Implications of dominance hierarchy on hummingbird-plant interactions in a temperate forest in Northwestern Mexico

Gabriel López-Segoviano[1], Maribel Arenas-Navarro[2], Laura Edith Nuñez-Rosas[3] and, María del Coro Arizmendi[3]

[1] Escuela Nacional de Estudios Superiores (ENES) Unidad Morelia, Universidad Nacional Autónoma de México (UNAM), Morelia, Michoacán, México.

[2] Instituto de Investigaciones en Ecosistemas y Sustentabilidad (IIES), Universidad Nacional Autónoma de México (UNAM), Morelia, Michoacán, México.

[3] Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México, Tlalnepantla, Edo. México, México.

Corresponding author:

María del Coro Arizmendi

Laboratorio de Ecología, UBIPRO Facultad de Estudios Superiores Iztacala, Universidad Nacional Autónoma de México Av. de los Barrios 1, Los Reyes Iztacala, Tlalnepantla, Edo. México, México, CP 54090.

Email address: coro@unam.mx

Dio formato: Inglés (Estados Unidos)

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ABSTRACT

The structuring of plant-hummingbird networks can be explained by multiple factors, including species abundance (i.e. the neutrality hypothesis), matching of bill and flower morphology, phenological overlap, phylogenetic constraints, and feeding behavior. The importance of complementary morphology and phenological overlap on the hummingbird-plant network has been extensively showed, while the importance of hummingbird behavior has received less attention. In this work, we evaluated the relative importance of species abundance, morphological matching, and floral energy content~~, and phenological overlap~~ in predicting the frequency of hummingbird-plant interactions. ~~match, nectar energy, and phenological overlap in predicting the frequency of interactions.~~ Then, we determined whether the hummingbird species' dominance hierarchy is associated with modules within the network. Moreover, we evaluated whether hummingbird specialization (*d'*) is related to bill morphology (bill length and curvature) and dominance hierarchy. Finally, we determined whether generalist core hummingbird species are lees dominant in the community. We recorded plant-hummingbird interactions and behavioral dominance of hummingbird species in a temperate forest in Northwestern Mexico (El Palmito, Mexico). We measured flowers' corolla length and nectar traits and hummingbirds' weight and bill traits. We recorded 2272 interactions among 13 hummingbird and 10 plant species. The main driver of plant-hummingbird interactions was species abundance, consistent with the neutrality interaction theory. Hummingbird specialization was related to dominance and bill length, but not to bill curvature of hummingbird species. However, generalist core hummingbird species (species that interact with many plant species) were less dominant. The frequency of interactions between hummingbirds and plants was determined by the abundance of hummingbirds and their flowers, and the dominance of hummingbird species determined the separation of the different modules and specialization. Our study suggests that abundance and feeding behavior may play an important role in North America's hummingbird-plant networks.

Keywords: Ecological networks, aggressive dominance, morphological traits, David's score.

INTRODUCTION

Ecological network theory allows the comparison of interactions among highly diverse ecological communities and provides methods to quantify and compare interaction patterns across communities (Bascompte & Jordano, 2006, 2007a). Network structure can result from the simultaneous influence of species abundance and the constraints imposed by complementarity in species phenotypes, phenologies, spatial distributions, phylogenetic relationships, and sampling artifacts (Vázquez, Chacoff & Cagnolo, 2009). As a result, two main hypotheses have been postulated as the main factors modulating the occurrence of plant-pollinator interactions (Sazatornil et al., 2016). The neutrality hypothesis refers to the presumption that species abundances drive interaction frequencies, with more abundant species having more interaction partners and higher interaction frequencies than rarer species (Vázquez et al., 2007, 2009; Krishna et al., 2008; Vázquez, Chacoff & Cagnolo, 2009; Sazatornil et al., 2016; Simmons et al., 2021). In contrast, the forbidden links hypothesis postulates that network patterns are constrained by morphological trait-matching, phenologies, spatial distributions, and phylogenetic relationships of plants and pollinators (Jordano, Bascompte & Olesen, 2003; Vázquez, Chacoff & Cagnolo, 2009; Vizentin-Bugoni, Maruyama & Sazima, 2014; Sazatornil et al., 2016; Simmons et al., 2021). Thus, two species cannot interact if their phenologies do not overlap or do not match morphologically (Vázquez, Chacoff & Cagnolo, 2009; Vizentin-Bugoni, Maruyama & Sazima, 2014). For example, phenological overlap is an important driver of hummingbird-plant assemblages in some places in Mexico (Martín González et al., 2018; Chávez-González et al., 2020). In seasonal regions, for instance, phenological overlap may be particularly important because hummingbirds' migratory behavior leads to high seasonal turnover in species composition (Sonne et al., 2020).

