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FINDING THE MISSING LINKS: KNOWLEDGE SHORTFALLS IN PLANT–HUMMINGBIRD INTERACTION NETWORKS ACROSS THE AMERICAS

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Abstract: Interactions between plants and hummingbirds form a key mutualistic pollination system crucial for the functioning of Neotropical ecosystems, and understanding their structure and variability is essential for predicting ecosystem responses to climate change and habitat loss. However, most evidence comes from local interaction networks with limited geographic and temporal sampling, generating major knowledge gaps in the documented biotic interactions (Eltonian shortfall). In this study, we conducted a continental-scale synthesis of published plant–hummingbird interaction networks across the Americas to evaluate how well current data represent geographic, environmental, taxonomic, and trait dimensions of the Trochilidae and their plant partners. The compiled dataset includes 12,658 recorded interactions involving 214 hummingbird species (~60% of the family) and 1,757 plant species. Network records are strongly concentrated in a few countries and predominantly in warm, humid, tree-covered environments, leaving large geographic regions and seasonal climates underrepresented. Taxonomic coverage is uneven, with Emerald and Hermit clades relatively well represented in published networks, while approximately 40% of all hummingbird species remain entirely unrecorded. Representation of threatened species is particularly limited, with very few Endangered or Critically Endangered species recorded. Cross-network centrality analyses show that a small subset of hummingbird and plant species repeatedly occupy central interactive roles, but these patterns are closely aligned with sampling intensity rather than geographic range size, indicating potential bias in inferred functional importance. By integrating network structure, species traits, and environmental characterization, this study provides a macroecological assessment of current knowledge on plant–hummingbird interactions. Our results identify priority gaps in species and regional coverage and highlight the need for targeted sampling to improve ecological inference and conservation planning for hummingbird pollination systems across the Americas.

Key words: ecological networks, Eltonian shortfall, flower visitor networks, Trochilidae.

Introduction

Mutualistic interactions are fundamental to ecosystem functioning, biodiversity maintenance and shape the ecological dynamics of communities and the evolution of species (Andersen et al. 2018; Bascompte, 2019). Among these interactions, plant-pollinator relationships play a key ecological role in the communities, as nearly 300,000 species of plants rely on animal pollinators for successful reproduction (Ollerton et al. 2011). In the Americas, hummingbirds (Trochilidae) represent one of the most diverse, ecologically dominant, and specialized groups of pollinators, forming a classic model of plant–pollinator coevolution. Through long-term reciprocal selection, plants and hummingbirds have evolved tightly matched morphological traits (e.g., floral tube shape and bill length) that enhance foraging efficiency for birds and reproductive success for plants (Barreto et al. 2024). As a result, more than 4,000 plant species interact with hummingbirds, many of which rely almost exclusively on them for pollination (Rodríguez-Flores et al. 2019).

Given their ecological relevance, understanding the structure and variability of plant–hummingbird interactions is essential for predicting ecosystem responses to anthropogenic pressures such as climate change, habitat

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loss, and land-use change (Tylianakis et al. 2007). In the last decades, ecological interaction networks have become one of the most widely used frameworks to characterize community structure and species roles, allowing researchers to quantify patterns such as specialization, redundancy, and species importance across scales (Martín-González et al. 2015; Rico-Guevara et al. 2021). In fact, network approaches have been applied to systems ranging from local assemblages to broad macroecological analyses, revealing geographic variation in network structure and testing large-scale ecological hypotheses (Andresen et al. 2018). As a result, interaction networks are now central tools for linking local ecological processes with large-scale biodiversity patterns, making their coverage, representativeness, and potential biases critically important for ecological inference.

Despite the rapid growth of studies on plant–hummingbird interaction networks, the accumulated knowledge generated by using these network approaches is potentially affected by strong and largely unquantified biases (de Aguiar et al. 2019). Most interaction networks are built from local studies conducted at limited spatial extents, often concentrated in a few regions, habitats, or climatic conditions (Poisot et al. 2020). Consequently, it remains unclear to what extent current plant–hummingbird network research's systematic sampling biases limit our understanding of the geographic, environmental, and taxonomic diversity of this interaction across the Americas. These sampling and representation biases in network studies generate and reinforce greater gaps that many studies have addressed as the biodiversity shortfalls. These shortfalls are persistent knowledge gaps in biodiversity studies regarding the limitations when evaluating the identity, distribution, evolution, ecological traits, population dynamics, abiotic tolerances limits and ecological interactions of species (Brown & Lomolino, 1998; Lomolino, 2004; Cardoso et al. 2011; Diniz-Filho et al. 2013; Hortal et al. 2015). Regarding ecological interaction networks (Fig. 1), our incomplete knowledge of species' geographic distributions combined with the Eltonian shortfall (i.e., which refers to the lack of information on species interactions and ecological roles) are particularly relevant (Damos, 2024). Even when species co-occur within a region, incomplete interaction data (often driven by limited sampling effort, temporal mismatches, or detectability constraints rather than true ecological absence) may lead to biased inferences about community structure, species importance, and network resilience (Terry & Lewis, 2020). Altogether, these limitations constrain our ability to generalize from existing plant–hummingbird networks, potentially leading to incomplete or biased interpretations of community structure and ecosystem functioning at continental scales.

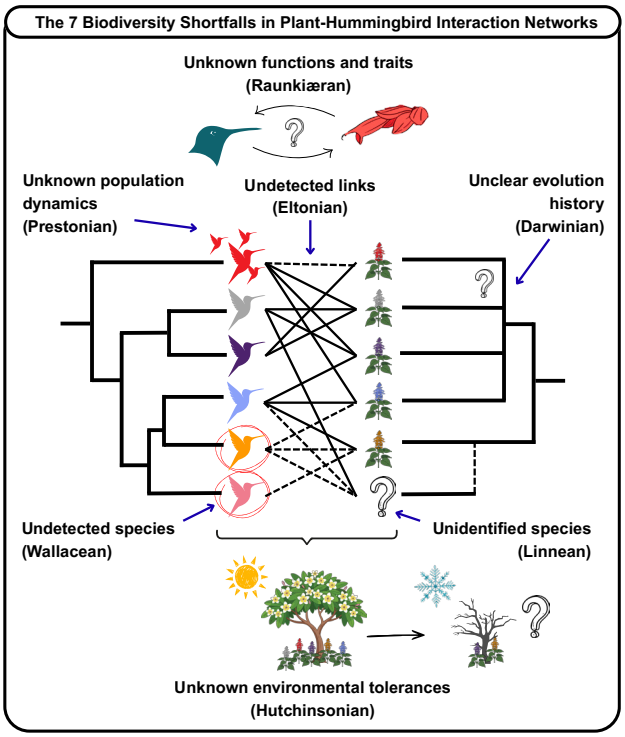

Figure 1. Representation of the shortfalls in plant-hummingbird interaction networks studies. When evaluating the interactions of a community there are a number of unidentified species (Linnean shortfall) that come from several unknown lineages (Darwinian shortfall), with incomplete information about their distribution (Wallacean shortfall), physiological-tolerance (Hutchinsonian shortfall), population dynamics (Prestonian shortfall), ecological roles (Raunkiaeran shortfall) and interactions with other species (Eltonian shortfall).

