



## Mapping the Interactions Between Hummingbirds and Plants in a Region of the Colombian Andes

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### Highlights

- This study provides a detailed characterization of a plant–hummingbird interaction network in a high-Andean forest of southwestern Colombia, a region with limited empirical information on pollination networks.
- The research integrates long-term field observations with bipartite network analysis to examine the structure and organization of hummingbird–plant interactions in a natural montane ecosystem.
- The study combines ecological network theory with applied conservation perspectives, explicitly linking interaction networks to national pollinator conservation frameworks.
- The approach emphasizes the importance of considering species interactions, rather than species richness alone, when assessing ecosystem integrity and restoration priorities.
- The work contributes baseline information for future monitoring, conservation planning, and restoration strategies in high-mountain ecosystems of the tropical Andes.

## EARLY VIEW

### Mapping The Interactions Between Hummingbirds And Plants in A Region of The Colombian Andes

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Running head: Hummingbird–Plant Interactions in The Colombian Andes

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**Abstract:** Pollination is a key ecological process that ensures plant reproduction and supports the stability and biodiversity of natural ecosystems. In high Andean environments, hummingbirds act as essential pollinators due to their physiological adaptations that allow them to forage in extreme climatic conditions and at high elevations. However, the ongoing transformation of these ecosystems driven by deforestation, land-use change, and climate variability highlights the urgent need to understand the structure and resilience of pollination networks. In this study, we analyzed the interaction network between hummingbirds and ornithophilous plants in a remnant of Andean forest in southwestern Colombia. Interactions were documented through trail surveys, focal observations, and mist-netting over a three-year sampling period. We recorded 269 interactions between 10 hummingbird species and 28 plant species, achieving 95% sampling completeness. Network analysis revealed low specialization, intermediate modularity, and a predominance of generalist species, suggesting a relatively cohesive but potentially vulnerable system. These findings contribute

valuable empirical evidence on how mutualistic interactions are structured in tropical montane forests and highlight the importance of preserving not only species richness but also the ecological interactions that sustain ecosystem function. This knowledge is essential for designing conservation and restoration strategies that enhance the resilience of high mountain ecosystems in the face of current and emerging threats.

**Keywords:** Pollination networks, Hummingbird-plant interactions, Andean forest ecosystems, Ecological resilience, Conservation strategies.

## INTRODUCTION

Plant–hummingbird interaction networks in the Andean forests of Colombia play a pivotal role in pollination, a fundamental ecological process that sustains biodiversity and ecosystem stability (Bascompte & Jordano, 2007). These mutualistic relationships, particularly between nectarivorous birds like hummingbirds and flowering plants, ensure the continuity of reproductive cycles and maintain ecological functionality (Fenster *et al.* 2004; Jordano *et al.* 2007). Hummingbirds are particularly relevant in high Andean ecosystems due to their exceptional physiological adaptations that allow them to forage under extreme climatic conditions, making them key pollinators in these environments (Sonne *et al.* 2020; Leimberger *et al.* 2022).

Pollination networks are increasingly affected by anthropogenic pressures, including habitat fragmentation, land-use change, deforestation, and climate change—recognized as major drivers of biodiversity loss in tropical montane forests (Carranza-Quiceno *et al.* 2024; Sánchez *et al.* 2024). Although the use of artificial feeders has been noted to alter interaction patterns in urban or semi-urban environments (Echeverry-Galvis *et al.* 2024), in natural landscapes, the main threats stem from broader environmental transformations. These factors can compromise both the frequency and the specificity of interactions, potentially leading to the disruption of key ecological processes.

Theoretical advances in mutualistic network ecology have revealed complex patterns such as nestedness, modularity, asymmetry, and resilience to perturbations (Bascompte & Jordano, 2007; Olesen & Jordano, 2002). Studies on plant–hummingbird networks in the Neotropics have examined the influence of species richness, phenology, morphological matching, and environmental gradients on network structure (Dalsgaard *et al.* 2009; Lara *et al.* 2012; Maruyama *et al.* 2018; Sonne *et al.* 2020). However, empirical data from high

Andean forests of Colombia remain limited (Ramírez *et al.* 2017; 2022), and most existing research has focused on other latitudinal or altitudinal ranges (González & Loiselle, 2016). Understanding the structure and functioning of pollination networks in these ecosystems is also relevant from an applied perspective. Hummingbirds are pollinators for many wild and cultivated plant species, contributing to food security and ecosystem service provision (Sekercioglu, 2006; De Groot *et al.* 2002). Nevertheless, recent research has shown that agroecosystems such as shaded coffee plantations may reduce the specialization and robustness of hummingbird-plant interactions, potentially threatening their long-term resilience (López-Flores *et al.* 2024). Such findings underline the need to analyze these networks in natural settings, where conservation and restoration priorities can be more effectively informed.

