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Morphological Traits and Specialization of Neotropical Flower-hummingbird Networks

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Biological specialization plays a central role in species coexistence. While many studies focus on hummingbird pollination, research on the effects of morphological traits of both hummingbirds and plants on the specialization of interaction networks remains scarce. In this study, we aim to address the following questions: i) does the dominance of ornithophilous plant species increase the specialization of hummingbird-plant interaction networks?; ii) do ornithophilous plants exhibit a greater diversity of interactions with hummingbirds compared to non-ornithophilous plants?; iii) do the beak size and body weight of hummingbirds influence the diversity of their interactions? Research was conducted on hummingbird-plant interactions in the Neotropical region. We investigated hummingbird-plant interactions in the Neotropical region by compiling 24 networks from the literature, comprising 1,182 interactions between 34 hummingbird species and 326 plant species. We found no effect of ornithophilous plant dominance on the structure (connectance and modularity) of the networks. However, species-level interactions were influenced by morphological attributes of both plants and hummingbirds. Interaction similarity among plant species was greater for ornithophilous plants than for non- ornithophilous plants. Additionally, beak size positively influenced the degree and specialization of hummingbird interactions. Our findings demonstrate that the morphological characteristics of hummingbird and plant species directly influence the diversity of interactions in Neotropical hummingbird-plant networks and species specialization.

Key words: Morphological correspondence, Ornithophily, Plant-animal interactions, Specialization, Trochilidae

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BACKGROUND

Several ecological processes involve interactions among species, which can be studied through the approach of ecological complex networks (Delmas et al. 2009; Landi et al. 2018; Poisot et al. 2016). Studies involving ecological networks can be characterized in various ways; however, they are typically grouped into antagonistic and mutualistic networks (Ings et al. 2009; Landi et al. 2018). Mutualistic associations between animal pollinators and flowering plants are widely studied from a network perspective (*e.g.*, Bascompte and Jordano 2013; Olesen et al. 2007), due to their well-recognized ecological, evolutionary, and economic importance for the functioning and maintenance of ecological communities (Ollerton 2017; Rech et al. 2016; Ratto et al. 2018). Generally, plant-pollinator networks exhibit a nested structure where specialist species interact primarily with generalists (Bascompte et al. 2006). Despite significant advances in studies aimed at describing temporal (Dalsgaard et al. 2011) and geographical patterns (Moreira et al. 2020) of plant-pollinator networks, few studies have addressed how morphological traits of interacting species affect the structural characteristics of these networks in Neotropical ecosystems.

The plant-pollinator interaction occurs through the provision of floral resources by plants to visitors that, during foraging, subsequently pollinate them (Agostini et al. 2014; Willmer 2011). Many plant species depend on animals as pollination agents and it is estimated that at least 87.5% of the world's angiosperms are pollinated by animals (Ollerton et al. 2011). Among vertebrates that act as pollinators, birds represent one of the most diverse groups (Regan et al. 2015), with hummingbirds (Aves: Trochilidae) being the primary pollinators of approximately 15% of the plant species in the Neotropical region (Bawa 1990; Las-Casas et al. 2012). However, this process often involves the participation of multiple species with different degrees of specialization (Waser and Ollerton 2006; Bender et al. 2017; Rodríguez-Flores et al. 2019). In this sense, hummingbird species tend to visit plants with specific floral morphological characteristics, commonly referred to as ornithophilous or trochilophilous (see Fenster 2004; Maglianesi et al. 2015).