These shortfalls become particularly problematic when interaction networks are used to infer broad ecological patterns or to guide conservation planning (Jongman, 1995). Many network properties, including centrality and specialization, are directly influenced by species richness and the number of recorded interactions. Similarly, the metrics commonly used to quantify these properties (e.g., degree and specialization indices) are highly sensitive to network size and sampling completeness. Consequently, systematic biases in the representation of species, habitats, climates, or geographic regions may lead to conclusions that fail to accurately capture the true variability of ecological interactions across environmental and spatial gradients (Poisot et al., 2020). For hummingbirds, a taxonomically well-known group with well-described traits and distributions, this raises a critical question: how representative is the existing body of plant–hummingbird interaction networks of the family as a whole and of the environments

they inhabit? To address these gaps, we conducted a continental-scale synthesis of published plant–hummingbird interaction networks across the Americas. By compiling and standardizing quantitative network data from multiple studies, we aimed to evaluate the extent to which existing research captures the taxonomic, geographic, and environmental diversity of plant–hummingbird interactions, and to identify persistent knowledge gaps linked to biodiversity shortfalls. Specifically, we (i) quantified the richness of plant species, hummingbird species, and unique interactions represented in published networks; (ii) assessed the geographic and environmental coverage of these studies across climatic gradients and land-cover types; (iii) evaluated the taxonomic, morphological, trophic niche, migratory, and conservation-status representativeness of hummingbird species included in interaction networks; and (iv) identified plant and hummingbird species that frequently appear as central nodes across multiple networks. By integrating network structure, environmental context, and species traits, our synthesis provides a macroecological perspective on the current state of knowledge of plant–hummingbird interactions and highlights priority gaps for future research and conservation efforts.

Methods

Data compilation on plant-hummingbird interaction networks

To assess the geographic distribution and identify potential sampling gaps in studies of plant-hummingbirds interaction networks, we performed a comprehensive search in the Web of Science core database using the following query string: "hummingbird" AND "interaction network" OR "pollination network" OR "floral-visitor network" OR "floral visitor network". We considered studies in English, Spanish and Portuguese and going as back as 1960. From the initial results, studies were included based on these criteria: i) the study presented an original quantitative plant-hummingbird interaction network (i.e., a matrix or list of pairwise interactions), ii) the complete network data was accessible, either through publication supplements, public repositories, or direct author provision and, iii) the data allowed for the unambiguous interpretation of specific links between plant and hummingbird species, meaning that, studies presenting networks solely in graphical format (i.e. low-resolution figures) without supporting numerical data were excluded to ensure accuracy. Given that some publications are compilations of multiple networks, we traced and incorporated all original source studies referenced therein to avoid duplication and ensure a complete dataset. The final bibliography used is provided in Table S1. Since each network differ in sampling effort, both in time and geographic extension, and information such as interaction frequency cannot be compared between networks, all weighted networks (i.e. visitation rates) were transformed into binary networks (interaction/no interaction). For each selected study, we extracted the following information: the complete list of pairwise plant-hummingbird interactions, year or period of data collection, country of study, and geographic coordinates (latitude and longitude) of the study site. To ensure spatial independence among networks in close geographic proximity, we applied a 1 km buffer around each study site and merged overlapping points into a single composite network. When coordinates were not explicitly stated, they were manually approximated based on the provided location description.

To ensure taxonomic consistency, we standardized all species names to their currently accepted nomenclature. Hummingbirds (Trochilidae) were updated according to Birds of the World (Winkler et al., 2024), and plants according to the Plants of the World Online (POWO, 2026) and The Leipzig Catalogue of Vascular Plants (Freiberg et al., 2020). During this process, we implemented a validation filter to remove plants' records that were identified at taxonomic levels above species and taxonomically or geographically improbable records (e.g., plant species absent from the Americas or records that did not match any names in the plant taxonomy databases), which were presumed to be identification errors that could not be verified from the information in the articles. From each curated interaction network, we derived three key descriptors to characterize network structure at each location: (i) hummingbird species richness, (ii) plant species richness, and (iii) the total number of unique interactions. Although sampling effort varies across studies, we included studies that considered both dry and rain seasons. Then, we generated a latitudinal gradient map that shows the representation of the three descriptors, to visualize the variation in network attributes across the geographic range of the studies.

Environmental characterization

To characterize the environmental context of the compiled plant-hummingbird interaction networks, we extracted climatic and land-cover data for each study location. The analysis was performed using R (R Core Team, 2025) and the terra package (Hijmans et al., 2022). Initially, we extracted the climatic variables from the WorldClim 2.1 database (Fick & Hijmans, 2017), which provides a standard set of 19 bioclimatic variables. To capture potential micro-scale variation between network sites, some of which were located less than 5 km apart, we used data at the finest available spatial resolution (30 arc-seconds, approximately 1 km²).

We selected the following subset of variables to characterize climatic conditions: Bio 1, Bio 2, Bio 5, Bio 6, Bio 7, Bio 10, Bio 11, Bio 12, Bio 13, Bio 14, Bio 16, Bio 17, Bio 18 and Bio 19. Variables without standard units (Bio 3: Isothermality), those representing seasonal variation (Bio 4: Temperature Seasonality, Bio 15: Precipitation Seasonality), and those constructed using combinations of temperature and precipitation (Bio 8: Mean Temperature of Wettest, Bio 9: Driest Quarter) were excluded, as they are not directly comparable to absolute temperature or precipitation measures without transformation. Additionally, we obtained land-cover information from the European Space Agency (ESA) WorldCover 2020 product (Zanaga et al., 2022). This global dataset provides 11 discrete land-cover classes (Tree cover, Shrubland, Grassland, Cropland, Built-up, Bare/sparse vegetation, Snow and ice, Permanent water bodies, Herbaceous wetland, Mangrove, and Moss and lichen) at a very high spatial resolution (10 m). Because of the temporal mismatch between the WorldCover dataset and the network sampling periods, only studies conducted between 2019 and 2021 were included in this analysis. This fine resolution enabled a precise characterization of the habitat surrounding each network study site. For each network location, we generated a 1 km buffer and extracted, for all cells within this area, the values of the selected bioclimatic variables and the dominant land-cover class, which were then summarized as mean values and the most frequent category to represent each network. The environmental space occupied by the sampled networks was then assessed by comparing the ranges of the climatic variables and the frequency distribution of land-cover categories across all sites.

