world, 1758-2005* (p. 222). Cambridge: Harvard University Press.
- Boudinot, B. E., Sumnicht, T. P., & Adams, R. M. (2013). Central American ants of the genus *Megalomyrmex* Forel (Hymenoptera: Formicidae): six new species and keys to workers and males. *Zootaxa*, 3732(1), 1-82.
- Brandão, C. R. F. (1990). Systematic revision of the Neotropical ant genus *Megalomyrmex* Forel (Hymenoptera: Formicidae: Myrmicinae), with the description of thirteen new species. *Arquivos de Zoologia*, 31(5), 1-91.
- Brown Jr, W. L., & Wilson, E. O. (1959). The evolution of the dacetine ants. *The Quarterly Review of Biology*, 34(4), 278-294.
- Campbell, L. C., Kiers, E. T., & Chomicki, G. (2022). The evolution of plant cultivation by ants. *Trends in Plant Science*.
- Céréghino, R., Leroy, C., Dejean, A., & Corbara, B. (2010). Ants mediate the structure of phytotelm communities in an ant-garden bromeliad. *Ecology*, 91(5), 1549-1556.
- Chao, A., & Chiu, C. H. (2016). Species richness: estimation and comparison. *Wiley StatsRef: statistics reference online*, 1, 26.

- Chao, A., & Jost, L. (2012). Coverage-based rarefaction and extrapolation: standardizing samples by completeness rather than size. *Ecology*, 93(12), 2533-2547.
- Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecological monographs*, 84(1), 45-67.
- Corbara, B. (2021). Ant Gardens. In *Encyclopedia of social insects* (pp. 35-38). Cham: Springer International Publishing.
- DaRocha, W. D., Neves, F. S., Dáttilo, W., & Delabie, J. H. (2016). Epiphytic bromeliads as key components for maintenance of ant diversity and ant–bromeliad interactions in agroforestry system canopies. *Forest Ecology and Management*, 372, 128-136.
- Davidson, D. W. (1988). Ecological studies of neotropical ant gardens. *Ecology*, 69(4), 1138-1152.
- Davidson, D. W., & Patrell-Kim, L. (1996). Tropical arboreal ants: why so abundant?. In *Neotropical biodiversity and conservation* (pp. 127-140). Mildred E. Mathias Botanical Garden.
- Davidson, D. W., Cook, S. C., Snelling, R. R., & Chua, T. H. (2003). Explaining the abundance of ants in lowland tropical rainforest canopies. *Science*, 300(5621), 969-972.
- De Queiroz, K. (2007). Species concepts and species delimitation. *Systematic biology*, 56(6), 879-886.

- Dejean, A., Orivel, J., Leponce, M., Compin, A., Delabie, J. H., Azémar, F., & Corbara, B. (2018). Ant–plant relationships in the canopy of an Amazonian rainforest: the presence of an ant mosaic. *Biological Journal of the Linnean Society*, 125(2), 344-354.
- Donoso, D. A., & Ramón, G. (2009, January). Composition of a high diversity leaf litter ant community (Hymenoptera: Formicidae) from an Ecuadorian pre-montane rainforest. In *Annales de la Société entomologique de France* (Vol. 45, No. 4, pp. 487-499). Taylor & Francis Group.
- Eisenhauer, N., Bonn, A., & A. Guerra, C. (2019). Recognizing the quiet extinction of invertebrates. *Nature communications*, 10(1), 50.
- Erwin, T. L. (1982). Tropical forests: their richness in Coleoptera and other arthropod species. *The Coleopterists Bulletin*.
- Fagua, J. C., & Ramsey, R. D. (2019). Geospatial modeling of land cover change in the Chocó-Darién global ecoregion of South America; One of most biodiverse and rainy areas in the world. *PloS one*, 14(2), e0211324.
- Fernandez, F., Guerrero, R. J., & Sanchez-Restrepo, A. F. (2021). Systematics and diversity of Neotropical ants. *Revista Colombiana de Entomología*, 47(1).
- Fiorentino, G., Lattke, J., Troya, A., Sosiak, C., Dong, M., & Barden, P. (2023). Deep time extinction of largest insular ant predators and the first fossil *Neoponera* (Formicidae: Ponerinae) from Miocene age Dominican amber. *BMC biology*, 21(1), 1-12.
- Floren, A., Biun, A., & Linsenmair, E. K. (2002). Arboreal ants as key predators in tropical lowland rainforest trees. *Oecologia*, 131, 137-144.