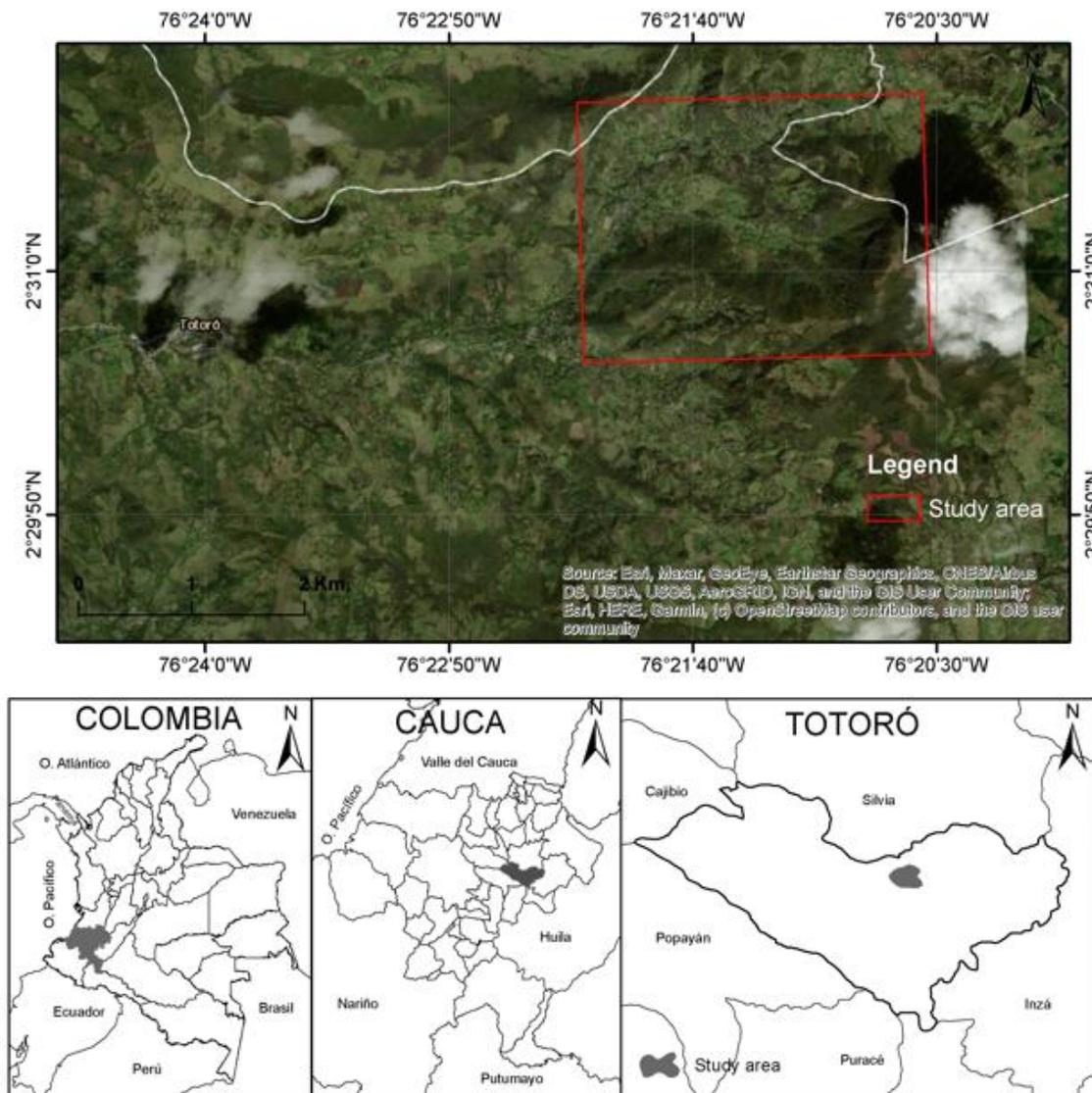
In this study, we examine the hummingbird–plant interaction network in a remnant of high Andean forest in southwestern Colombia, within the Guanacas–Puracé–Coconucos páramo complex. Our objective is to characterize the structure and key properties of this mutualistic network, including its richness, specialization, modularity, robustness, and species roles, and to link our findings explicitly with national conservation frameworks, especially the ICP 2018, the “Colombian Pollinators Initiative”, which establishes strategic actions for the conservation and sustainable management of pollinators and pollination services in Colombia (ICP 2018). This research contributes to filling regional knowledge gaps and aligns with national conservation efforts, including the Colombian Pollinators Initiative (ICP, 2018), by highlighting the ecological and conservation relevance of mutualistic interactions in tropical montane ecosystems.

## **MATERIALS AND METHODS**

### **Study Area**

The study was conducted at the Potrero del Río farm, located in El Cofre village, Totoró municipality, Cauca department, southwestern Colombia (2°23'10.4"N, -76°24'36.8"W; Fig. 1). The area lies on the western flank of the Central Andes, within the upper Cauca River basin. It includes bioclimatic zones ranging from sub-Andean forest to páramo and forms part of the Guanacas–Puracé–Coconucos páramo complex (IAvH, 2012). The elevation ranges from 2750 to over 3000 m a.s.l., with an average annual rainfall of 2000 mm and a mean temperature of 10.3 °C (IDEAM, 2023). According to Holdridge’s life zone

classification, the study area corresponds to a montane very humid forest (Bmh-MB/T) (Holdridge, 1974).