Missing hummingbirds and networks representation for the family

Using the final compiled dataset, we identified hummingbird species that are absent from all available interaction network studies using as reference the most recent and complete list of accepted hummingbird species, which was proposed by Birds of the World (Winkler et al., 2024). Since there is a high uncertainty regarding subspecies identification and taxonomy, we decided to consider only accepted species and performed a throughout revision of the species reported in each network considering their known geographic distribution and recent taxonomic changes to ensure taxonomic confidence. These unsampled species represent a critical knowledge gap, as no data exist on their roles within plant-hummingbird interaction networks. To evaluate whether the absence of these species from the sampled networks introduces a systematic bias in our understanding of the family Trochilidae, we compared the ecological and morphological traits of sampled versus unsampled species. For each species in the family, we compiled the following trait data: *Morphology*: Key morphological measurements from the AVONET database (Tobias et al., 2022); *Trophic Niche*: Trophic guild classifications from AVONICHE (Sayol et al., 2026); *Migratory Behavior:* Migration patterns as documented in Birds of the World (Winkler et al., 2024); and *Conservation Status*: Vulnerability categories from the IUCN Red List (IUCN, 2025).

All the traits information was integrated into the dataset for every species present in the networks (see Table S2). For each of those four traits, we compared the species in the networks vs the species absents in the networks to assess the representativeness of the sampled data. For the trophic niche, migratory behavior and conservation status, we compared the proportion of each category in each group. For morphological traits, since variables did not present a normal distribution, we performed Mann–Whitney tests to compare each trait.

Cross-network analysis of species centrality

To identify species that consistently play a central role in plant-hummingbird interaction networks, we evaluated the interactive role of each species within each network. We quantified this role using the network metric degree centrality (D), defined as the number of distinct interactions partners a species has within a network (Freeman, 1977). In ecological terms, a species with a high degree could be considered a generalist and a potentially key node in the network's structure. For each compiled network, we calculated the degree centrality for every hummingbird and plant species. Subsequently, we identified the species with the highest degree in both the hummingbird and plant assemblages for that specific network. To evaluate their consistency across the geographic range of the study, we calculated the frequency with which each species had the highest degree centrality across all networks. This frequency-based cross-network analysis allowed us to distinguish locally important species from those that exhibit consistently high interactive roles in multiple, geographically distinct communities. Because degree is influenced by network size and sampling intensity (Vanbergen et al. 2016; Martin & Niemeyer, 2021), we did not directly compare absolute degree values across networks. Rather, we evaluated species' interaction roles based on their relative position within each network (i.e., identifying the most connected species locally), which provides a more robust basis for comparison across studies with heterogeneous sampling designs (Henriksen et al. 2018).

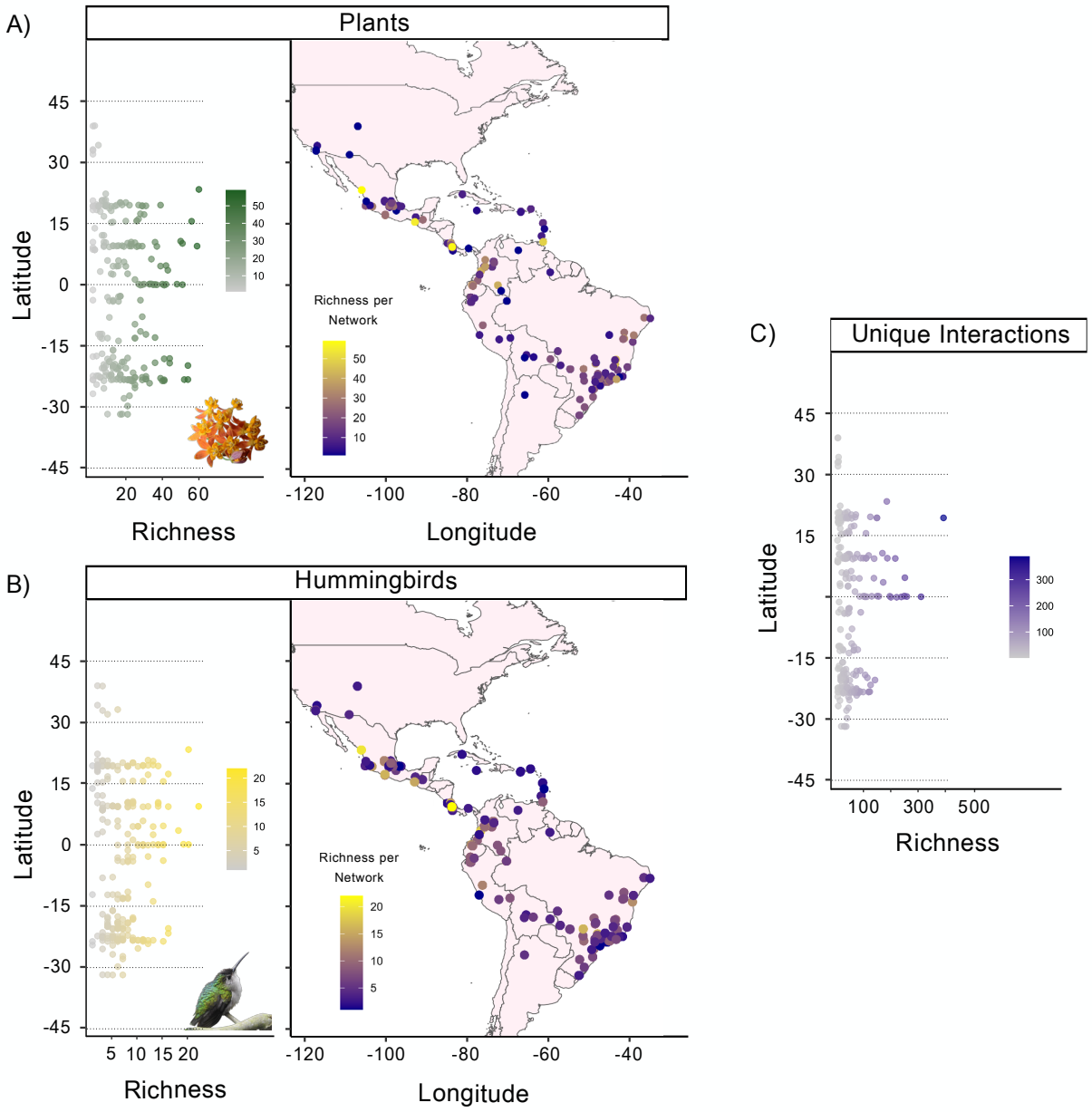

Figure 2. Geographic distribution of plant–hummingbird interaction networks across the Americas and their latitudinal gradients for (A) plant species richness, (B) hummingbird species richness, and (C) number of unique interactions per network. Panels A and B also show species richness per network. Plant (*Asclepias curassavica*) and hummingbird (*Pampa curvipennis*) photographs by Alejandro R. Villa.

Results

The plant-hummingbird networks in America

Our continental-scale compilation resulted in a final dataset of 12,658 recorded interactions (representing 8,890 unique pairwise links) derived from 233 distinct interaction networks published across 118 studies. These data encompass 214 hummingbird species (60% of the family Trochilidae) and 1,757 plant species. The plant species most frequently represented in the networks belonged to the families Rubiaceae, Heliconiaceae, Lamiaceae, Bromeliaceae, and Fabaceae. Among hummingbirds, the Emeralds (subfamily Trochilinae) and the Hermits (subfamily Phaethornithinae) were the tribes with the highest total number of reported interactions (Table 1).