- Floren, A., Wetzel, W., & Staab, M. (2014). The contribution of canopy species to overall ant diversity (Hymenoptera: Formicidae) in temperate and tropical ecosystems. *Myrmecological News*, 19(1), 65-74.
- Fox, G. A., Negrete-Yankelevich, S., & Sosa, V. J. (Eds.). (2015). *Ecological statistics: contemporary theory and application*. Oxford University Press, USA.
- Frank, J. H., & Lounibos, L. P. (2009). Insects and allies associated with bromeliads: a review. *Terrestrial arthropod reviews*, 1(2), 125-153.
- Frank, J. H., Sreenivasan, S., Benschhoff, P. J., Deyrup, M. A., Edwards, G. B., Halbert, S. E., ... & Welbourn, W. C. (2004). Invertebrate animals extracted from native *Tillandsia* (Bromeliales: Bromeliaceae) in Sarasota county, Florida. *Florida Entomologist*, 87(2), 176-185.
- Geiger, R. (1965). The climate near the ground harvard university press. *Massachusetts, Cambridge*.
- Gonçalves-Souza, T., Brescovit, A. D., Rossa-Feres, D. D. C., & Romero, G. Q. (2010). Bromeliads as biodiversity amplifiers and habitat segregation of spider communities in a Neotropical rainforest. *The Journal of Arachnology*, 38(2), 270-279.
- Greer, J. A., & Moreau, C. S. (2021). Phylogenetic analysis and trait evolution of ant cocoons. *Insect Systematics & Evolution*, 53(1), 60-77.
- Guayasamin, J. M., Vandegrift, R., Policha, T., Encalada, A. C., Greene, N., Ríos-Touma, B., ... & Roy, B. A. (2021). Tipping point towards biodiversity conservation? Local and global consequences of the application of 'Rights of Nature' by Ecuador.

- Heil, M., & McKey, D. (2003). Protective ant-plant interactions as model systems in ecological and evolutionary research. *Annual Review of Ecology, Evolution, and Systematics*, 425-453.
- Herz, H., Beyschlag, W., & Hölldobler, B. (2007). Herbivory rate of leaf-cutting ants in a tropical moist forest in Panama at the population and ecosystem scales. *Biotropica*, 39(4), 482-488.
- Hölldobler, B., & Wilson, E. O. (1990). *The ants*. Harvard University Press.
- Hölldobler, B., & Wilson, E. O. (1998). *Journey to the ants: a story of scientific exploration*. Harvard University Press.
- Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). *Methods in Ecology and Evolution*, 7(12), 1451-1456.
- Hsieh, T., Ma, K., & Chao, A. (2016). A quick introduction to iNEXT via examples. Available in: <http://chao.stat.nthu.edu.tw/wordpress>.
- Janicki, J., Narula, N., Ziegler, M., Guénard, B., & Economo, E. P. (2016). Visualizing and interacting with large-volume biodiversity data using client-server web-mapping applications: The design and implementation of antmaps.org. *Ecological informatics*, 32, 185-193.
- Jepson, J. (2000). *The tree climber's companion: a reference and training manual for professional tree climbers*. Drayer Fachhandel.
- Jetz, W., & Rahbek, C. (2001). Geometric constraints explain much of the species richness pattern in African birds. *Proceedings of the National Academy of Sciences*, 98(10), 5661-5666.

- Justicia, R. M. (2007). Ecuador's Chocó Andean Corridor: *A landscape approach for conservation and sustainable development* (Doctoral dissertation, University of Georgia).
- King, J. R., Warren, R. J., & Bradford, M. A. (2013). Social insects dominate eastern US temperate hardwood forest macroinvertebrate communities in warmer regions. *PLoS One*, 8(10), e75843.
- Kleiber, C., Zeileis, A., & Zeileis, M. A. (2020). Package 'aer'. R package version, 12(4).
- Lach, L., Parr, C., & Abbott, K. (Eds.). (2010). *Ant ecology*. Oxford university press.
- Leroy, C., Carrias, J. F., Céréghino, R., & Corbara, B. (2016). The contribution of microorganisms and metazoans to mineral nutrition in bromeliads. *Journal of Plant Ecology*, 9(3), 241-255.
- Longino, J. T. (2010). A taxonomic review of the ant genus *Megalomyrmex* Forel (Hymenoptera: Formicidae) in Central America. *Zootaxa*, 2720(1), 35-58.
- Longino, J. T., & Nadkarni, N. M. (1990). A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. *Psyche: A Journal of Entomology*, 97(1-2), 81-93.
- Longino, J. T., Branstetter, M. G., & Ward, P. S. (2019). Ant diversity patterns across tropical elevation gradients: effects of sampling method and subcommunity. *Ecosphere*, 10(8), e02798.
- Lowman, M. D., & Rinker, H. B. (2004). *Forest canopies*. Elsevier.
- Mangiafico, S. S. (2016). Summary and Analysis of Extension. Program Evaluation in R, version, 1(1).