Angiosperms exhibit extreme diversity in their floral traits (Dafni et al. 2005), and certain characteristics may favor the attractiveness to different types of animals. Plants adapted to hummingbird pollination display morphological, structural, and phenotypic traits associated with the ornithophilous syndrome (Faegri and Van Der Pijl 1979). Among these, flowers with tubular corollas and reduced diameter, contrasting colors (*e.g.*, orange, red, and violet), lack of scent, diurnal anthesis, high nectar production, and spatial separation of the nectar chamber from the stigmas and anthers are notable (Castellanos et al. 2004). Additionally, trochilophilous plants feature pendant flowers favoring the hovering flight of hummingbirds (Faegri and Van Der Pijl 1979). However, plant communities in the Neotropical region exhibit flowers with a wide morphological variation (Dafni et al. 2005). These flowers may present varying degrees of morphological specialization concerning corolla length and shape (Waser and Ollerton 2006), as well as compatibility with the beak morphology of hummingbirds (Maruyama et al. 2014). Some flower plants are visited by multiple animal species, while others have morphology that restricts their use solely by hummingbirds (Maruyama et al. 2014; Strauss and Irwin 2004).

Morphological characteristics of hummingbirds, such as beak length and body mass, can directly reflect on their success in resource acquisition (Rico-Guevara et al. 2019), as well as on the foraging strategies they employ (Mendonça and Anjos 2005). However, while body mass is of great importance in hummingbird-plant interactions (Araya-Salas et al. 2018), it is more closely associated with behavioral dominance systems among hummingbirds (*e.g.*, Marquez-Luna et al. 2019). Thus, larger-sized hummingbird species with greater body mass tend to be dominant over smaller hummingbirds, restricting their access to defended flowers (Claudino et al. 2021). On the other hand, some studies indicate that beak length is the most important variable in explaining interaction frequency and specialization in hummingbird-plant networks (*e.g.*, Maglianesi et al. 2014; Claudino et al. 2021). This is because beak size is directly related to morphological fit with the corolla of flowers, causing hummingbirds with different beak sizes to also use distinct floral resources (Brown and Bowers 1985; Machado 2009).

Based on ecological and behavioral observations, a certain level of morphological fit between hummingbirds and plants is expected (Castellanos et al. 2004). However, morphological and phenotypic incongruities can restrict the type, number, and strength of interactions exerted by a particular species (Junker et al. 2013; Stang et al. 2009). Additionally, factors such as seasonal resource availability can make hummingbirds versatile in their foraging, also exploiting non-ornithophilous plant species during times of food scarcity (Machado 2009). The inclusion of non-ornithophilous plants in their diet can directly influence the specialization of pollinator communities and, consequently, the formation of modules (i.e. subsets of species) in the interaction networks. Since species with more specialized connections tend to form groups that interact with each other (Olesen et al. 2007).

Although many studies address pollination performed by hummingbirds, including from the perspective of hummingbird-plant interaction networks (*e.g.*, Vizentin-Bugoni et al. 2014), studies focusing on the effects of morphological traits of plants and hummingbirds on network topology are scarce. We characterized the hummingbird-plant networks using the topological descriptors at the network level and at the species level (Dormann et al. 2009). At the network level, we used network connectance that is a descriptor of the level of connectivity (*i.e.*, specialization) among these species (Antoniazzi et al. 2018), and the network modularity which is a measure of the modular arrangement of interactions between species within the network (*i.e.*, occurrence of specialized subsets of interacting animals and plants) (Olesen et al. 2007). At the species level, we used the descriptors degree, specialization, and interaction similarity, which measure the diversity, specificity, and sharing of interactions between species, respectively. In this context, this study aims to answer the following questions: i) does the dominance of ornithophilous plant species increase the specialization of interactions in hummingbird-plant networks?; ii) do ornithophilous plants exhibit greater diversity of interactions with hummingbirds than non-ornithophilous flowers?; iii) does hummingbird beak length and body mass influence the diversity of their interactions? We expect that: i) high proportions of ornithophilous species positively influence the structure of interaction networks by increasing their connectivity and decreasing their modularity; ii) ornithophilous plant species have greater diversity and specialization of interactions within networks compared to non-ornithophilous species; iii) hummingbirds with larger beaks are more specialized compared to hummingbirds with smaller or intermediate beak sizes. On the other hand, hummingbirds with greater body mass will have a greater number of interactions within networks.