The compiled networks exhibited a distinct latitudinal gradient in network complexity. Species richness (for both plants and hummingbirds) and the number of unique interactions increased toward the equator, peaking in Ecuador (Fig. 2). Furthermore, research effort across the continent is disproportionately distributed, with most studies focused

Table 1. Top 10 plant (P) and hummingbird (H) genera and species with the highest number of reported interactions across all networks.

Group	Order/Family (P) or subfamily/tribe (H)	Taxa	Number of reported interactions
Plant genera	Gentianales/Rubiaceae	*Palicourea*	628
	Zingiberales/Heliconiaceae	*Heliconia*	577
	Lamiales/Lamiaceae	*Salvia*	463
	Poales/Bromeliaceae	*Aechmea*	296
	Poales/Bromeliaceae	*Guzmania*	265
	Fabales/Fabaceae	*Erythrina*	252
	Lamiales/Gesneriaceae	*Columnea*	243
	Poales/Bromeliaceae	*Tillandsia*	234
	Myrtales/Onagraceae	*Fuchsia*	229
	Poales/Bromeliaceae	*Vriesea*	205
Hummingbird genera	Phaethornithinae (hermits)	*Phaethornis*	1859
	Trochilinae/Trochilini (emeralds)	*Thalurania*	689
	Trochilinae/Trochilini (emeralds)	*Chloristilbon*	505
	Trochilidae/Mellisugini (bees)	*Selasphorus*	484
	Lesbiinae/Heliantheini (brilliants)	*Coeligena*	484
	Trochilinae/Trochilini (emeralds)	*Chionomesa*	448
	Lesbiinae/Heliantheini (brilliants)	*Heliodoxa*	443
	Trochilinae/Trochilini (emeralds)	*Eupetomena*	425
	Trochilinae/Lampornithini (mountain gems)	*Lampornis*	399
Plant species	Gentianales/Rubiaceae	*Bouvardia ternifolia*	123
	Lamiales/Orobanchaceae	*Castilleja tenuiflora*	104
	Fabales/Fabaceae	*Erythrina speciosa*	98
	Gentianales/Rubiaceae	*Palicourea padifolia*	65
	Poales/Bromeliaceae	*Aechmea nudicaulis*	64
	Lamiales/Gesneraceae	*Besleria solanoides*	64
	Lamiales/Bignonaceae	*Spathodea campanulata*	61
	Fabales/Fabaceae	*Inga vera*	60
	Fabales/Fabaceae	*Bauhinia variegata*	58
	Gentianales/Rubiaceae	*Hamelia patens*	56
Hummingbird species	Trochilinae/Trochilini (emeralds)	*Chlorostilbon lucidus*	432
	Trochilinae/Trochilini (emeralds)	*Eupetomena macroura*	405
	Trochilinae/Trochilini (emeralds)	*Thalurania glaucopis*	359
	Phaethornithinae (hermits)	*Phaethornis eurynome*	352
	Trochilinae/Trochilini (emeralds)	*Chionomesa fimbriata*	282
	Trochilinae/Trochilini (emeralds)	*Basilinna leucotis*	278
	Phaethornithinae (hermits)	*Phaethornis striigularis*	271
	Phaethornithinae (hermits)	*Ramphodon naevius*	258
	Trochilinae/Trochilini (emeralds)	*Amazilia tzacatl*	250

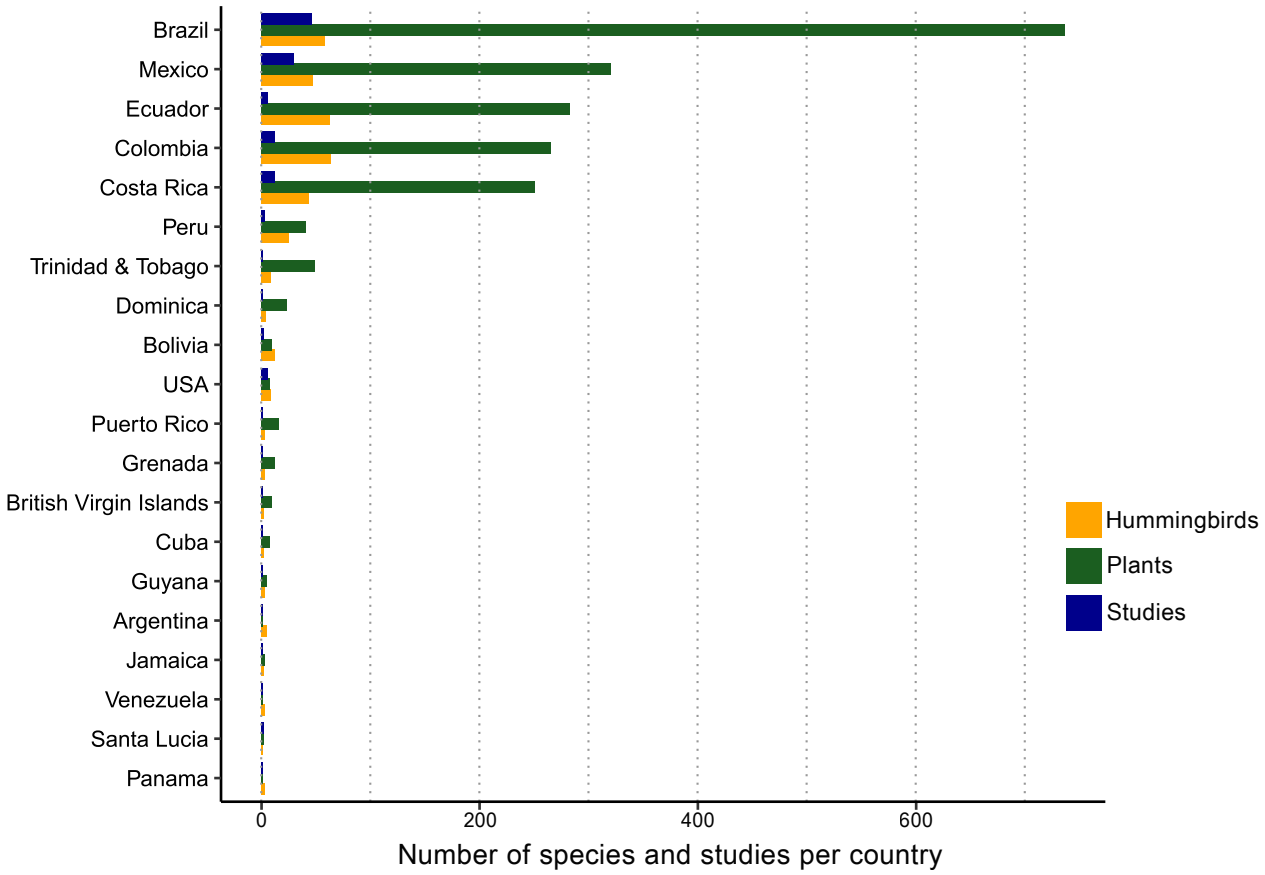

Figure 3. Number of recorded species and studies per country. Orange bars indicate hummingbird species, green bars plant species, and blue bars the number of network studies.

in a few countries. Brazil (n = 96, 41.2%), Mexico (n = 42, 18.02%), Costa Rica (n = 27, 11.58%), Ecuador (n = 21, 9.01%) and Colombia (n = 19, 8.15%) together contained most of studies, reported the highest species richness, and accounted for most recorded interactions (Fig. 3).