- McCaig, T., Sam, L., Nakamura, A., & Stork, N. E. (2020). Is insect vertical distribution in rainforests better explained by distance from the canopy top or distance from the ground?. *Biodiversity and Conservation*, 29(3), 1081-1103.
- McCracken, S. F., & Forstner, M. R. (2008). Bromeliad patch sampling technique for canopy herpetofauna in Neotropical forests. *Herpetological Review*, 39, 170-174.
- McCracken, S. F., & Forstner, M. R. J. (2014). Herpetofaunal community of a high canopy tank bromeliad. *Aechmea zebrina*, 65-75.
- Morales-Linares, J., García-Franco, J. G., Flores-Palacios, A., Valenzuela-González, J. E., Mata-Rosas, M., & Díaz-Castelazo, C. (2017). Spatial structure of ant-gardens: vertical distribution on host trees and succession/segregation of associated vascular epiphytes. *Journal of Vegetation Science*, 28(5), 1036-1046.
- Moreau, C. S., Bell, C. D., Vila, R., Archibald, S. B., & Pierce, N. E. (2006). Phylogeny of the ants: diversification in the age of angiosperms. *science*, 312(5770), 101-104.
- Myers, N., Mittermeier, R. A., Mittermeier, C. G., Da Fonseca, G. A., & Kent, J. (2000). Biodiversity hotspots for conservation priorities. *Nature*, 403(6772), 853-858.
- Padial, J. M., Miralles, A., De la Riva, I., & Vences, M. (2010). The integrative future of taxonomy. *Frontiers in zoology*, 7(1), 1-14.
- Parker, G. G. (1995). Structure and microclimate of forest canopies. *Forest canopies*, 73-106.
- Perillo, L. N., Castro, F. S. D., Solar, R., & Neves, F. D. S. (2021). Disentangling the effects of latitudinal and elevational gradients on bee, wasp, and ant diversity in an ancient neotropical mountain range. *Journal of Biogeography*, 48(7), 1564-1578.

- Petruzzellis, F., Palandrani, C., Savi, T., Alberti, R., Nardini, A., & Bacaro, G. (2017). **Sampling intraspecific variability in leaf functional traits: Practical suggestions to maximize collected information.** *Ecology and evolution*, 7(24), 11236-11245.
- Philpott, S. M., Serber, Z., & De la Mora, A. (2018). **Influences of species interactions with aggressive ants and habitat filtering on nest colonization and community composition of arboreal twig-nesting ants.** *Environmental entomology*, 47(2), 309-317.
- Prieto Munoz, J. G. (2021). **The Los Cedros forest has rights. The Ecuadorian constitutional court affirms the rights of nature.** *Verfassungsblog: On Matters Constitutional*.
- Ribeiro, S., Espirito Santo, N., Delabie, J., & Majer, J. (2013). **Competition, resources and the ant (Hymenoptera: Formicidae) mosaic: a comparison of upper and lower canopy.** *Mycological Progress*, 18, 113-120.
- Richardson, M. J., Richardson, B. A., & Srivastava, D. S. (2015). **The stability of invertebrate communities in bromeliad phytotelmata in a rain forest subject to hurricanes.** *Biotropica*, 47(2), 201-207.
- Roy, B. A., Zorrilla, M., Endara, L., Thomas, D. C., Vandegrift, R., Rubenstein, J. M., ... & Read, M. (2018). **New mining concessions could severely decrease biodiversity and ecosystem services in Ecuador.** *Tropical Conservation Science*, 11, 1940082918780427.
- Sánchez-Bayo, F., & Wyckhuys, K. A. (2019). **Worldwide decline of the entomofauna: A review of its drivers.** *Biological conservation*, 232, 8-27.