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Trait matching between hummingbird's bill traits and flowers' corolla traits are an important driver of hummingbird-plant assemblages (Wolf & Stiles 1989, Maglianesi et al. 2014a, Sonne et al. 2019). This morphological matching reflects coevolutionary processes that are understood as increasing species' coexistence and decreasing competition for floral resources and pollinators (Wolf & Stiles, 1989; Cotton, 1998). In this context, specialization (species that interacts with a relatively small number of the available partners; Vázquez & Aizen 2005) and modularity (interactions organized in sets of interacting species or modules; Olesen et al. 2007) can be related to trait matching in hummingbird-plant networks (Sonne et al., 2020; Dalsgaard et al., 2021). However, matching between hummingbirds' bills and the flowers' corollas declines along latitudinal and altitudinal gradients, where strong seasonality in terms of temperature makes phenological overlap the main driver of hummingbird-plant interaction frequencies (Sonne et al., 2020). Accordingly, hummingbird communities of North America have less diverse bill morphology than communities in tropical environments (Stiles, 1981; Kodric-Brown et al., 1984; Brown & Bowers, 1985), leading to less specialized and less modular networks (Dalsgaard et al., 2011; Sonne et al., 2020).

In the Mexican hummingbird-plant assemblage, migratory behavior is apparently as important as hummingbird and flower morphological traits for structuring interactions at the community level (Martín González et al., 2018; Chávez-González et al., 2020). In addition to morphological restrictions, inter and intraspecific competition could be important factors for structuring hummingbird-plant networks (Feinsinger, 1976; Wolf, Stiles & Hainsworth, 1976; Maglianesi, Böhning-Gaese & Schleuning, 2014). For example, some studies have focused on the importance of dominance hierarchy in network structure and its relationship with core-periphery species (Dworschak & Blüthgen, 2010; Dáttilo, Díaz-Castelazo & Rico-Gray, 2014).

Dominance hierarchy among species can affect the visitation frequency of a hummingbird to a specific plant species (Wolf, Stiles & Hainsworth, 1976; López-Segoviano, Bribiesca & Arizmendi, 2018). The strength of species interactions plays an essential role in determining the specialization, modularity, and core-periphery status (Blüthgen, Menzel & Blüthgen, 2006; Dormann & Strauss, 2014; Martín González et al., 2020). Hence, dominance hierarchy could influence the structure of hummingbird-plant networks and determine hummingbird specialization (Ramírez-Burbano et al., 2022). The existence of a dominance hierarchy may lead to differential utilization of plants by hummingbirds depending on the hummingbird's place in the hierarchy and the caloric value of the plant's nectar, with the most dominant hummingbird species feeding mainly on plant species that offer more calories per flower (López-Segoviano, Bribiesca & Arizmendi, 2018). Therefore, we expect that the dominant hummingbird species can act as specialized and the less dominant species as~~ act~~ generalists in the hummingbird-plant network.

In a temperate forest located in northwestern Mexico—El Palmito, Sinaloa—14 hummingbird species coexist during fall and winter, when there is a high abundance of flower resources and several migratory hummingbird species arrives (López Segoviano 2018, López-Segoviano et al. 2018b, a, 2021). At El Palmito, the hummingbird community is structured by aggressive dominance relationships associated with the quality of floral resources (López-Segoviano, Bribiesca & Arizmendi, 2018). Therefore, in this work, we assessed the dominance hierarchy of hummingbird species and its influence on species' roles (specialization), as well as its association with module separation within the hummingbird-plant visitation network. To do this, we first evaluated the relative importance of species abundance, morphological match, and nectar energy~~, and phenological overlap~~ in predicting the frequency of interactions. Then, we determined whether the hummingbird species' dominance hierarchy is associated with modules within the network. Moreover, we evaluated whether hummingbird specialization (*d'*) is related to bill morphology (bill length and curvature) and dominance hierarchy. Finally, we determine whether generalist core hummingbird species are lees dominant in the community.