Environmental characterization of the studies

The compiled networks encompass a wide range of climatic conditions. Across all study sites, precipitation variables ranged from 0 (minimum value for Bio17) to approximately 1,600 mm (the maximum value recorded for the wettest quarter, Bio16). The mean values of the temperature variables ranged between 10 (Bio02 mean = 10.73) to 27°C (Bio5 mean = 26.79) (Fig. 4). Land-cover representation across networks was highly homogeneous. From the 233 studies, 92 studies (39.4%) were conducted between 2019 and 2021, only in 6 countries (Figure 5). The majority conducted in areas classified as "Tree cover" (n = 65), followed by "Built-up" (n = 16), "Grassland" (n = 5), Cropland (n = 3) and "Shrubland" (n = 3). Geographic analysis revealed that Brazil and Mexico contained the greatest diversity of land-cover types in their study sites (5 categories). Conversely, networks in Costa Rica, Ecuador, Colombia and the British Virgin Islands were each documented three or less land-cover types (Tree cover, Grassland and Built-Up).

Sampling gaps and trait representativeness

Of the 358 recognized hummingbird species, 214 (60%) were recorded in at least one interaction network, leaving 144 species (40%) absent from the compiled dataset. To assess potential sampling bias, we compared the traits of species present in the networks against those absent in the networks. In this case, we only found significant morphological differences between species recorded in the networks and those that were absent in beak traits (Fig. 6, Table S3). For the trophic guild, the original data AVONICHE database reported only three species with an omnivore diet: *Lophornis magnificus* (50% nectar, 50% insects), *Lophornis ornatus* (50% nectar, 50% insects) and *Archilochus colubris* (60% nectar, 40% insects), with the rest of the species having a diet consisting mainly of nectar (90% or more). In the compiled networks we found only

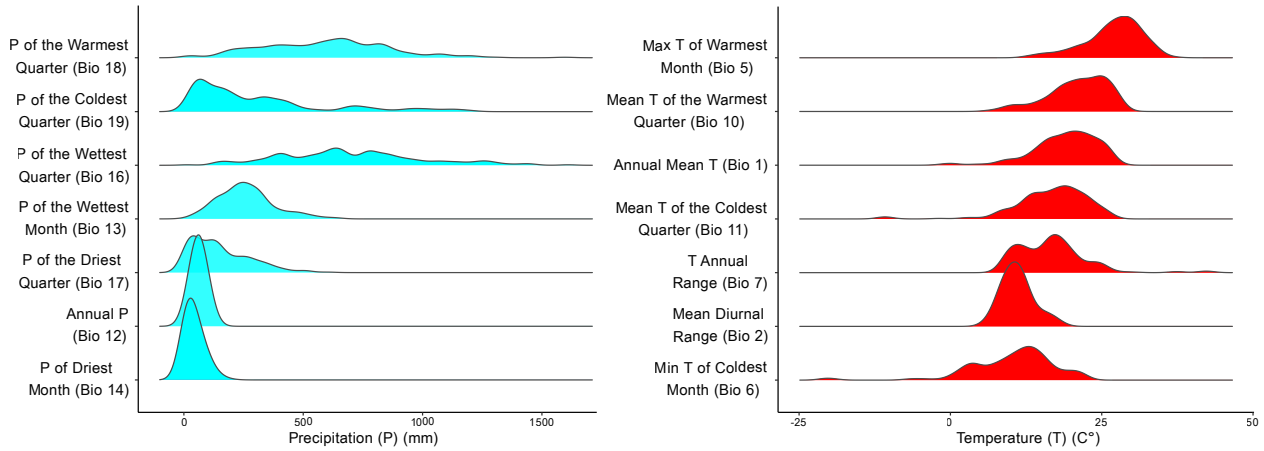

Figure 4. Climatic coverage of network studies across selected bioclimatic variables. Left panels show precipitation-related variables (P; blue), and right panels show temperature-related variables (T; red).