MATERIALS AND METHODS

Data collection

We used the database from the study by Moreira et al. (2020), which compiled 28 hummingbird-plant interaction networks distributed in the Neotropical region. The networks included in the database were based on studies that met the following criteria: (1) presentation of a basic description of the study area, containing a geographic coordinate; (2) listing of hummingbird species recorded on each plant species; (3) at least five plant species and five hummingbird species listed, totaling at least 10 species; and (4) a minimum of 80% of the hummingbird identified at the species level. For the taxonomic classification of plant species, we used the database of Flora e Funga do Brasil 2020 (https://floradobrasil.jbrj.gov.br/). For hummingbird species, the scientific nomenclature follows the arrangement proposed by the Brazilian Committee of Ornithological

Records (Pacheco et al. 2021). For further details regarding the compilation of hummingbird-plant interactions see Moreira et al. (2020).

Defining the morphological traits of species

All recorded plant species in our database were categorized in two categories: ornithophilous plants and non-ornithophilous plants. For this, we used the database available in Rodríguez-Flores et al. (2019), which characterized botanical families according to the floral morphology of their species. Thus, for botanical families with well-defined floral morphology, the species were easily categorized into ornithophilous and non-ornithophilous plants following the general characteristic of the family (Rodríguez-Flores et al. 2019). However, there are some botanical families with species that have variable floral morphology, being these categorized as "intermediate" by Rodríguez-Flores et al. (2019). For our plant species belonging to families with 'intermediate' floral morphology, we conducted additional searches in the literature for studies related to the description of the species of interest. Thus, we consulted the literature to define the floral morphology of the species, considering the corolla shape (tubular, bell-shaped, etc.), corolla size (in centimeters) and corolla color of the plant species. To determine corolla color, flowers were divided into four color categories: white (including all white or pale flowers); yellow (including different shades of yellow); warm colors (including all orange, red, and pink/salmon flowers); and cool colors (including all blue and purple flowers) (Carvalheiro et al. 2014). Flowers with more than one color were classified according to the predominant color (see Carvalheiro et al. 2014). Based on the determined characteristics, it was possible to categorize the different types of flowers of plant species, from flowers with ornithophilous syndrome (*i.e.*, flowers with tubular corollas, larger in size, and with contrasting colors such as orange, red, and violet) to those considered entomophilous – non-ornithophilous plants (Castellanos et al. 2004).

For plant species identified at the genus level, it was not possible to accurately determine the pollination syndrome, and such species were excluded from the networks. Networks with more than 5% of plant species for which ornithophilous and non-ornithophilous categorization was not possible were not included in our analyses. Based on these criteria, only 24 out of the hummingbird-plant networks compiled by Moreira et al. (2020), were considered in this study (Fig. 1; Table S1).