**Figure 1:** Location of the study area in Totoró, Cauca, Colombia.

### **Documentation of Hummingbird–Plant Interactions**

Interactions were recorded along a single 1 km trail encompassing both forest interior and edges, targeting ornithophilous plants in bloom (Rocca & Sazima, 2010). This was the only trail used for data collection, and all sampling took place within the same study area. Each

focal plant was observed for 30 minutes, following standardized protocols (González, 2011). In addition to trail walks, five fixed observation points were established in flower-rich areas to ensure repeated sampling throughout the study

Bird identification relied on Bushnell 10×50 binoculars and the field guides by Ayerbe (2018a, 2018b). Plant identification was based on Arcos (2009), complemented by comparisons with herbarium specimens from the Universidad del Cauca. Sampling was carried out between February 2018 and April 2021, covering all months of the year. A total of 17 field trips and 40 effective sampling days yielded 202 hours of observation and 248 hours of mist netting. Nets were placed near flowering plants, following Rodríguez & Stiles (2005) and Ramírez (2013).

### **Structure of the Interaction Network**

A plant-centered interaction matrix was constructed, where rows represented plant species and columns represented hummingbird species. Cell values indicated the number of observed visits by hummingbirds to flowers. Interactions not recorded were marked as zero (Medel *et al.* 2009).

The bipartite network was visualized and analyzed using the bipartite package in R version 4.4.1 (R Core Team, 2024), following Dormann *et al.* (2009, 2022). The analysis was structured according to Becoche (2023), including metrics such as connectance, nestedness, interaction asymmetry, and robustness.

### **Identification of Key Species**

Key species were identified using three centrality metrics: degree, closeness centrality, and betweenness centrality (Bascompte & Jordano, 2007; Medel *et al.* 2009). Species with the highest degree values were considered more generalist, while high closeness centrality indicated greater influence within the network structure. Betweenness centrality identified species acting as critical connectors, facilitating interactions across otherwise disconnected modules (Ramírez *et al.* 2017).

This approach aligns with recent findings emphasizing the role of key mutualistic species in maintaining the structural and functional integrity of ecological networks (Vitali *et al.* 2021). In restoration contexts, identifying core plant species is critical to re-establish

plant–pollinator communities, as demonstrated in Andean hummingbird networks (Crespo *et al.* 2021).

### **Network Metrics and Null Models**

The estimated interaction richness was calculated using rarefaction and extrapolation via the iNEXT online tool, incorporating Hill numbers (Chao & Jost, 2015; Chao *et al.* 2015). This method also considered forbidden links ecologically implausible interactions due to morphological or phenological mismatches (Chacoff *et al.* 2012).

To assess network structure, we calculated connectance (C), nestedness (NODF), interaction asymmetry, interaction strength, extinction slope, and robustness (Medel *et al.* 2009; Ramírez *et al.* 2007; Becoche, 2023). Robustness was defined as the area under the secondary extinction curve.

To determine whether the observed structure deviated from random expectations, we generated 1000 random matrices using the Patefield algorithm (Patefield, 1981) in bipartite, following García (2013). Z-scores were calculated to compare observed metrics with null distributions (Blüthgen *et al.* 2008; CaraDonna *et al.* 2017).

## **RESULTS**

### **Community of Plants Visited by Hummingbirds**

The plant community visited by hummingbirds in the Andean forest comprised 28 species, distributed across 18 families and 23 genera (Table 1). The families with the highest number of species were Bromeliaceae (5 species), Ericaceae, Melastomataceae, and Rubiaceae (3 species each), while the remaining families were represented by a single species (Supplementary file 1).

The plants exhibited a variety of growth forms. Shrubs, particularly those from the genera *Tibouchina* and *Palicourea*, predominated (50%), followed by epiphytes such as *Tillandsia* (17.8%), trees from the genera *Gaiadendrum* and *Bejaria* (14.2%), and large lianas like *Psammisia* and *Passiflora* (14.2%), which were observed climbing on tree trunks. Herbaceous species were represented solely by the genus *Rubus* (3.5%).

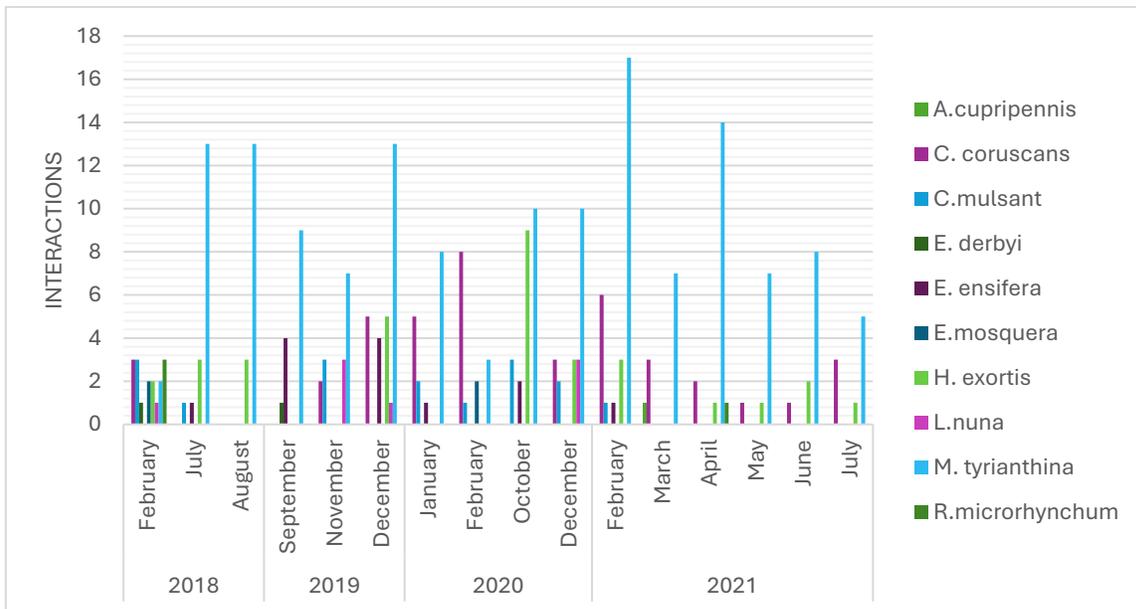
**Table 1:** Plant species visited by hummingbirds in the Andean forest of Totoró and the sampling methods used for their registration.