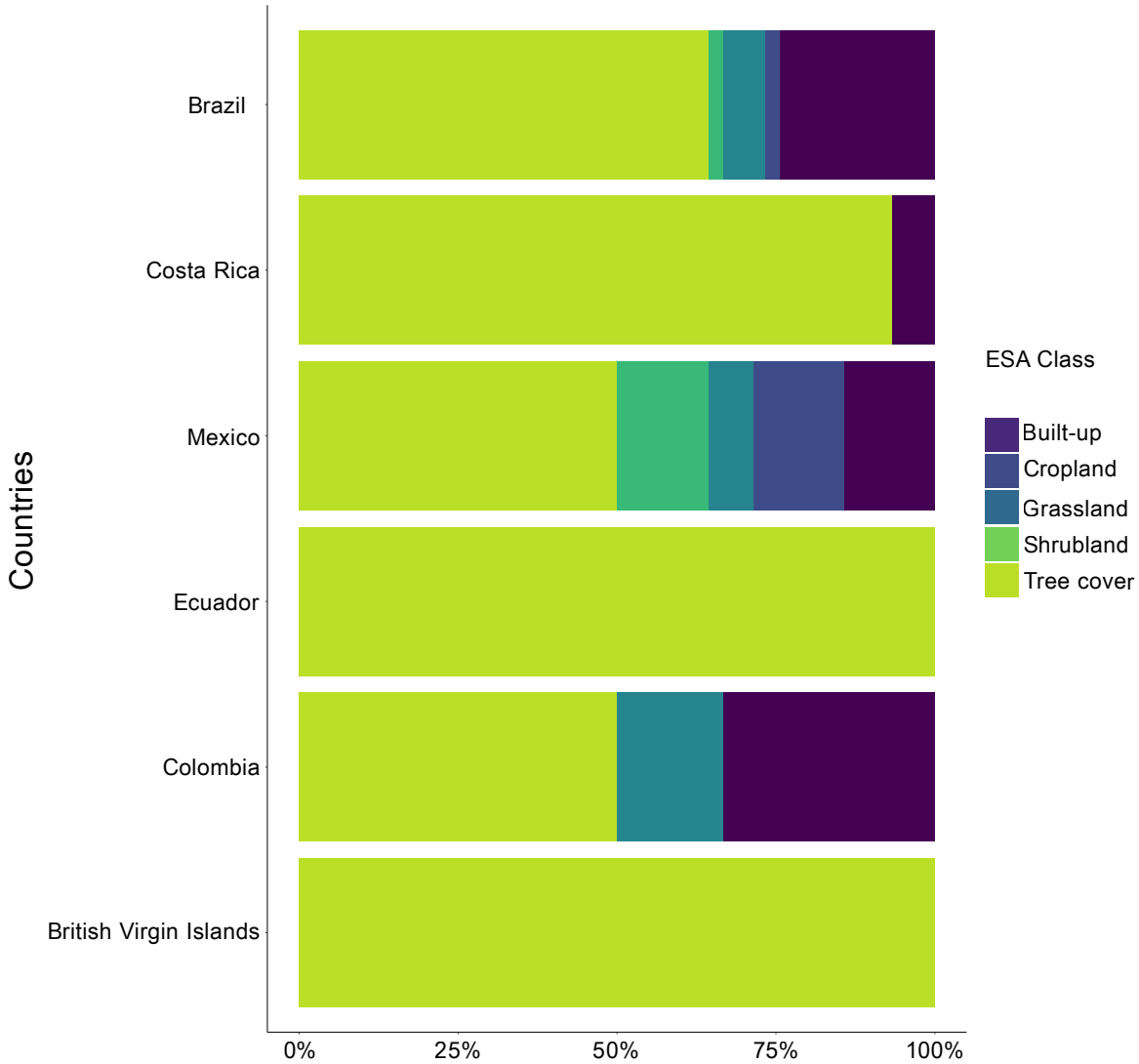

Figure 5. Proportion of land-cover categories (based on the ESA WorldCover classification) represented by network locations in each country.

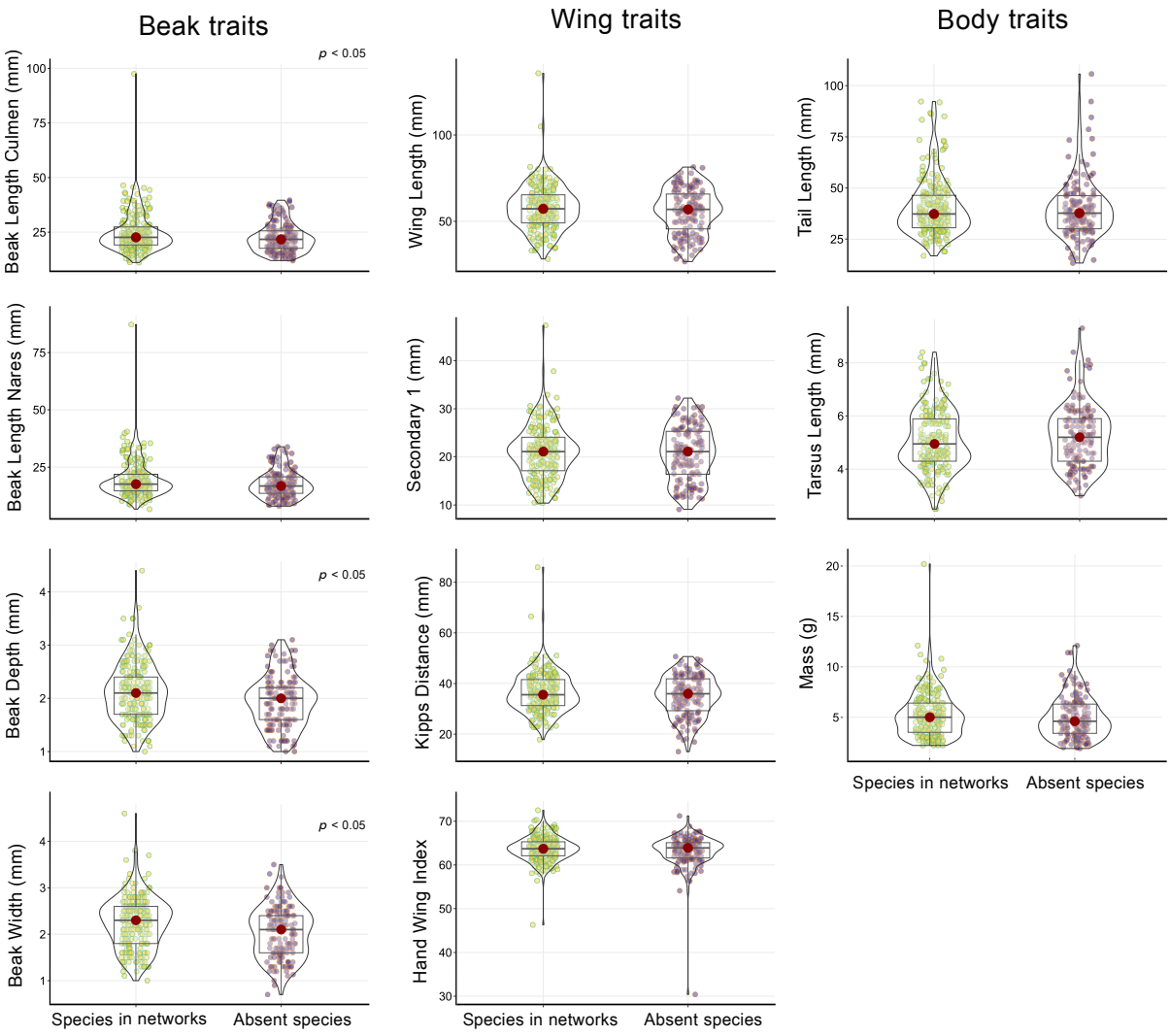

Figure 6. Comparison of morphological trait distributions between hummingbird species included in networks and the entire Trochilidae family across 11 traits. Left column: bill traits (culmen length, bill length to nares, bill depth, bill width); middle column: wing traits (wing length, secondary length, Kipp's distance, hand-wing index); right column: body traits (tail length, tarsus length, body mass).

Archilochus colubris and *Lophornis magnificus*, present in 22 and 3 networks respectively. Regarding the species vulnerability status, the networks studies have representation of only one of all the species categorized as "Endangered" and "Critically Endangered", and less than half of the "Vulnerable" and "Near Threatened" species (Fig. 7A). Finally, regarding migratory status, all of the species with full or mixed migration were present in the networks (Fig. 7B).

Cross-network centrality

For hummingbirds the species with highest interactive roles across multiple networks were *Basilinna leucotis* (n = 15), *Chlorostilbon lucidus* (n = 14) , *Eupetomena macroura* (n = 13), *Chionomesa fimbriata* (n = 12), *Phaetornis eurynome* (n = 11), *Amazilia tzacalt* (n = 10), *Hylocharis chrysura* (n = 9) and *Ramphodon naevius* (n = 8), while in plants were *Erythrina speciosa* (n = 6), *Bouvardia ternifolia* (n = 6), *Aechmenia nudicaulis* (n = 4), *Hamelia patens* (n = 4) and Palicourea padifolia (n=4) (Fig. 8).