METHODS

Study Area

The study site is located in the Sierra Madre Occidental near the community of El Palmito, Concordia (23°35'20 N, 105°52'0 W) in Sinaloa, Mexico, between 1,800 and 2,200 m asl. The climate is temperate sub-humid, with an average annual precipitation of 1,247 mm (SMN, 2016). Vegetation is constituted mainly of pine-oak, oak-pine, and pine forest, cloud forest, and riparian and secondary vegetation (Ávila-González et al., 2019). Fieldwork was conducted from 10 November 2010 to 24 February 2011 in a 300 ha area presenting a mixture of these vegetation types. The largest number of hummingbird species and floral resources are present in El Palmito during the fall/winter season (López Segoviano, 2018).

Hummingbird interactions

The quantitative hummingbird–plant interaction network was constructed based on observations of legitimate visits (when hummingbirds contacted the flowers' reproductive structures). We considered the number of visits to be a measure of the strength of the interactions. A visit was defined as when a hummingbird probed at least one flower on an individual plant species (Maruyama et al., 2019). We quantified the visitation rate and interactions among hummingbirds by conducting observations at a distance of ~8 m from the plant species (following Cotton 1998). We observed 338 hours of hummingbirds visits to ten plant species (*Salvia elegans*, *S. gesneriiflora*, *S. iodantha*, *S. mexicana*, *Cuphea watsoniana*, *C. pinetorum*, *Loeselia mexicana*, *Cestrum thyrsoideum*, *Castilleja arvensis* and *Agave inaequidens* subsp. *barrancensis*). The number of observed hours for each plant species was proportional to its abundance in the study area (described below). ~~Behavioural~~Behavioral observations were performed daily by two observers at one-hour intervals between 07:00 and 15:00 h, recording the hummingbird species, visitation to flowers, and the outcomes of aggressive interactions between hummingbirds. We considered aggressive interactions when hummingbird chase, vocalize and attack other hummingbirds (Kodric-Brown et al., 1984; Cotton, 1998; Camfield, 2006). We identified the winner of an aggressive interaction as the hummingbird that returned to feed or perch after it had successfully defended and/or chased off another hummingbird from a floral patch (Justino, Maruyama & Oliveira, 2012).

Hummingbird and flowers ~~phenology and~~ abundance

To evaluate the ~~phenology and~~ abundance of hummingbirds and the flowers they visited, we counted hummingbirds in fixed-radius plots (25 m radius) and flowers along transects measuring 40 m in length and 5 m in width within each fixed-radius plot (López-Segoviano et al. 2018a). We established 20 plots separated by at least 188 m, which were fixed and distributed to represent the heterogeneity of the study site (López-Segoviano et al. 2018a). During 10 min, two observers identified and counted all hummingbirds visually or acoustically detected in a plot (Tinoco, Santillán & Graham, 2018); when the bird survey was finished, we counted all flowers in a transect. We excluded hummingbirds flying over the fixed-radius plot to avoid an

Comentado [AMf1]: Did you consider time in your dominance data? I just saw one interaction matrix without any time data. What data did you use for the elo-rating method? Please add raw data!

Comentado [AMf2]: If a hummingbird vocalizes and the others don't leave, that means the hummingbird that vocalize lost the interaction? How did you handle this type of behaviors?

Comentado [AMf3]: Did you have a hummingbird defending the flower patch? Did you consider the interaction of these individual repeatedly with others? This individual represents the total of the species or it was only that VERY aggressive individual?

Comentado [AMf4]: How did you know it was the same individual? Or did you consider also when it chased the other individual without caring if that individual came back?

overestimation of hummingbird abundance. All plots and transects were sampled every ten days from 12 November to 20 February in 2010–2011, resulting in 11 samples.

Comentado [AMf5]: Nice!

Hummingbird and flowers traits

We measured bill morphological traits (bill length and curvature) in live-caught hummingbirds and museum specimens housed at the Museum of Zoology ‘Alfonso L. Herrera’ (MZFC, UNAM) and Colección Nacional de Aves (Instituto de Biología, UNAM). Three standard mist nets (12 x 3 m) were placed near flowering sites to capture hummingbirds during fieldwork. Mist nets were operated for an eight hour period beginning at sunrise during four days in each sampling period. Ten sampling periods were conducted from 12 November 2010 to 26 February 2011. Following Maglianesi et al. (2014a), we measured bill length and curvature, since these morphological traits have been found to affect plant–hummingbird interactions. Bill length (mm) of each captured individual was measured using a calliper, and bill curvatures (°) was calculated with the angle tool using ImageJ software (http://rsbweb.nih.gov/ij/) from lateral photographs from each individual.