- Sarkar, S., Sánchez-Cordero, V., Londoño, M. C., & Fuller, T. (2009). Systematic conservation assessment for the Mesoamerica, Chocó, and Tropical Andes biodiversity hotspots: a preliminary analysis. *Biodiversity and Conservation*, 18, 1793-1828.
- Sarnat, E. M., Fischer, G., Guénard, B., & Economo, E. P. (2015). Introduced Pheidole of the world: taxonomy, biology and distribution. *ZooKeys*, (543), 1.
- Schär, S., Talavera, G., Rana, J. D., Espadaler, X., Cover, S. P., Shattuck, S. O., & Vila, R. (2022). Integrative taxonomy reveals cryptic diversity in North American *Lasius* ants, and an overlooked introduced species. *Scientific Reports*, 12(1), 5970.
- Scheffers, B. R., & Williams, S. E. (2018). Tropical mountain passes are out of reach—but not for arboreal species. *Frontiers in Ecology and the Environment*, 16(2), 101-108.
- Schmidt, C. A., & Shattuck, S. O. (2014). The higher classification of the ant subfamily Ponerinae (Hymenoptera: Formicidae), with a review of ponerine ecology and behavior. *Zootaxa*, 3817(1), 1-242.
- Schonberg, L. A., Longino, J. T., Nadkarni, N. M., Yanoviak, S. P., & Gering, J. C. (2004). Arboreal Ant Species Richness in Primary Forest, Secondary Forest, and Pasture Habitats of a Tropical Montane Landscape 1. *Biotropica*, 36(3), 402-409.
- Schultz, T. R., Sosa-Calvo, J., Brady, S. G., Lopes, C. T., Mueller, U. G., Bacci Jr, M., & Vasconcelos, H. L. (2015). The most relictual fungus-farming ant species cultivates the most recently evolved and highly domesticated fungal symbiont species. *The American Naturalist*, 185(5), 693-703.

- Sierra, R. (1999). *Propuesta preliminar de un sistema de clasificación de vegetación para el Ecuador continental*. Proyecto INEFAN/GEF-BIRF, Quito (Ecuador) EcoCiencia, Quito (Ecuador).
- Smith, C., & Warren, M. (2019). *GLMs in R for Ecology*.
- Stein, A., Gerstner, K., & Kreft, H. (2014). Environmental heterogeneity as a universal driver of species richness across taxa, biomes and spatial scales. *Ecology letters*, 17(7), 866-880.
- Szewczyk, T., & McCain, C. M. (2016). A systematic review of global drivers of ant elevational diversity. *PloS one*, 11(5), e0155404.
- Talaga, S., Dézerald, O., Carteron, A., Petitclerc, F., Leroy, C., Céréghino, R., & Dejean, A. (2015). Tank bromeliads as natural microcosms: a facultative association with ants influences the aquatic invertebrate community structure. *Comptes Rendus Biologies*, 338(10), 696-700.
- van Elst, T., Eriksson, T. H., Gadau, J., Johnson, R. A., Rabeling, C., Taylor, J. E., & Borowiec, M. L. (2021). Comprehensive phylogeny of Myrmecocystus honey ants highlights cryptic diversity and infers evolution during aridification of the American Southwest. *Molecular phylogenetics and evolution*, 155, 107036.
- Vergara-Torres, C. A., Vásquez-Bolaños, M., Corona-López, A. M., Toledo-Hernández, V. H., & Flores-Palacios, A. (2017). Ant (Hymenoptera: Formicidae) diversity in the canopy of a tropical dry forest in Tepoztlán, Central Mexico. *Annals of the Entomological Society of America*, 110(2), 197-203.
- Vieites, D. R., Wollenberg, K. C., Andreone, F., Köhler, J., Glaw, F., & Vences, M. (2009). Vast underestimation of Madagascar's biodiversity evidenced by an integrative

amphibian inventory. *Proceedings of the National Academy of Sciences*, 106(20), 8267-8272.

Ward, P. S., Brady, S. G., Fisher, B. L., & Schultz, T. R. (2015). The evolution of myrmicine ants: phylogeny and biogeography of a hyperdiverse ant clade (hymenoptera: Formicidae). *Systematic Entomology*, 40(1), 61-81.

Wilson, E. O. (1987). The arboreal ant fauna of Peruvian Amazon forests: a first assessment. *Biotropica*, 245-251.

Wilson, E. O. (1987). The little things that run the world (the importance and conservation of invertebrates). *Conservation biology*, 344-346.

Wilson, E. O. (2003). *Pheidole in the New World: a dominant, hyperdiverse ant genus (Vol. 1)*. Harvard University Press.