Discussion

Our continental-scale synthesis reveals a strong imbalance in the geographic, environmental, and taxonomic coverage of interaction data across the Americas. Although the dataset includes 60% of all hummingbird species, network records are highly concentrated in a small number of countries which together account for most studies,

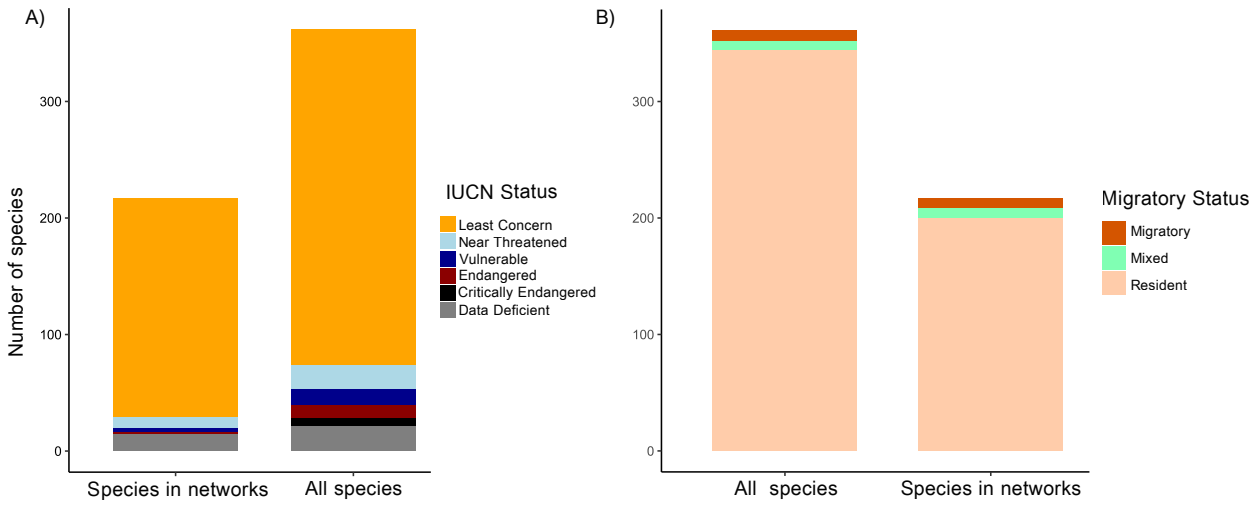

Figure 7. Species representation in networks compared with the entire Trochilidae family. (A) Number of species per threat category according to the International Union for Conservation of Nature (IUCN). (B) Number of resident, migratory, and partially migratory species.

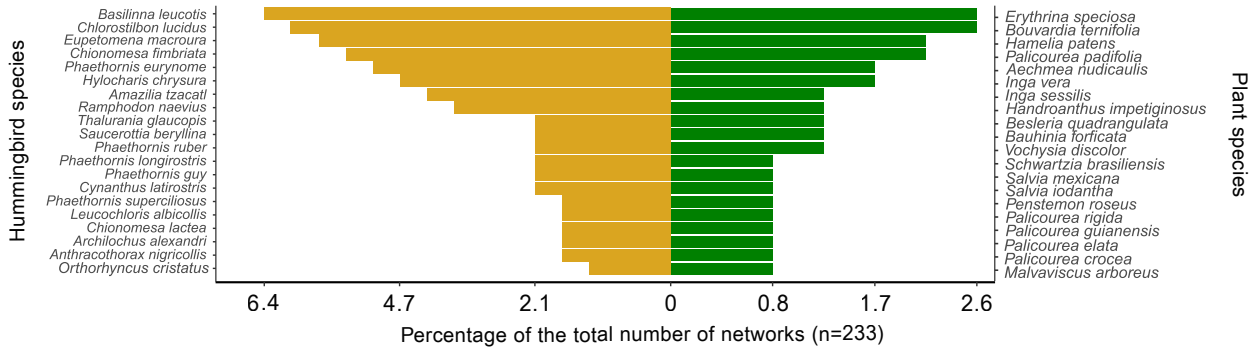

Figure 8. Top 20 species with the highest interactive roles across all compiled networks in the Americas. The y-axis lists species (hummingbirds in orange, plants in green), and the x-axis shows the proportion of networks in which each species occupied the highest interactive role.

species records, and interaction links. Within the available networks, network richness and interaction diversity peak near the equator and decline toward higher latitudes, while large portions of South America, Central America, and the Caribbean remain poorly represented or completely unsampled. In addition, threatened species are rarely included in networks, and interactive roles are dominated by a small subset of frequently sampled species. Together, these patterns indicate that current knowledge of plant–hummingbird interaction structure is shaped as much by sampling distribution as by biological processes.

Knowledge shortfalls in species distributions and ecological interactions have received increasing attention across taxa and regions (Marshall et al. 2024). Methodological advances, particularly species distribution and ecological niche models (i.e., Wallacean shortfall) have reduced some geographic gaps in occurrence data (Terribile et al. 2018; Vieira et al. 2024). However, interaction networks depend on intensive local sampling and therefore capture only a fraction of the spatial variability in species interactions (Oliveira et al. 2025). Shortfalls are therefore not limited to where species occur but extend to where interactions are documented and how network structure is inferred. Our results indicate that these interaction shortfalls are substantial at continental scale and influence multiple dimensions simultaneously, leading studies to reinforce biases by concentrating in few countries (i.e. Brazil, Mexico) with similar environmental conditions

(i.e. environmental concentration in warm humid regions) and underrepresenting threatened species and their roles in their communities.

The compiled networks also show a latitudinal gradient in species richness and number of unique interactions, with three main peaks (Mexico, the Ecuador and Brazil) and declines toward higher latitudes. Importantly, the gradient is not limited to species counts but extends to interaction richness, indicating that these diverse regions also sustain a greater diversity of interaction links. This supports previous evidence that specialization and interaction turnover tend to increase in species-rich hummingbird–plant systems (Dalsgaard et al. 2011). Although this pattern is consistent with the classic latitudinal diversity gradient (Hillebrand 2004), widely documented for both hummingbirds and flowering plants (Rahbek & Graves 2000; Cartier et al. 2021; Jiang et al. 2023), this uneven spatial aggregation also suggests that there is biased research effort and sampling intensity. The missing information of the latitudes between the three identified peaks (Mesoamerica and the Atlantic Forest) may enhance misinterpretation of other geographic gradients patterns, further increasing the Eltonian shortfall.

The environmental space represented by available plant–hummingbird networks is uneven and concentrated in relatively warm and humid conditions. Most studies were conducted in regions with moderate to high temperatures and precipitation, whereas highly seasonal or cold environments are poorly represented. The few networks associated with low temperature extremes occur mainly in the USA and are linked to variables that capture seasonal minima rather than the typical thermal conditions under which hummingbird–plant interactions occur (Abrahamczyk et al. 2011). As a result, regions with strong climatic seasonality—such as large portions of the USA and Canada in the north and Chile and Argentina in the south—remain sparsely covered in the network literature. A similar imbalance appears in habitat representation since most networks are in areas currently classified as tree cover, and the widest diversity of land-cover categories occurs in Brazil and Mexico, again mirroring the geographic concentration of sampling effort. However, this pattern should be interpreted with caution because contemporary global land-cover information (Zanaga et al. 2022) reflects recent landscape conditions, whereas many interaction networks were sampled decades ago. In landscapes that have undergone rapid land-use change, urban expansion, or agricultural conversion, current classifications such as built-up or cropland may not match the habitat structure present at the time of sampling. This temporal mismatch can introduce classification error when linking network structure to environmental context and may obscure historical interaction patterns. Incorporating historical land-cover reconstructions or time-matched environmental layers would substantially improve inference about how habitat conditions shape plant–hummingbird interaction networks.