<b>Family</b>	<b>Specie</b>	<b>Flower Color</b>
<b>ACANTHACEAE</b>	<i>Aphelandra acanthus</i>	Yellow
<b>ALSTROEMERIACEAE</b>	<i>Bomarea multiflora</i>	Orange
<b>ASTERACEAE</b>	<i>Gynoxys columbiana</i>	Yellow
<b>ASTERACEAE</b>	<i>Bernadesia spinosa</i>	Pink
<b>BERBERIDACEAE</b>	<i>Beberis grandiflora</i>	Orange
<b>BROMELIACEAE</b>	<i>Tillandsia sp.</i>	White
	<i>Tillandsia compacta</i>	Purple
	<i>Tillandsia complanata</i>	Purple-red
	<i>Racinea tetrantha</i>	Yellow
	<i>Tillandsia fendleri</i>	Purple
<b>CAMPANULACEAE</b>	<i>Siphocampylus giganteus</i>	Yellow
<b>ELAEOCARPACEAE</b>	<i>Vallea stipularis</i>	Pink
<b>ERICACEAE</b>	<i>Bejaria mathewsii</i>	Fuchsia
	<i>Psammisia graebneriana</i>	Red
	<i>Thibaudia floribunda</i>	Red
<b>LORANTHACEAE</b>	<i>Gaiadendron punctatum</i>	Yellow
<b>MELASTOMATACEAE</b>	<i>Tibouchina grossa</i>	Red
	<i>Tibouchina mollis</i>	Purple
	<i>Miconia orcheotoma</i>	White
<b>ONAGRACEAE</b>	<i>Fuchsia caucana</i>	Red
<b>PASSIFLORACEAE</b>	<i>Passiflora mixta</i>	Orange
<b>PENTAPHYLACACEAE</b>	<i>Freziera canescens</i>	White
<b>ROSACEAE</b>	<i>Rubus robustus</i>	White
<b>RUBIACEAE</b>	<i>Palicourea amethystina</i>	Blue
	<i>Palicourea garciae</i>	White
	<i>Palicourea heterochroma</i>	Yellow
<b>SOLANACEAE</b>	<i>Brugmansia sanguinea</i>	Red
<b>VERBENACEAE</b>	<i>Duranta obtusifolia</i>	Blue

## Hummingbird Community Visiting the Plants

The hummingbird community recorded in the study area included 10 species (Table 2). *Metallura tyrianthina* registered the highest number of visits (146), followed by *Colibri coruscans* (42), totaling 269 interactions. In contrast, species such as *Aglaeactis cupripennis* (1) and *Eriocnemis derbyi* (2) showed minimal interaction frequencies.

Seasonal patterns revealed that *M. tyrianthina* was recorded in all sampled months, suggesting year-round activity. Conversely, *E. derbyi* and *E. mosquera* were occasional visitors, indicating potential altitudinal or phenological restrictions (Fig. 2).