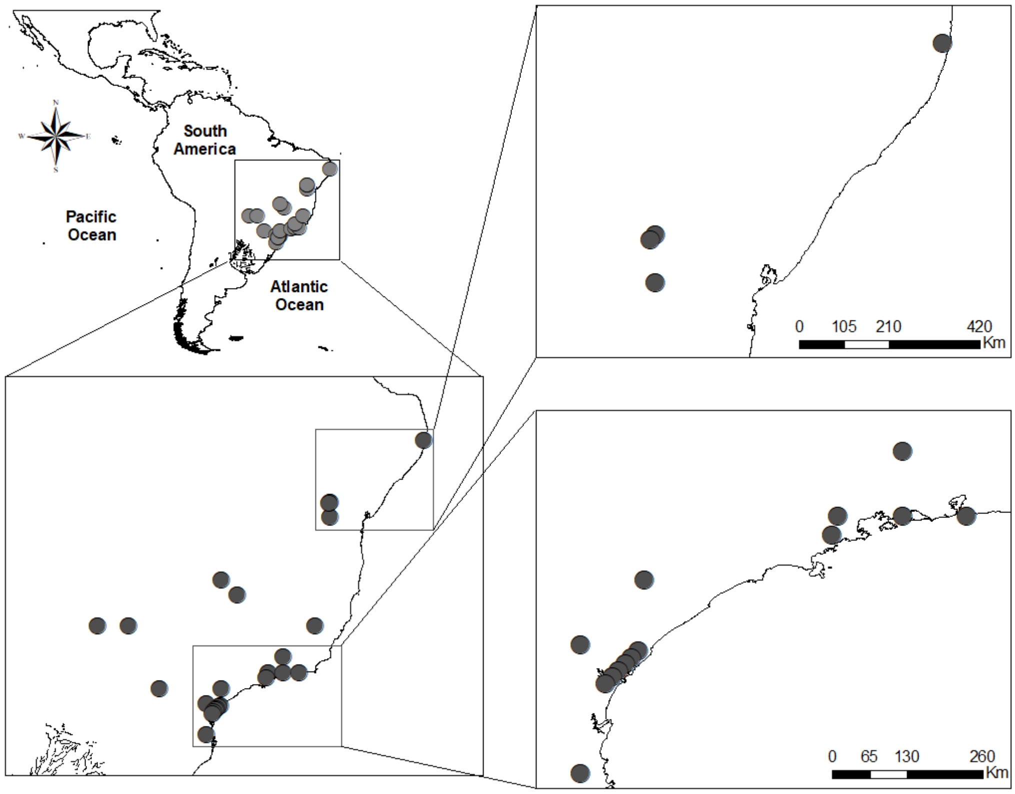

Fig. 1. Distribution of the 24 flower-hummingbird networks analyzed in the study. At this map scale, the overlay networks have been enlarged for better visualization.

Additionally, we also estimated the beak size (mm) and body weight (g) for hummingbird species. Beak size is typically measured as the length of the beak from the tip to the base and body weight is commonly measured using a precision scale capable of accurately measuring small weights. We obtained the mean values of these measurements from information available in the literature (*e.g.*, Grantsau 1998). These measurements provide crucial data for understanding morphological variations among hummingbird species and their potential effects on ecological interactions (Araya-Salas et al. 2018; Claudino et al. 2021).

Network analyses

From the compiled interaction data, we constructed binary matrices with hummingbird species *i* represented in the columns and plant species *j* in the rows. The resulting interactions from these matrices yield graphical representations, as species at the same trophic level do not interact with each other (Bascompte and Jordano 2006). Since we evaluated networks extracted from different studies, only presence-absence data could be analyzed. To describe the structure of hummingbird-plant networks, we used the descriptors connectance (C) and modularity (M). Connectance is the proportion of possible interactions that are realized in the network, being usually used to describe the specialization of qualitative bipartite networks because the higher the connectivity, the lower the specialization of the networks (*e.g.*, Rodríguez-Flores et al. 2019). To calculate the network modularity, we used the bipartite modularity index *Q* (Barber 2007) through the *LPAb+* algorithm to detect modules present in the networks (Beckett 2016). For the calculation of these descriptors, we used the *bipartite* package (Dormann et al. 2008) in the R software (R Core Team 2024).

To characterize species-level interactions for hummingbird-plant networks, we calculated the degree (k), specialization (d'), and interaction similarity for each plant species and each hummingbird species present in the matrices. The degree of a species is a measure related to the number of species with which a given species interacts. The d' index is a robust measure of specialization that compares the observed frequency distribution of interactions of a species to the availability of interacting partners (Blüthgen et al. 2006). Additionally, the d' index varies from 'one' for a completely specialized species to 'zero' for a completely generalist species (Blüthgen et al. 2006). The similarity index was used to quantify the similarity between species interactions, for which Jaccard similarity (1 - Jaccard dissimilarity, ranging from 0 to 1) was calculated for plant species and hummingbird species. The *bipartite* package (Dormann et al. 2008) will be used for index calculations.