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We measured flower morphology (corolla's length, diameter, and curvature) and nectar characteristics (concentration, volume, and calories) of plant species visited by hummingbirds (Maglianesi et al., 2014). To calculate corolla curvatures (°), we used the same method of bill curvature. We quantified the mean sugar production per flower for each species by measuring the nectar produced and sugar concentration from recently opened flowers that were bagged for 24 h (Tinoco, Santillán & Graham, 2018). Nectar was extracted using microcapillary tubes, and nectar concentration was measured using a portable refractometer (0–32 Brix). Calories produced per flower was calculated by multiplying nectar volume (µL) by sugar concentration (mol) by 1.34, as proposed by Stiles (1975). We calculated mean values for each of the ten plant species using 11–134 individuals (depending on their abundance).

Dominance hierarchy

We calculated the hummingbird species' dominance hierarchy at El Palmito using David's score (Ds = $w + w^2 - l - l^2$). This score reflects the proportion of wins by species i in its interactions with species j, as $w + w^2 - l - l^2$, where w is the number of i’s wins, l is i’s losses, $w^{(2)}$ is the wins of species defeated by i, and $l^{(2)}$ is the losses of species to whom i lost (David, 1987; de Vries, 1998). This index for ranking dominance was designed for an incomplete data matrix, with paired comparisons in which not all species compete against each other (David, 1987). The resulting David's scores indicate the dominance rank of each hummingbird species within the interspecific interaction matrix (López-Segoviano, Bribiesca & Arizmendi, 2018), in this case, 13 hummingbird species.

Like David's score, Elo-rating has been used to assess the dominance hierarchies of the hummingbirds previously (Márquez-Luna et al., 2022), and this two methods allow us ratings parametric statistical testing (Sánchez-Tójar, Schroeder & Farine, 2018). In recent years, Sánchez-Tójar et al. (2018) added quantifying the uncertainty of an inferred dominance hierarchy, and Neumann and Fischer (2022) incorporated the Bayesian approach to estimate Elo-rating dominance hierarchies. The original Elo-rating method was established by Elo (Elo, 1961),

Comentado [AMf6]: This method is a method for the sequential estimation of dominance strengths, so you need time data. Do you have this?

Con formato: Sangría: Primera línea: 1,25 cm, Interlineado: sencillo where the rating of the contest's winner is increased by an amount that depends on the chance of winning: the amount is negligible if the chance of winning is high vice versa (Albers & De Vries, 2001). Also, the order in which the contests were held affects the inference of the contestants' dominant rank since after knowing each contest's result, the contenders' score is updated (Márquez-Luna et al., 2022). The Elo-rating calculation procedure assumes that the chance of A winning from B is a function of the difference in the current ratings of the two contestants (Albers & De Vries, 2001).

$$pA=1/(1+\exp(-0.01(EloA-EloB)))$$

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where pA is the probability that the species A wins, while $EloA$ is the punctuation of the species A before the contest, and $EloB$ indicates the punctuation of species B before the contest. Neumann and Fischer (2022) implemented a Bayesian framework for Elo-rating called STEER (Steepness estimation with Elo-rating), which captures uncertainty on multiple levels: first, the uncertainty arising from the sequence itself, that is, by randomizing the order in which interactions are considered; second, from the actual rating process, that is, using Bayesian estimates of k and start ratings. The new method is based on the following: A has the highest rating among the four individuals, and we can calculate A's expected winning probabilities with the three remaining individuals (Neumann & Fischer, 2023). Since A's rating is the highest rating of all individuals, all its winning probabilities are larger than 0.5 and turn out to be all larger than 0.8 (Neumann & Fischer, 2023). We used an interaction matrix (477 interactions between 13 species) to perform~~ant~~ the analysis with 20 randomized sequences and 2000 iterations with the function elo_steepness_from_matrix of the R package EloSteepness (Neumann, 2022)~~.~~