Yu, D. W. (1994). The structural role of epiphytes in ant gardens. *Biotropica*, 222-226.

Tables

Table 1. Diversity and abundance of Formicidae found in the canopy of the cloud forests of Mashpi-Tayra Reserves, Ecuador.

Subfamily	Genera	Morphospecies	Abundance
Dolichoderinae	<i>Tapinoma</i>	3	43
Dolichoderinae	<i>Azteca</i>	2	23
Dolichoderinae	<i>Dolichoderus</i>	1	10
Ectatomminae	<i>Holcaponera</i>	1	1
Formicinae	<i>Nylanderia</i>	3	74
Formicinae	<i>Camponotus</i>	5	35
Formicinae	<i>Brachymyrmex</i>	1	32
Heteroponerinae	<i>Acanthoponera</i>	1	1
Myrmicinae	<i>Solenopsis</i>	2	158
Myrmicinae	<i>Pheidole</i>	5	165
Myrmicinae	<i>Megalomyrmex</i>	1	557
Myrmicinae	<i>Crematogaster</i>	2	69
Myrmicinae	<i>Apterostigma</i>	2	32
Myrmicinae	<i>Cyphomyrmex</i>	2	3
Myrmicinae	<i>Wasmannia</i>	1	82
Myrmicinae	<i>Acromyrmex</i>	1	2
Ponerinae	<i>Rasopone</i>	1	2
Ponerinae	<i>Mayaponera</i>	1	6
Ponerinae	<i>Odontomachus</i>	1	2
Ponerinae	<i>Anochetus</i>	1	7
Ponerinae	<i>Neoponera</i>	2	3
Ponerinae	<i>Pachycondyla</i>	1	2
Ponerinae	<i>Hypoponera</i>	1	1

Table 2. Subfamilies and bromeliad occurrence of Formicidae found in the canopy of the cloud forests of Mashpi-Tayra Reserves, Ecuador.

Subfamily	Bromeliad occurrence
Myrmicinae	62
Formicinae	27
Dolichoderinae	16
Ponerinae	14
Ectatomminae	1
Heteroponerinae	1

Table 3. Genera and bromeliad occurrence of Formicidae found in the canopy of the cloud forests of Mashpi-Tayra Reserves, Ecuador.

Genera	Bromeliad occurrence
Megalomyrmex	21
Pheidole	17
Nylanderia	16
Camponotus	9
Solenopsis	8
Tapinoma	7
Anochetus	5
Crematogaster	5
Dolichoderus	5
Wasmannia	5
Azteca	4
Apterostigma	3
Neoponera	3
Brachymyrmex	2
Cyphomyrmex	2
Odontomachus	2
Acanthoponera	1
Acromyrmex	1
Holcoponera	1
Hypoconera	1
Mayaponera	1
Pachycondyla	1
Rasopone	1

Table 4. Asymptotic estimates of ant species richness and diversity indexes (ChaoShannon and ChaoSimpson) in the sampled bromeliads.

	Assemblage	Diversity	Observed	Estimator	Standard Error	Lower Control Limit	Upper Control Limit
1	<i>Formicidae</i>	Species richness	41	60.93359	15.13197	41	90.5917
2	<i>Formicidae</i>	Shannon diversity	27.82461	36.653	3.814616	29.17649	44.12951
3	<i>Formicidae</i>	Simpson diversity	18.46154	21.47727	3.479073	14.65842	28.29613

Table 5. Diversity estimates with rarefied and extrapolated samples, size-based (the diversity estimates with respect to sample size).

Assemblage	t	Method	Order.q	Quartile Deviation	Quartile Deviation Lower Control Limit	Quartile Deviation Upper Control Limit	Sampling Coverage	Sampling Coverage Lower Control Limit	Sampling Coverage Upper Control Limit
<i>1</i>	1	Rarefaction	0	1.875	1.529464	2.220536	0.08730159	0.06265662	0.1119466
<i>10</i>	32	Rarefaction	0	29.37335	24.796656	33.950042	0.74273291	0.67645297	0.8090129
<i>20</i>	65	Observed	0	41	34.09587	47.90413	0.85208696	0.79393016	0.9102438
<i>30</i>	96	Extrapolation	0	47.84051	38.88215	56.798865	0.9028455	0.83932428	0.9663667
<i>40</i>	130	Extrapolation	0	52.80231	41.112647	64.491966	0.93966349	0.8790658	1

Table 6. Diversity estimates with rarefied and extrapolated samples, coverage based (the diversity estimates with respect to sample coverage).