Data analyses

To measure the dominance of ornithophilous plant species in the networks, we used the proportion of ornithophilous species relative to the total number of plant species in each network. We employed Generalized Linear Models (GLMs) with Gaussian error distribution (for data with normal distribution) to test the effect of the proportion of ornithophilous plants on the connectivity and modularity of the networks. In these models, the size of the networks (*i.e.,* the total number of interactions between hummingbirds and plants) was used to control for potential effects of species richness on network topology. All statistical analyses were conducted using the R statistical software (R Core Team 2024).

To analyze whether network descriptors at the species level (degree, specialization, and similarity) differ between groups of ornithophilous and non-ornithophilous plants, Generalized Linear Mixed Models (GLMMs) were employed. In these models, the plant species was used as a random effect variable to control for potential intrinsic differences between species that may affect hummingbird-plant interactions. GLMMs were also used to test the effect of beak size (mm) and body weight (g) on the degree, specialization, and similarity of hummingbird species. In these models, the hummingbird species was used as a random effect variable. For this analysis, were used only hummingbird species for which reliable morphometric data were obtained. All GLMMs were constructed using the *lme4* package (Bates et al. 2015).

RESULTS

In total, the 24 analyzed networks were composed of 34 hummingbird species, 311 plant species, and 1,028 distinct interactions (Table S2). The most frequent hummingbird species in the database were *Chionomesa fimbriata*, represented in 62.5% of the compiled networks and *Chlorostilbon lucidus* and *Eupetomena macroura* present in 54.2% of the networks each. The hummingbird species that interacted with the highest number of plant species were *Thalurania glaucopis* (*n* = 139), *Phaethornis eurynome* (n = 125), and *Chlorostilbon lucidus* (n = 104). The largest number of plant species recorded in our study (199 species or 63.78%) belonged to the group of ornithophilous plants. Meanwhile, 34.29% (107 species) of species were determined as non-ornithophilous, and 1.92% (six species) were categorized as undetermined.

The connectance of the hummingbird-plant networks ranged from 0.21 to 0.57 (mean 0.33 ± SD 0.09). Meanwhile, the modularity of the networks ranged from 0.16 to 0.55, with an average value of 0.36 (± 0.10). There was no effect of the proportion of ornithophilous species on the connectance and modularity of the networks (Table 1). Similarly, the connectance and modularity of the networks were not affected by network size.

Table 1. Results of the models (GLMs) showing the effects of the proportion of ornithophilous plant species (%) and network size on the topological descriptors (connectance and modularity) of Neotropical hummingbird-plant networks

Response variables	Explanatory variables	*d.f.*	Sum. Sq.	Mean. Sq.	*F*	*P*
Network connectance	Proportion of ornithophilous plant species	1	0.002	0.002	0.307	0.584
	Network size	1	0.012	0.012	1.852	0.187
Network modularity	Proportion of ornithophilous plant species	1	0.012	0.012	1.678	0.209
	Network size	1	0.015	0.015	2.130	0.159

The similarity of interactions among plant species differs significantly between groups of ornithophilous and non-ornithophilous plant species ($\chi^2 = 7.49$, $p = 0.006$; Table 2). We found higher interaction similarity for ornithophilous plant species compared to non-ornithophilous ones

(Fig. 2). However, no differences were observed in the degree and specialization of interactions between ornithophilous and non-ornithophilous plant species.