Comentado [AMf7]: This method gives you the certainty of the whole dominance hierarchy. I recommend to use a method that gives you the dominance certainty per species, especially because you have a matrix with multiple zeroes (which is expected in a community interaction matrix). I recommend to use the Bayesian method of Adams (2005) and the dominance certainty method (Cowan et al. 2022)

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Network Analysis

Specialization

To calculate the degree of specialization (*d'*) of hummingbirds and plant species within the interaction network, we used the function "*specieslevel"* in the *bipartite* package (Blüthgen, Menzel & Blüthgen, 2006; Dormann, Gruber & Fründ, 2008). The d' value is derived from the Kullback-Leibler distance; it measures the deviation of the actual interaction frequencies from a null model that assumes that all partners interact in proportion to their availability (Blüthgen, Menzel & Blüthgen, 2006). The *d'* value ranges from 0 for the most generalized to 1 for the most specialized species (Blüthgen, Menzel & Blüthgen, 2006). The d' values were weighted by total interaction frequencies of hummingbirds (square root transformed) following Maglianesi et al. (2014a).

Core-periphery

To determine the hummingbird species' core and periphery roles within the interaction network, we used the function "*CPness"* in the *econetwork* package (Miele et al., 2020; Martín González et al., 2020; Miele, Ramos-Jiliberto & Vázquez, 2020). The *CPness* function displays a matrix of core-periphery structure, and there is a species ordering such that interactions are distributed in an L-shape composed of four blocks of varying connectance (see Martín González et al. 2020, Miele et al. 2020b). The core-periphery species was determined by *CPness*=(E11+E12+E21)/E, where

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Eij is the number of interactions (edges) or the sum of weights for each block (Eij for block ij) or for the entire network (E) (Miele et al., 2020; Martín González et al., 2020).

Modularity

To calculate the modularity (*Q*) within the network we used the Beckett algorithm (DIRTLPAwb+) for weighted (quantitative) bipartite networks (Dormann & Strauss, 2014), for maximized weighted modularity in bipartite networks (Beckett, 2015). The modularity (*Q*) measures aggregated sets of interacting species within the network, ranging from 0 to 1 (Dormann & Strauss, 2014). Modularity values are highest when each module is isolated from the rest of the network (Beckett, 2015). We used the number of Markov chain Monte Carlo (MCMC) moves to yield no improvement before the algorithm stops set to 10^7 steps (Dormann & Strauss, 2014). Higher *Q* values indicate that the data support the division of a network into modules. Following Maruyama et al. (2014), we performed 50 independent runs and retained the module conformation with the highest *Q* value. Because the algorithm is stochastic, the module arrangement can vary between each run, so we evaluated whether the *Q* value of each network was different than expected by chance, performing a null model (“Patefield algorithm”) for *Q* values with 100 randomly generated network replicates using the observed species richness and interaction heterogeneity. We used the Q values in the randomizations to calculate the z-score, which is the number of standard deviations a datum is above the mean of the 100 randomized networks (Maruyama et al., 2014).

Constructing and contrasting interaction probability matrices

To evaluate which factors contributed to the structure of the observed flower-hummingbird interactions, we constructed interaction probability matrices and used the likelihood approach proposed by Vázquez et al. (2009) and later modified by Vizentin-Bugoni et al. (2014). We built an observed matrix (O) with the total number of interaction plant-hummingbird events detected where rows corresponded to plant species (*i*) and columns to pollinators (*j*). Additionally, we constructed four probability matrices based on ~~phenological overlap (F),~~ morphological match (M) as a forbidden link model, abundance (A) as a neutrality model, and caloric value (C). ~~The probability matrix based on phenological overlap (F) contained the 11 sampling sessions in which each plant and hummingbird co-occurred.~~ The probability matrix based on morphological match (M) was based on hummingbird bill length and curvature and flower corolla length and curvature, following Sonne et al. ~~considering the interaction possible (1) if a given hummingbird species had a bill length (+ tongue) equal~~(~~Sonne et al.,~~ 2019) ~~to or longer than the corolla length and not possible (0) otherwise. We added 70 % to the bill's total length to account for the tongue, since hummingbirds can extract nectar efficiently when extending their tongue beyond the bill by about 70 % of the bill length (Grant & Temeles, 1992)~~: first standardizing all trait variables to zero mean and unit variance, second, the morphological match was calculated as the Euclidean distance in traits between each hummingbird–plant pair. Then, we inverted the values of the Euclidean distance matrix using Excel's MINVERSE function so that species with closed matches had higher values and *vice versa*.~~.~~ The probability matrix based on abundance (A) contained flower abundance per plant species and the abundance of hummingbird species