Patterns of trait coverage across networks revealed marked contrasts among different dimensions of species representation. For morphological traits, only the three beak-related variables (i.e., culmen length, depth, and width) showed significant differences between species present in the networks and those absent from them, whereas wing and body traits did not differ between these groups. Specifically, species represented in the networks encompassed a broader range of beak morphologies, while absent species tended to exhibit shorter, narrower, and less conspicuous beaks. This pattern may be associated with more generalist feeding habits among underrepresented species (Claudino et al., 2022). However, because information on diet composition and the structural roles of these missing species within interaction networks remains largely unavailable, this interpretation should be treated with caution, as it cannot be directly supported by our dataset without becoming speculative. Future studies should therefore prioritize investigating the dietary ecology and functional roles of these underrepresented species to better understand the mechanisms underlying their historical absence from plant–hummingbird network studies.

Migratory status and trophic guild are broadly captured in the available datasets, with all fully or partially migratory hummingbird species appearing in at least one network, yet taxonomic completeness remains limited, as 40% of hummingbird species are still absent from published interaction networks. Representation is even more restricted for IUCN-Red list conservation status categories, with only a small fraction of Vulnerable, Endangered, and Critically Endangered species included. Because hummingbirds constitute a well-resolved and intensively studied clade (Jetz et al. 2012), it is possible to estimate with reasonable confidence how many species are missing from network datasets and to characterize the direction of this taxonomic gap. Performing an equivalent assessment for plants is considerably more difficult, since hummingbird-visited species are phylogenetically dispersed across many angiosperm families and lack a unified, interaction-defined lineage. Therefore, plant-side gaps are likely substantially larger but also less visible and harder to quantify, which can propagate additional uncertainty into estimates of interaction diversity, specialization patterns, and network-level trait structure.

Species' interactive roles across networks provide a clear illustration of the depth of the Eltonian shortfall and

the biases produced by incomplete and uneven sampling. We detected a pronounced asymmetry in species contributions, with several hummingbird species occupying central positions across multiple networks, whereas only a small number of plant species recur as central nodes and in far fewer cases. For example, *Basilinna leucotis* was the most central species in 15 different networks, while only 11 plant species were central in more than one network, each in fewer than six cases (notably *Erythrina speciosa* and *Bouvardia ternifolia*). This asymmetric contribution is consistent with the typical structure of hummingbird–plant networks (Bascompte et al. 2006), where plant richness often exceeds hummingbird richness and interactions are not reciprocally specialized (Chavez-González et al. 2020; Infante et al. 2020; Sánchez & Lara 2024; Izquierdo-Palma et al. 2021). However, centrality patterns are strongly shaped by sampling distribution. The species most frequently identified as central are concentrated in the countries with the greatest number of studies, showing how geographic bias propagates into functional interpretations. This effect is illustrated by *B. leucotis*, whose distribution is restricted from northern Mexico to Nicaragua yet appears as central in more networks than *Anthracothorax nigricollis*, a species with more than twice the geographic range but occurring largely in regions with few or no network studies (Arizmendi et al. 2021; Greeney 2023). Such contrasts indicate that apparent differences in species-level importance may reflect data availability more than true ecological dominance. Missing species further amplify this distortion: several hummingbirds absent from network datasets are known to interact with multiple plant taxa and to be locally common, but without network-level data their specialization, competitive interactions, and functional roles remain unresolved. These absences bias estimates of network structure and species roles and directly contribute to interaction-level shortfalls (Nunes-Martínez & Pires 2024).

Overall, we found a pronounced geographic concentration of network studies. Brazil and Mexico alone account for nearly 60% of all compiled networks, with Costa Rica, Ecuador, and Colombia contributing most of the remainder. Although these countries are indeed centers of hummingbird and plant diversity (Dalsgaard et al. 2011), diversity alone does not explain the magnitude of the imbalance. Several countries with high hummingbird richness (including Venezuela, Peru, Paraguay, Uruguay, Suriname, French Guiana, and Chile) have few or no documented networks. A similar pattern occurs in Central America and the Caribbean, where most networks are concentrated in Costa Rica while multiple countries remain unrepresented. This uneven distribution of research effort suggests that continental patterns of interaction structure are currently inferred from a geographically restricted subset of communities. These gaps likely reflect structural and economic inequalities in research capacity rather than biological absence of interactions and could distort our understanding of macroecological patterns (Wojciechowski et al. 2017; Culumber & Tobler, 2019). In this regard, network studies are logistically demanding and resource-intensive, requiring repeated field sampling, taxonomic expertise, and coordinated teams (Nielsen & Bascompte 2007; Delmas et al. 2018). Limitations in funding, infrastructure, and long-term monitoring programs can therefore strongly constrain where, when and how often networks are documented, further deepening the existing biodiversity shortfalls (Zhang et al. 2023; Hortal et al. 2015). Expanding interaction datasets will depend not only on identifying priority regions, but also on strengthening collaborative and financial support mechanisms that enable network sampling in underrepresented areas.

By compiling the currently available plant–hummingbird networks across the Americas, we identified substantial gaps in geographic, environmental, taxonomic, and interaction-role coverage. These shortcomings, particularly those related to the geographic and environmental distribution of network studies (i.e., climate and vegetation types), are especially relevant in the context of biodiversity shortfalls, as they may bias macroecological inferences, including patterns of species richness, unique interaction richness, and centrality metrics (e.g., degree). Furthermore, because many vulnerable, endangered, and critically endangered species remain absent from network studies, the lack of information on their ecological interactions with plants represents a major limitation for conservation planning and management. Addressing these gaps will require targeted sampling in underrepresented regions, greater inclusion of threatened species with few or no recorded interactions, and improved integration of temporal and environmental dimensions into ecological network studies. Although this study focused on the Eltonian shortfall, evaluating the remaining biodiversity shortfalls (i.e., Wallacean, Hutchinsonian, Prestonian, Linnean, Raunkiaeran, and Darwinian) would provide a broader understanding of potential biases in current knowledge and help clarify the complex structure and dynamics of plant–hummingbird interactions. Such efforts could provide a practical roadmap for advancing ecological network research, reducing persistent biodiversity shortfalls, and improving our understanding of the ecological and evolutionary processes shaping plant–hummingbird interactions across environmental and biogeographic gradients.

Author Contributions

A.R.V. and W.D. conceptualized the project, discussed and designed the methodology. A.R.V. collected and curated the plant-hummingbird interaction data, reviewed the taxonomy of species, performed the analysis and created the figures. A.R.V and W.D. wrote the first draft of the manuscript. W.D. supervised the project.

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Conflict of Interest Statement

The authors have declared that no competing interests exist.

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