**Figure 2:** Temporal variation in hummingbird visits to plants in the Andean forest of Totoró, Cauca.

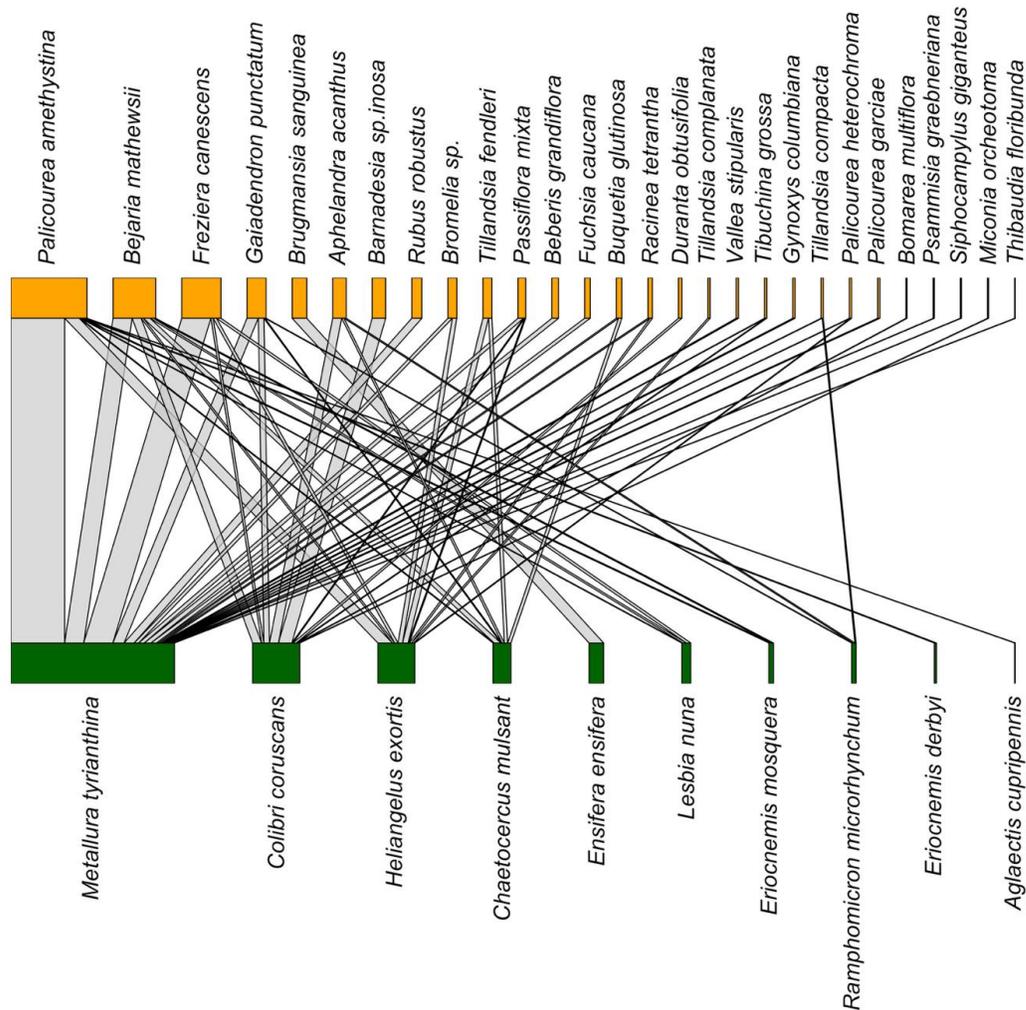
**Table 2:** Hummingbird species visiting ornithophilous plants in the study area.

Family	Specie	Common name
TROCHILIDAE	<i>Aglaeactis cupripennis</i>	Buff-winged Starfrontlet
	<i>Chaetocercus mulsant</i>	White-booted Racket-tail
	<i>Colibrí coruscans</i>	Sparkling Violetear
	<i>Ensifera ensifera</i>	Sword-billed Hummingbird
	<i>Eriocnemis derbyi</i>	Black-thighed Puffleg
	<i>Eriocnemis mosquera</i>	Mosquera Puffleg
	<i>Heliangelus exortis</i>	Tourmaline Sunangel
	<i>Lesbia nuna</i>	Black-tailed Trainbearer
	<i>Metallura tyrianthina</i>	Tyrian Metaltail
	<i>Ramphomicron microrhynchum</i>	Short-billed Starfrontlet

### Network Topology

The resulting interaction network consisted of 10 hummingbird species and 28 plant species, yielding a bipartite matrix of 38 nodes. From the 280 possible pairwise interactions, 269 were recorded in the field, achieving a high sampling coverage of 95%.

Species with few connections, such as *E. mosquera* and *Tibouchina grossa*, coexisted with highly connected species like *M. tyrianthina* and *Palicourea amethystina* (Fig. 3). Visit intensity varied across species pairs, with *M. tyrianthina* and *P. amethystina* showing a particularly strong interaction.



**Figure 3.** Bipartite graph of hummingbird (green) and plant (yellow) interactions. Top: 28 plant species; Bottom: 10 hummingbird species.

From the plant perspective, the families with the highest number of interactions were Rubiaceae (72), Ericaceae (40), Pentaphylacaceae (35), Bromeliaceae (24), Loranthaceae (17), Asteraceae (14), and Solanaceae (13). Dominant genera included *Palicourea* (68), *Bejaria* (38), *Freziera* (35), *Tillandsia* (20), *Gaiadendrum* (17), and *Brugmansia* (13).

The hummingbirds with the most interactions were *M. tyrianthina* (146 interactions, 54.2%), followed by *C. coruscans* (42) and *Heliangelus exortis* (33). Not all hummingbirds visited the same set of floral resources, highlighting heterogeneity in foraging preferences and floral specialization.

## Network Structure and Metrics

At the network level, connectance was calculated at 0.20, indicating a relatively low proportion of realized interactions compared to the total possible. This value was significantly lower than expected under the null model ( $z = -9.09$ ,  $p < 0.05$ ). The specialization index ( $H2 = 0.20355$ ) suggests a predominance of generalist behavior, with both hummingbirds and plants engaging in multiple interactions. Specialization also differed significantly from null expectations ( $z = 17.49$ ,  $p < 0.05$ ). Key generalist species included *M. tyrianthina*, *C. coruscans*, *P. amethystina*, and *B. mathewsii*. Nestedness, measured by the NODF index (458.89), was considered low because the observed value was significantly lower than expected under the randomized null model ( $z = -4.59$ ,  $p < 0.05$ ), indicating a reduced pattern of specialist–generalist subsets. In this context, “low nestedness” reflects fewer redundant interactions compared to a random network of similar size. This implies limited redundancy in the network structure, potentially reducing resilience.