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recorded in the plots. Each flower abundance per plant species was multiplied by the abundance of each hummingbird species to generate a matrix representing the product of all plant and pollinator abundances (Vizentin-Bugoni, Maruyama & Sazima, 2014). The caloric value probability matrix (C) was based on the calories produced as nectar per flower multiplied by average number of flowers for each plant species combined with the hummingbird's weight as proposed by Maruyama et al. (2014). They combine the hummingbird weight with nectar availability to incorporate species-specific differences among hummingbird species in the probability of the interactions (Maruyama et al., 2014). Based on the rationale that larger hummingbirds have a higher probability of interacting with plants providing higher rewards due ~~to~~ excluding smaller hummingbirds through aggressive behavior (Maruyama et al., 2014).

We also constructed probability matrices with all the possible combinations (i.e. AC, MA, ~~FM, F~~MC, and ~~F~~MAC) and normalized all probability matrices by dividing each cell by the matrix sum (Vizentin-Bugoni, Maruyama & Sazima, 2014). For example, the cell values in abundance (A) matrix were normalized by dividing each cell by the matrix sum such that its elements totaled one, resulting in a probability matrix A (Vizentin-Bugoni, Maruyama & Sazima, 2014). We evaluate whether a probability matrix could predict the observed interactions by determining whether cells with higher probability in our models also had a higher number of interactions in the observed matrix (Vizentin-Bugoni, Maruyama & Sazima, 2014). We used the difference in Akaike's Information Criterion (ΔAIC) to compare the predictive ability among models. ΔAIC is the value obtained by subtracting the best-fitting AIC from the best-fitting AIC of each model (Vázquez, Chacoff & Cagnolo, 2009; Vizentin-Bugoni, Maruyama & Sazima, 2014). We considered that a model matrix better predicted the observed matrix when it has a smaller AIC value, and models with ΔAIC <14 were considered equivalent (Burnham, Anderson & Huyvaert, 2011).

Statistical Analysis

To examine if the hummingbird and plant species were grouped into modules and which are the most important traits, we performed a principal component analysis (PCA) for each group. The first PCA was done with the hummingbird traits (David´s score, weight, bill length, and curvature) by species and a second with the floral traits (nectar volume, concentration and calories, and corolla length, width, and curvature) by species. To evaluate whether hummingbird species specialization (*d'*) was related to the dominance hierarchy, we performed a linear regression between the hummingbirds' dominance hierarchy (Ds and Elo-rating) and their degree of specialization (*d'*). Also, we evaluated the relationship between bill length and curvature with the degree of specialization (*d'*). We performed all analyses in R software version 4.2.3 ~~3.6.3.~~ (R Core Team, 2023).

Comentado [AMf8]: Again, please use the dominance hierarchy just with the species with high dominance certainty. If not, you may be assuming dominance relationships.

RESULTS

We recorded 2 272 interactions among 13 hummingbird species and 10 plant species (Table S1). The best predictor model for the hummingbird-plant interactions was the abundance (A) matrix, followed by the combination between the abundance (A) and ~~morphology~~ caloric (C~~M~~) matrices (Fig. 1).

The agonistic interaction network (477 interactions between 13 individuals) has 36.7 interactions per individual, 6.1 interactions per dyad, and 0.551 proportion of unknown relationships. The credible interval (89 %) was between 0.81 and 0.87, and the mean steepness was 0.84 (SD = 0.02). Both ratings evaluate that Rivoli's Hummingbird (*Eugenes fulgens*), Mexican Violetear (*Colibri thalassinus*), and Blue-throated Mountain-gem (*Lampornis clemenciae*) were~~are~~ the more~~st~~ dominant in the community (Table 1).

Comentado [AMf9]: They are identified? How do you know they are the same individuals?