Table 2. Results of models (GLMMs) evaluating the effects of plant groups (ornithophilous plants and non-ornithophilous plants) on the response variables (degree, specialization, and similarity) of plant species in Neotropical hummingbird-plant networks. The chi-square and P values represent the regression coefficients of the overall model

Response variables	Model	Parameters		
Degree	Randon effects	Groups	Variance	Std.Dev.
		Plant species	0.896	0.946
		Residuals	2.663	1.632
	Fixed effects	Explanatory variables	Chi-square	p
		Plant group	1.131	0.288
Specialization (*d'*)	Randon effects	Groups	Variance	Std.Dev.
		Plant species	0.001	0.024
		Residuals	0.019	0.136
	Fixed effects	Explanatory variables	Chi-square	p
		Plant group	0.004	0.949
Similarity	Randon effects	Groups	Variance	Std.Dev.
		Plant species	0.008	0.089
		Residuals	0.030	0.173
	Fixed effects	Explanatory variables	Chi-square	p
		Plant group	7.490	0.006**

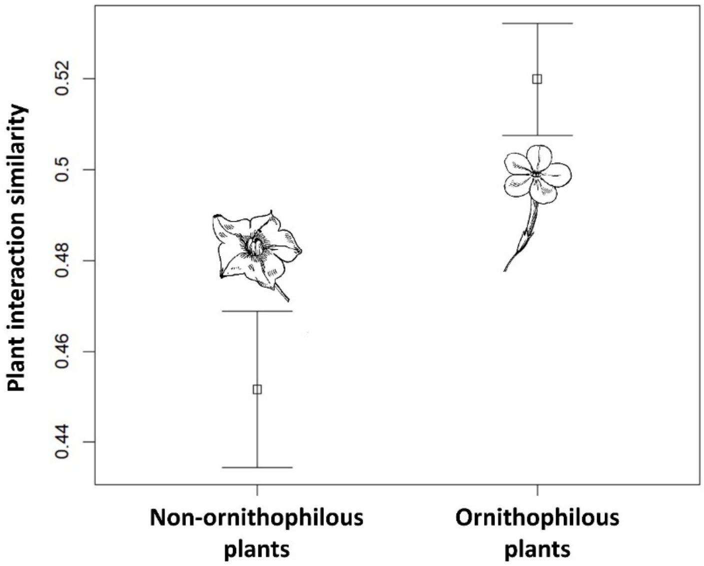

Fig. 2. Comparison of interaction similarity between groups of ornithophilous and non-ornithophilous plant species in Neotropical hummingbird-plant networks.

Our results also show that there are effects of hummingbird body structure on their interactions (Table 3). Beak size positively influenced both the degree ($\chi^2 = 4.086$, $p = 0.043$; Fig. 3) and specialization ($\chi^2 = 14.58$, $p < 0.001$; Fig. 4) of hummingbird species interactions. On the other hand, beak size did not affect interaction similarity. Meanwhile, body weight did not influence any of the analyzed structural parameters.

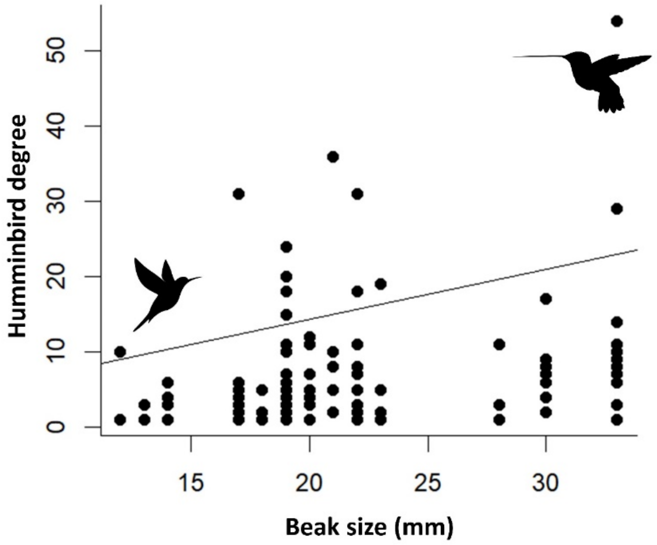

Fig. 3. Effect of beak size (mm) on the degree of hummingbird species in Neotropical hummingbird-plant networks.