Assemblage	Sampling Coverage	t	Method	Order.q	Quartile Deviation	Quartile Deviation Lower Control Limit	Quartile Deviation Upper Control Limit
<i>1</i>	0.08730159	1	Rarefaction	0	1.875	1.529464	2.220536
<i>10</i>	0.74273304	32	Rarefaction	0	29.37335	24.796656	33.950042
<i>20</i>	0.85208696	65	Observed	0	41	34.09587	47.90413
<i>30</i>	0.9028455	96	Extrapolation	0	47.84051	38.88215	56.798865
<i>40</i>	0.93966349	130	Extrapolation	0	52.80231	41.112647	64.491966

Table 7. Summary table of all the variables measured in this study, from the abiotic variables (*Elev*, *Hei*, *TE*, *TI*, *pH*, and *Am*) and biotic variables such as the diversity indices (*Den*, *Bs*, *Bsi*, *Ev*, *Ab*, *Riq*).

Variables	Min	Median	Mean	Max.	Standard Deviation	Standard Error	Code	Unit
<i>Elevation</i>	775.00	882.00	920.50	1295.00	146.90	18.22	<i>Elev</i>	meters above the sea level (m.a.s.l)
<i>Bromeliad Height from the ground</i>	17.26	24.10	24.47	35.30	3.92	0.49	<i>Hei</i>	meters (m)
<i>Enviromental temperature</i>	19.60	22.80	22.87	27.10	1.71	0.21	<i>TE</i>	celsius (°C)
<i>Bromeliad Internal temperature</i>	19.10	20.80	21.11	24.00	1.08	0.13	<i>TI</i>	celsius (°C)
<i>Potential of hydrogen</i>	2.00	4.50	4.55	6.90	0.77	0.10	<i>pH</i>	pH
<i>Bromeliad Area</i>	0.58	2.55	3.04	8.08	1.69	0.21	<i>Am</i>	Square meters
<i>Species density</i>	0.00	14.52	51.19	383.66	88.48	10.98	<i>Den</i>	Individuals per unit area (ind/m ²)
<i>Shannon-Weaver Biodiversity index</i>	0.00	0.09	0.33	1.42	0.41	0.05	<i>Bs</i>	Shannon diveristy index
<i>Simpson Biodiversity index</i>	0.00	0.22	0.32	1.00	0.35	0.04	<i>Bsi</i>	Simpson diversity index
<i>Species Evenness</i>	0.00	0.57	0.53	1.00	0.37	0.06	<i>Ev</i>	Pielou's evenness index
<i>Abundance</i>	0.00	4.00	20.15	254.00	40.47	5.02	<i>Ab</i>	Individuals
<i>Species Richness</i>	0.00	2.00	1.86	7.00	1.45	0.18	<i>Riq</i>	Species number

Table 8. GLMs Coefficients Table of the fitted model:

$$Ab \sim Elev + Hei + TI + TE$$

	Estimate	Std. Error	z value	Pr(> z)	
<i>Intercept</i>	-3.9742067	0.7061833	-5.628	1.83E-08	***
<i>Elev</i>	-0.0001908	0.0002443	-0.781	0.435	
<i>Hei</i>	0.1289656	0.0066191	19.484	< 2e-16	***
<i>TI</i>	0.1732154	0.0335423	5.164	2.42E-07	***
<i>TE</i>	0.0077775	0.0225015	0.346	0.73	

Table 9. Analysis of Deviance (ANOVA) Table from the fitted model $Ab \sim Elev + Hei + TI + TE$ against a null model

Model 1: $Ab \sim Elev + Hei + TI + TE$

Model 2: $Ab \sim 1$

	Resid. Df	Resid. Dev	Degrees of freedom	Deviance	Pr(>Chi)	
<i>1</i>	60	2408.6				
<i>2</i>	64	2848.8	-4	-440.29	< 2.2e-16	***