According to extinction slope and robustness metrics (Table 3), hummingbirds were more sensitive to the loss of key plant species (robustness = 0.6105), whereas plants were more robust (0.7319), suggesting an asymmetry in network stability. Interaction strength asymmetry (ISA =  $-0.4736$ ) also showed a significant deviation from the null expectation ( $z = -6.07$ ,  $p < 0.05$ )

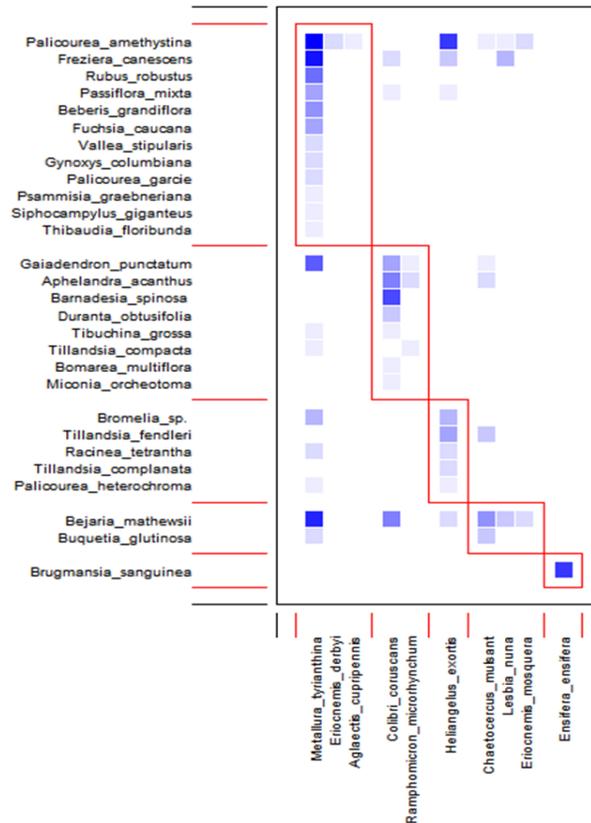
**Table 3:** Metrics at the plant-hummingbird network level in the Andean forest of Totoró.

Network Metrics	Value
Number of hummingbird species	10
Number of plant species	28
Interactions per species	14.736
Connectance	0.20
Nestedness (NODF)	458.891
H2	0.20355
Modularity	5
ISA	-0.4736
Hummingbird robustness	0.6105
Plant robustness	0.7319
Hummingbird extinction slope	16.057
Plant extinction slope	29.397

## Modular Structure of the Network

The network displayed a modular structure with five distinct modules (Fig. 4). Modules were not assigned subjectively; instead, they were calculated using an algorithmic community-detection approach based on weighted modularity optimization. Specifically, modules were identified with the DIRTLPA+ algorithm implemented in the *bipartite* package, which detects subgroups of species that interact more frequently with each other than with species in other parts of the network. These modules reveal functional subgroups of species within the community:

- Module 1: *P. amethystina*, *F. canescens*, *P. mixta* (plants); *M. tyrianthina*, *E. derbyi*, *A. cupripennis* (hummingbirds).
- Module 2: *A. acanthus*, *G. punctatum*, *B. spinosa*; *C. coruscans*, *R. microrhynchus*.
- Module 3: *R. tetrantha*, *T. complanata*; *H. exortis*.
- Module 4: *B. mathewsii*, *B. glutinosa*; *C. mulsant*, *L. nuna*, *E. mosquera*.
- Module 5 (isolated): *B. sanguinea* and *E. ensifera*.



**Figure 4:** Interaction matrix showing modular structure of the plant-hummingbird network. Dark squares represent strong interactions; red squares denote module boundaries.

### Key Species in the Network

Based on degree, centrality, and betweenness centrality metrics, four key plant species were identified: *Palicourea amethystina*, *Bejaria mathewsii*, *Freziera canescens*, and *Gaiadendron punctatum*. These species exhibited the highest values across the three metrics and served as primary floral resources in the network.

Similarly, four key hummingbird species were distinguished: *Metallura tyrianthina*, *Colibri coruscans*, *Heliangelus exortis*, and *Chaetocercus mulsant*, due to their high centrality and strong connector roles (Table 4). These species contribute significantly to the structural cohesion and potential resilience of the pollination network.

**Table 4:** Centrality metrics for key plant and hummingbird species in the Andean forest of Totoró.

	Species	Degree	Centrality	Betweenness centrality
Plants	<i>Palicourea amethystina</i>	7	1.136364	0.0478972
	<i>Bejaria mathewsii</i>	6	1	0.05140187
	<i>Freziera canescens</i>	4	1	0.05140187
	<i>Gaiadendron punctatum</i>	4	1.045455	0.05023364
	hummingbirds	<i>Metallura tyrianthina</i>	17	0.42142857
	<i>Colibri coruscans</i>	8	0.07142857	0.09868421
	<i>Heliangelus exortis</i>	7	0.02857143	0.10526316
	<i>Chaetocercus mulsant</i>	6	0.42142857	0.11842105

### Null Model Evaluation

Finally, the evaluation of metrics using null models (Table 5) indicated that the structure of the plant-hummingbird network was significantly different from a randomly assembled one ( $p < 0.05$ ). Specifically, connectance ( $z = -9.09$ ,  $p < 0.05$ ), specialization  $H2'$  ( $z = 17.49$ ,  $p < 0.05$ ), nestedness ( $z = -4.59$ ,  $p < 0.05$ ), and interaction strength asymmetry ( $z = -6.07$ ,  $p < 0.05$ ) all showed significant departures from null expectations. This suggests that ecological or evolutionary constraints shape the observed patterns of interaction.