Table 3. Results of models (GLMMs) evaluating the effects of beak size (mm) and body weight (g) on the response variables (degree, specialization, and similarity) of hummingbird species in Neotropical hummingbird-plant networks. The chi-square and P values represent the regression coefficients of the overall model

Response variables	Models	Parameters		
Degree	Randon effects	Groups	Variance	Std.Dev.
		Hummingbird species	0.841	0.917
		Residuals	62.460	7.903
	Fixed effects	Explanatory variables	Chi-square	p
		Beak size (mm)	4.086	0.043*
		Body weight (g)	0.173	0.678
Specialization (*d'*)	Randon effects	Groups	Variance	Std.Dev.
		Hummingbird species	0.000	0.012
		Residuals	0.024	0.156
	Fixed effects	Explanatory variables	Chi-square	p
		Beak size (mm)	14.587	< 0.001***
		Body weight (g)	0.166	0.684
Similarity	Randon effects	Groups	Variance	Std.Dev.
		Hummingbird species	0.012	0.111
		Residuals	0.040	0.201
	Fixed effects	Explanatory variables	Chi-square	p
		Beak size (mm)	2.194	0.139
		Body weight (g)	0.202	0.653

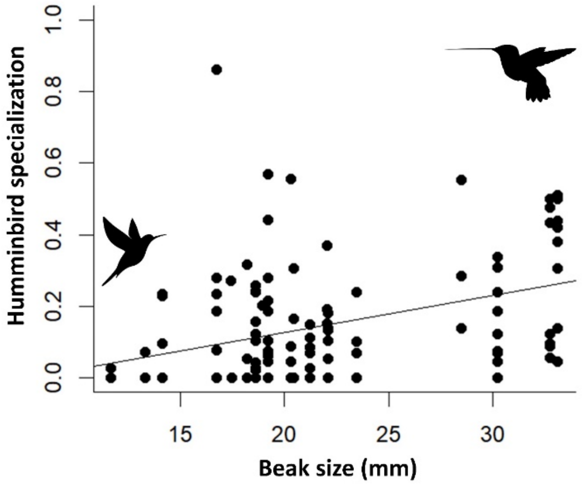

Fig. 4. Effect of beak size (mm) on the specialization of hummingbird species in Neotropical hummingbird-plant networks.

DISCUSSION

We did not find an effect of the dominance of ornithophilous plants on network-level topological descriptors (connectance and modularity), but our results show that both plant and hummingbird structural characteristics affect interaction descriptors at the species level in hummingbird-plant networks. For example, the similarity of interactions among plant species differed significantly between plant groups, with ornithophilous plant species showing higher interaction similarity. Additionally, our results show that hummingbird beak length influences specialization, with beak size positively affecting both the degree and specialization of hummingbird species interactions. These results suggest that morphological traits of both plants and hummingbirds can affect the specialization of interactions among these species.

The absence of an effect of ornithophilous plant dominance on network topology may be attributed to the high specialization (*i.e.*, low values of connectance and modularity) observed in these networks. This implies that, whether plant communities are dominated by ornithophilous species or not, the networks have low connectivity in the interactions (*e.g.*, Maglianesi et al. 2014; Claudino et al. 2021). The lack of effect regarding the dominance of ornithophilous plants on modularity may be related to the specialization of the ornithophilous plant group, resulting in high interaction similarity across the network. Thus, these intrinsic characteristics of the networks indicate that they have low connectance and low modularity regardless of the proportion of ornithophilous species in the networks.