Figures

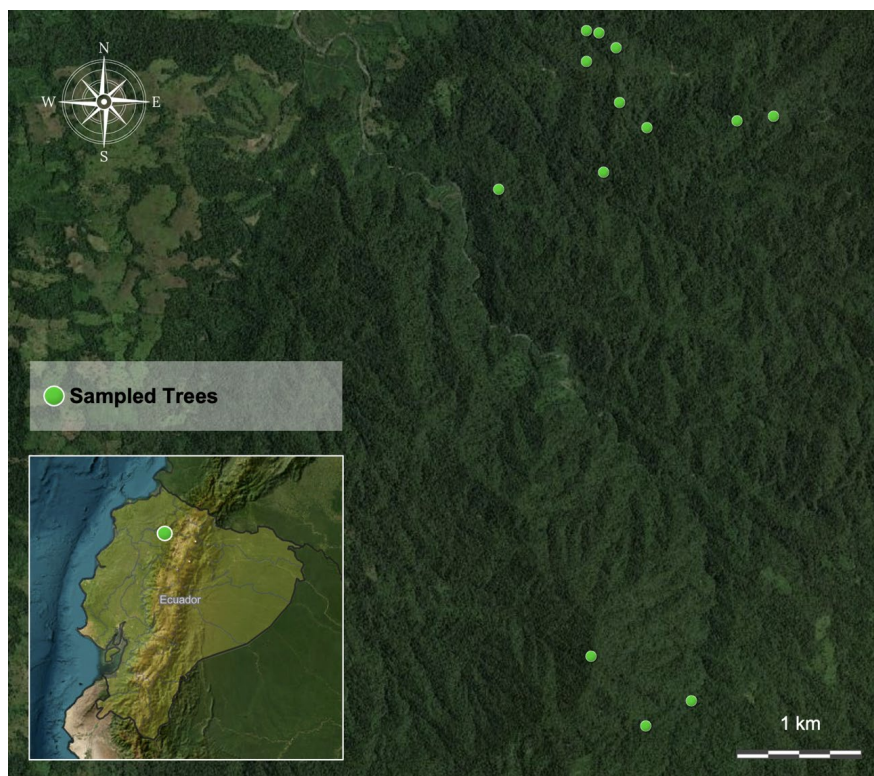


Figure 1. Sampling distribution, location of the 13 sampled trees located in Mashpi-Tayra.



Figure 2. Tree sampling in Mashpi-Tayra cloud forest. Left, FVE in the crown of a tree sampling a bromeliad. On the right, FVE uses the Single Rope Technique to reach the canopy of the cloud forest.

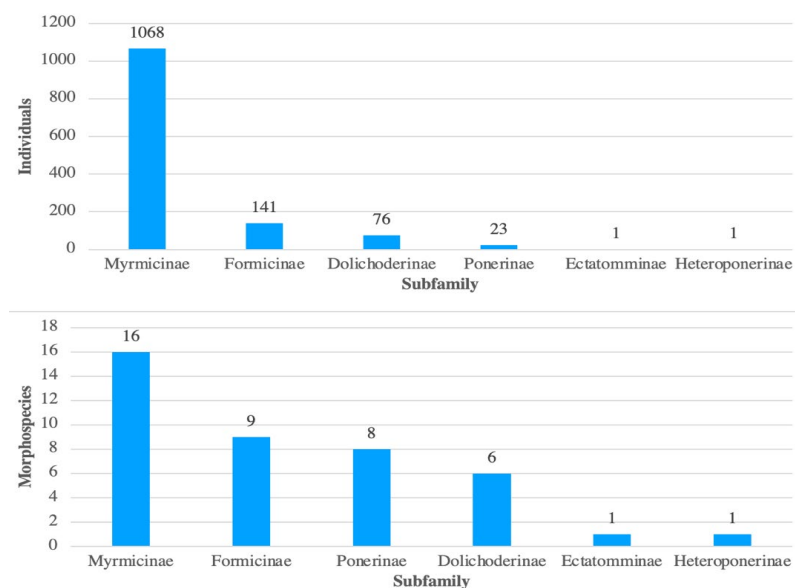


Figure 3. Bar chart of ants (Formicidae) abundance by subfamilies found in bromeliads from the canopy of cloud forest in the Andean Chocó bioregion (Above). Bar chart of ants (Formicidae) richness by subfamilies found in bromeliads from the canopy of cloud forest in the Andean Chocó bioregion (Below).



Figure 4. Collage showing some of the incredible diversity of Formicidae found in bromeliads from the canopy of cloud forest in the Andean Chocó bioregion.