**Table 5:** Null model comparison for connectance, specialization ( $H2'$ ), nestedness (NODF), and interaction strength asymmetry (ISA), including standard deviations, Fisher statistics, and p-values.

Evaluated Metrics	Observed	Null Model	ds	Z	p
Connectance	0,2	0,3036357	0,01139608	-9.093979	<0,05
H2	0.4405814	0.1212526	0.01825696	17.4908	<0,05
NODF	45.88915	67.07121	4.611532	-4.593281	<0,05
ISA	-0.225807	-0.1127609	0.01861641	-6.072428	<0,05

## Discussion

High-altitude pollination networks in Colombia are commonly dominated by plant families such as Ericaceae, Melastomataceae, Rubiaceae, and Bromeliaceae (García & Van der Hammen, 2007), a pattern that was also observed in this study. Nonetheless, the total richness of species, genera, and families recorded here was lower than in other Andean forests of the Central Cordillera (Rangel, 2015). This reduction can be attributed to several factors, including the higher elevation of the study site where species richness tends to decrease with altitude (Rangel, 2015) the prevalence of endemic taxa (Madriñán *et al.* 2013), and human disturbance such as the extraction of native species for firewood and fencing.

This reduced diversity of ornithophilous plants may also be reflected in the hummingbird community structure. Ramírez *et al.* (2017) documented a decrease in hummingbird species from 26 between 1500–2000 masl in Munchique National Park to 16 between 2700–3550 masl in Ranchería Park, Boyacá (Tolosa-Moreno *et al.* 2014), a trend corroborated by findings in the Galeras Volcano (Burbano, 2013) and elsewhere in Cauca (Ayerbe *et al.* 2008). These patterns may result not only from environmental filters such as elevation, but also from sampling constraints, since broader sampling efforts and the integration of complementary tools (e.g., video recording) have been shown to improve detection of rare interactions (Bugoni *et al.* 2016).

Understanding hummingbird natural history and foraging behavior is essential to elucidate the mechanisms shaping these networks (McGuire *et al.* 2009). The high interaction frequency of *M. tyrianthina* observed here is consistent with findings in Galeras, Nariño (Gutiérrez & Rojas, 2001), and likely reflects its territoriality and generalist diet. Conversely, subordinate or less abundant species such as *A. cupripennis* and *E. derbyi* may be limited by dominant individuals like *C. coruscans* (Vizentin *et al.* 2014), while the infrequent records of *Eriocnemis* might be linked to seasonal altitudinal migrations triggered by flowering peaks in páramo ecosystems (Moreno *et al.* 2014; Sentíes-Aguilar *et al.* 2024). From a structural perspective, the network exhibited a heterogeneous connectivity matrix dominated by generalist species, a configuration that supports network stability (Ramírez *et al.* 2022; Dunne *et al.* 2002). However, the low connectance observed may reflect either high biodiversity as common in tropical mutualisms (Dattilo & Rico-Gray, 2018) or anthropogenic disturbance such as deforestation, which can fragment habitats and disrupt interactions (Lara *et al.* 2012). Such disruptions can lead to the erosion of functional diversity

and the weakening of specialized interactions, particularly in the tropical Andes (Carranza-Quiceno *et al.* 2024).

The predominance of generalist species in this network also suggests an adaptive strategy to cope with fluctuations in floral resource availability (Maruyama *et al.* 2018; Sonne *et al.* 2020). Nonetheless, the case of *E. ensifera*, interacting exclusively with *B. sanguinea*, illustrates how morphological constraints such as bill curvature and flower depth drive specialization (Tinoco *et al.* 2017). Locally abundant species also tend to play generalist roles (Ramírez *et al.* 2022), although these do not necessarily translate into resilience. Vitali *et al.* (2021) demonstrated that even in the presence of keystone generalists, networks may be highly vulnerable to species loss, especially if mutualistic links are asymmetrically distributed.

The low nestedness value recorded could also reflect a limited number of species and the altered conservation status of the habitat (Bascompte & Jordano, 2007), making the network more sensitive to environmental perturbations (Lara *et al.* 2012). Modularity analysis revealed five distinct compartments, likely shaped by hummingbird morphology and floral resource specialization (Camargo & Rangel, 2015). For instance, *H. exortis* mostly visited bromeliads, while *E. ensifera* showed high fidelity to tubular flowers such as *B. sanguinea* (Luna *et al.* 2018; Olesen *et al.* 2007), reinforcing the idea that modularity contributes to ecosystem stability.

Extinction slope analyses confirmed that specialists are more vulnerable, particularly when associated plant species are lost (McGuire *et al.* 2012). CaraDonna *et al.* (2017) warned that removing highly connected or specialized taxa can trigger cascading effects that compromise the structure and function of the entire network. Thus, conservation efforts should prioritize key mutualists both pollinators and plants to maintain long-term ecosystem resilience. For instance, protecting generalists like *M. tyrianthina* and *C. coruscans*, as well as critical floral resources such as *P. amethystina*, is essential. Furthermore, restoration planning should consider the role of specific plant species in reassembling mutualistic networks, as demonstrated by Crespo *et al.* (2021) in the southern Andes of Ecuador.