Ornithophilous and non-ornithophilous plants differed significantly in their interaction similarity, with ornithophilous plants sharing a greater number of interactions (i.e., exhibiting higher similarity). According to Santamaría and Rodríguez-Gironés (2007), complementary traits directly affect species interaction. Thus, the set of traits present in the ornithophilous plant group (*e.g.*, diurnal anthesis, high nectar concentrations, flower color, corolla length, and curvature, among others) (Castellanos et al. 2004), which enhance attractiveness to hummingbirds, results in greater visitation frequency by pollinators (Forister et al. 2012). Therefore, hummingbirds tend to visit species of plants that are more morphologically similar, which can optimize resource use efficiency and/or reduce competition (Stiles 1981). Conversely, the lower similarity for non-ornithophilous plants may be related to the variation in functional and morphological traits of plants primarily adapted for insect pollination but occasionally visited by hummingbirds.

Our results indicate that certain morphological traits of hummingbirds (*e.g.*, beak length) drive higher specialization and a greater number of interactions, consistent with findings from other studies (*e.g.*, Maglianesi et al. 2014; Claudino et al. 2021). The increased number of interactions among hummingbirds with longer beaks is likely a result of morphological adaptation between the birds' beaks and the flower corolla, as species with longer beaks can interact both with small and larger corollas (Maglianesi et al. 2014). This trait enhances resource use efficiency, allowing hummingbirds to access nectar with less difficulty (Temeles et al. 2009). However, the lack of effect of body mass on the analyzed parameters is consistent with findings in the literature (*e.g.*, Lopez-Segoviano et al. 2018; Marquez-Luna et al. 2019). The body mass of hummingbirds is related to their dominance hierarchy, where larger hummingbirds tend to dominate, excluding smaller species from high-quality energy resources (Marquez-Luna et al. 2019). However, behavioral dynamics were not assessed in this study.

The largest number of hummingbird species compiled in our study belongs to the genus *Chionomesa*. It is worth noting that the genus *Chionomesa* was recently readopted to group the sister species *Chionomesa fimbriata* and *Chionomesa lactea* (see Pacheco et al. 2021), so the discussion presented here is based on publications about the former genus (*Amazilia*). This genus is composed of hummingbird species with a wide distribution in the Neotropical region. Studies indicate that species in the genus *Chionomesa* exhibit broad dietary and environmental plasticity, being capable of utilizing a diverse array of floral resources (Feinsinger 1976) and responding favorably to environmental changes and the presence of new resources. The species *Thalurania glaucopis* interacted with the highest number of plants in the study. This result may be related to the territorial behavior of the species as indicated by Machado and Semir (2006), in a study conducted in Atlantic Forest areas. Among the hummingbird species interacting with the highest number of plant species, the *Chlorostilbon lucidus* is a species with a wide geographical distribution and diversified diet, considered highly generalist regarding the resources they exploit (Machado 2009).

CONCLUSIONS

Our findings demonstrate that species-level interaction diversity tends to be more affected by morphological characteristics of plants and hummingbirds than topological descriptors at the network level. Thus, we show that the group of ornithophilous plants, sharing similar morphological traits, exhibits more ecologically similar interactions compared to plants with more variable morphology (non-ornithophilous plants). Additionally, our findings indicate that morphological variation among hummingbird species influences patterns of ecological specialization in the Neotropical region. Specifically, beak size was shown to be the most important trait influencing resource use efficiency, as it had a positive effect on the number and diversity of hummingbird interactions. This study represents the first systematic investigation evaluating the effects of plant characteristics on the specialization of Neotropical hummingbird-plant networks. Studies like this provide important insights into the functional factors shaping plant-pollinator networks.

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Authors' contributions: KCSC and WSA conceived and planned the study; KCSC compiled the database; KCSC, EVDF, and WSA performed data analyses; and KCSC, EVDF, and WSA wrote the manuscript.

Competing interests: KCSC, EVDF, and WSA declare that they have no conflict of interest.

Availability of data and materials: All of the authors agree with the publication of the data (supplementary material).

Consent for publication: All of the authors agreed to publish the paper.

Ethics approval consent to participate: Not applicable.

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