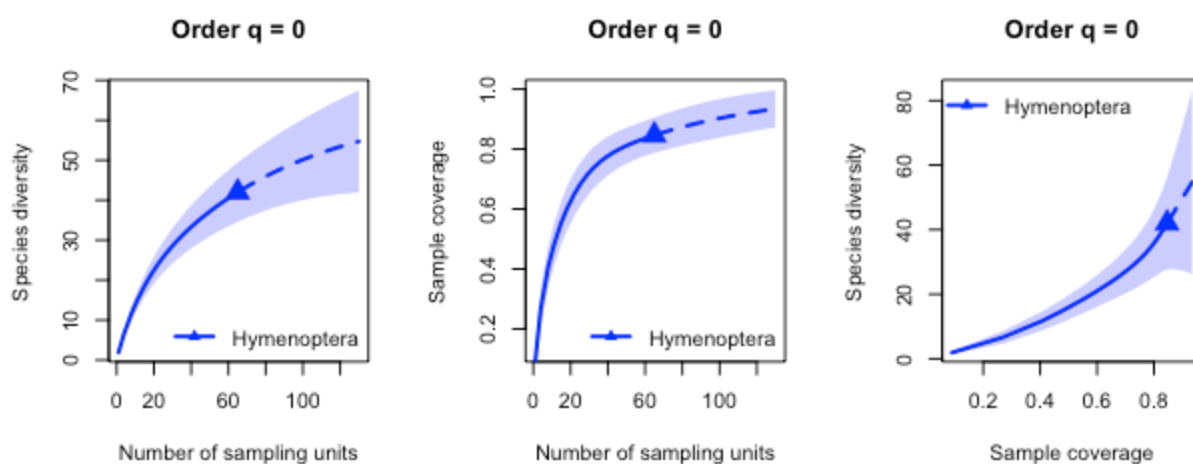


Figure 5. Interpolation and extrapolation for species diversity. (a) Sample-size-based and (c) coverage-based rarefaction (solid line segment) and extrapolation (dotted line segments) sampling curves for species richness ($q = 0$) with 95% confidence intervals for the canopy ant data. The solid dot represents the reference samples. (b) Sample completeness curves linking curves in (a) and (c). Sample-size-based (a) plots the diversity estimates with respect to sample size and Coverage-based (c) plots the diversity estimates with respect to sample coverage. statistically $2.2e-16$ (<0.05) (See Table. 9).

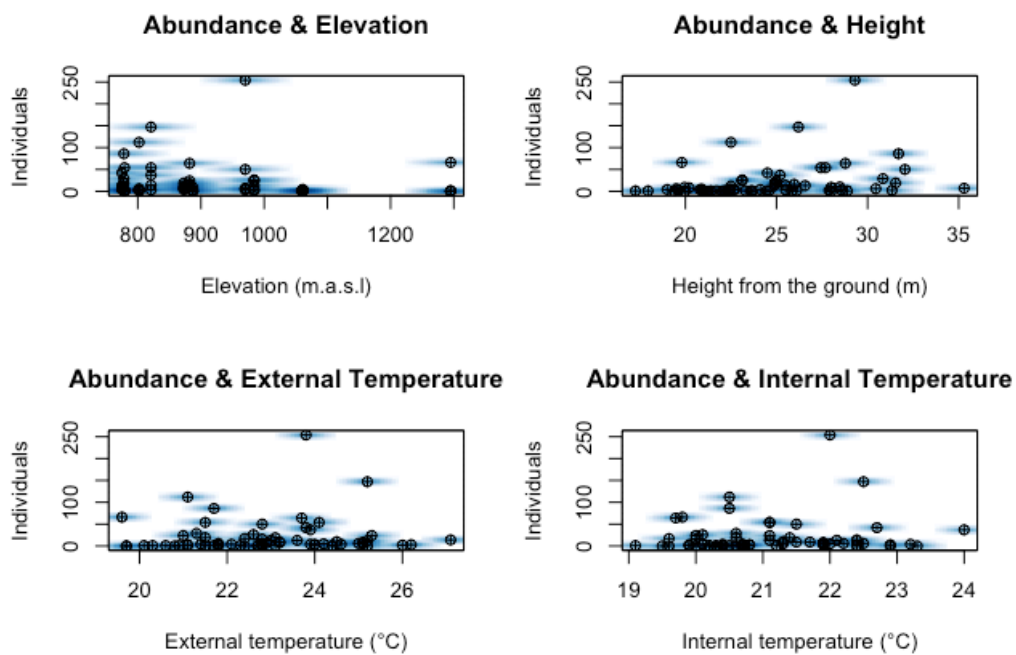


Figure 6. Formicidae abundance inside each bromeliad ($n = 65$) against the four analyzed variables. Height from the ground (Hei); Elevation (Elev); Internal temperature (TI); and External temperature (TE). All graphs by themselves have non-statistically significant coefficients of correlation.