Finally, it is important to acknowledge that the outcomes of this study are influenced by climatic variability and the flowering phenology of plant species during the sampling period. Although traditional methods provided robust data, the integration of emerging technologies such as automated sensors and longer sampling durations could help detect rare or seasonal interactions and further enrich our understanding of these networks.

## **CONCLUSIONS**

This study characterized a mutualistic plant-hummingbird network in a high-Andean forest of Totoró, documenting 269 interactions among 10 hummingbird species and 28 plant species. The predominance of generalist species highlights their functional importance in maintaining ecological cohesion and resilience at high altitudes. Plant families such as Bromeliaceae, Ericaceae, and Rubiaceae, as well as the dominance of shrubs and epiphytes, reflect floral adaptations to cold and humid conditions typical of the Central Andes.

The structure of the network characterized by low connectance and nestedness, and moderate modularity and specialization suggests limited robustness and potential vulnerability to environmental disturbances. Nonetheless, the presence of both generalist and specialist species indicates critical ecological roles, showing the need to protect mutualisms that ensure functional continuity. Hummingbirds such as *Metallura tyrianthina* and *Colibri coruscans*, along with plant species like *Palicourea amethystina*, emerged as structural pillars of the network. In view of the national policy context, these key species should be prioritized within the ICP 2018 framework for pollinator conservation and restoration actions, directing restoration efforts toward functional network reassembly, habitat connectivity and species-interaction integrity. Beyond its local focus, this research contributes to the broader understanding of plant-pollinator systems in montane tropical ecosystems and provides a baseline for future ecological monitoring. The integration of functional and structural aspects of mutualistic networks can guide conservation strategies in the Andes, especially in the face of climate change and land-use transformation. Future research and management actions should therefore consider explicit linkages between species-level interactions and national restoration priorities, aligning with the ICP 2018 targets of habitat restoration, pollinator service safeguarding and participatory community-based management. Protecting key species, restoring mutualistic interactions, and strengthening community participation are essential steps to maintain the integrity and ecological functionality of high-Andean ecosystems for future generations.

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## **AUTHOR CONTRIBUTIONS**

J.K.A.O. and J.M.B.M. conceived and designed the study. J.K.A.O. conducted fieldwork, collected data, and performed species identification. J.M.B.M. developed the methodological framework, performed network and statistical analyses, and led data interpretation. L.G.G.B. contributed to field supervision, taxonomic validation, and ecological interpretation. J.K.A.O. drafted the manuscript, and J.M.B.M. and L.G.G.B. critically revised it for intellectual content. All authors approved the final version of the manuscript.

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**SUPPLEMENTARY FILE 1**

	<i>Palicourea amethystina</i>	<i>Gaiadendron punctatum</i>	<i>Aphelandra acanthus</i>	<i>Racinea tetrantha</i>	<i>Bejaria mathewsii</i>	<i>Fuchsia caucana</i>	<i>Brugmansia sanguinea</i>	<i>Rubus robustus</i>	<i>Bromelia sp.</i>	<i>Tillandsia complanata</i>	<i>Vallea stipularis</i>	<i>Barnadesia spinosa</i>	<i>Passiflora mixta</i>
<i>Colibri coruscans</i>	0	5	8	0	8	0	0	0	0	0	0	12	1
<i>Eriocnemis derbyi</i>	2	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heliangelus exortis</i>	13	0	0	2	2	0	0	0	4	2	0	0	1
<i>Metallura tyrianthina</i>	48	10	0	2	17	5	0	9	4	0	2	0	5
<i>Ensifera ensifera</i>	0	0	0	0	0	0	13	0	0	0	0	0	0
<i>Chaetocercus mulsant</i>	1	1	2	0	6	0	0	0	0	0	0	0	0
<i>Lesbia nuna</i>	1	0	0	0	3	0	0	0	0	0	0	0	0
<i>Eriocnemis mosquera</i>	2	0	0	0	2	0	0	0	0	0	0	0	0
<i>Aglaectis cupripennis</i>	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Ramphomicron microhynchum</i>	0	1	2	0	0	0	0	0	0	0	0	0	0

(Continued)

	<i>Freziera canescens</i>	<i>Bomarea multiflora</i>	<i>Tibuchina grossa</i>	<i>Buquetia glutinosa</i>	<i>Duranta obtusifolia</i>	<i>Tillandsia fendleri</i>	<i>Beberis grandiflora</i>	<i>Gynoxys columbiana</i>	<i>Psammisia graebneriana</i>	<i>Tillandsia compacta</i>	<i>Siphocampylus giganteus</i>	<i>Palicourea heterochroma</i>	<i>Miconia orchetoma</i>	<i>Palicourea garciae</i>	<i>Thibaudia floribunda</i>
<i>Colibri coruscans</i>	2	1	1	0	3	0	0	0	0	0	0	0	1	0	0
<i>Eriocnemis derbyi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heliangelus exortis</i>	3	0	0	0	0	5	0	0	0	0	0	1	0	0	0
<i>Metallura tyrianthina</i>	26	0	1	2	0	0	6	2	1	1	1	1	0	2	1
<i>Ensifera ensifera</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Chaetocercus mulsant</i>	0	0	0	3	0	3	0	0	0	0	0	0	0	0	0
<i>Lesbia nuna</i>	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Colibri coruscans</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Eriocnemis derbyi</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Heliangelus exortis</i>	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0