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We found a low modularity value of the hummingbird-plant network ($Q = 0.201$) that was different from the null model when compared to the randomized differences of Q values (Z test, P-values > 0.05). We found three modules: the first module contained the most dominant hummingbird species (Rivoli's Hummingbird ~~*Eugenes fulgens*~~, and Blue-throated Mountain-gem ~~*Lampornis clemenciae*~~), which interacted mainly with *Agave inaequidens* flowers (Fig. 2 and Table 1). The second module contained three dominant hummingbirds (Berylline Hummingbird *Saucerottia beryllina*, Violet-crowned Hummingbird *Ramosomyia violiceps*, and Mexican Violetear *Colibri thalassinus*), and three less dominant hummingbird species (Ruby-throated Hummingbird *Archilochus colubris*, Costa’s Hummingbird *Calypte costae*, and Broad-billed Hummingbird *Cynanthus latirostris*) interacting mostly with *Cestrum thyrsoideum* flowers (Fig. 2 and Table 1). The third module contained five less dominant hummingbird species (White-eared Hummingbird *Basilinna leucotis*, Bumblebee Hummingbird *Selasphorus heloisa*, Calliope Hummingbird *S. calliope*, Rufous Hummingbird *S. rufus*, and Broad-tailed Hummingbird *S. platycercus*) that interacted mainly with flowers of *Salvia* species (Fig. 2 and Table 1).

The PCA with hummingbird traits and the Ds showed that the first two components of the PCA explained 95.9 % of the total variance. The first axis (PC1) explained 73.8~~75~~ % of the variance and was related to the Ds (with the highest contribution; Table S2). The second axis (PC2) explained 22.2~~15~~ % of the variance and was related to bill curvature (with the highest contribution) and bill length (Fig. 3A~~a~~). ~~The most dominant hummingbird species that belonged to module one were located in the positive quadrant of PCA1 and negative of PC2~~ (Fig. 3a). The second PCA with hummingbird traits and the Elo rating showed that the first two components of the PCA explained 94.6 % of the total variance. The first axis (PC1) explained 72.2 % of the variance and was related to weight (with the highest contribution; Table S2). The second axis (PC2) explained 22.2 % of the variance and was related to bill curvature (Fig. 3B). The more~~st~~ dominant hummingbird species in PCA1 and PCA2 that belonged to module one were located in the positive quadrant of PC1 and negative of PC2 in both PCA´s. The third ~~second~~ PCA with the floral traits (Fig. 3C) showed that the first two components of the PCA explained 71.97 % of the total variance (Table S3). The first axis ~~(PC1)~~ explained 52.13 % of the variance and was related to nectar volume (with the highest contribution) and sugar concentration (brix). The second axis ~~(PC2)~~ explained 19.84 % of the variance and was related to flower length (with the highest contribution) and width. ~~The flower species that belonged to module two were located in the positive quadrant of both axes~~. The species that make up module three were located in the positive quadrant of PCA1 and negative of PC2; while the species that belonged to module one and two were located dispersed in the rest of the quadrants (Fig. 3b).

We found that more specialized hummingbird species were Rivoli's Hummingbird, Violet-crowned Hummingbird, and Blue-throated Mountain-gem (Table S4). The species-level network specialization (*d'*) was related to dominance (-Ds: $R^2 = 0.78$, $F_{1,12} = 38.280$, $P < 0.001$ and~~;~~ Elo-rating: $R^2 = 0.71$, $F_{1,12} = 27.19$, $P < 0.001$; Fig. 4A and B), and bill length of hummingbird species ($R^2 = 0.81$, $F_{1,12} = 47.60$, $P < 0.001$; Fig. 4C), while bill curvature was not significantly associated ($R^2 = 0.12$, $F_{1,12} = 1.51$, $P = 0.244$; Fig. 4D).

White-eared and Rufous hummingbirds were identified as the generalist core species of the network (Fig. S1, and Table S4). These hummingbird species were the less dominant hummingbird species at this area (Table S4).

DISCUSSION

We found that one of the main drivers of plant-hummingbird interaction frequencies was each species' abundance, as proposed by the neutrality interaction theory (Vázquez et al., 2009). However, other studies have found that phenological overlap is the primary driver of the plant-hummingbird assemblage in Mexico (Martín González et al., 2018; Chávez-González et al., 2020). We do not include the phenological overlap to predict the frequency of hummingbird-plant interactions. The study covers part of the year when the blooming of flower resources influences the arrival of several migratory hummingbird species~~This may be explained by the fact that our research covers part of the year, when the arrival of several migratory hummingbird species influenced by the blooming of flower resources~~ (López-Segoviano et al., 2021). Thus, most flowering plants and hummingbirds coincide, and consequently, the phenological overlap between species is a less important ~~driver in predicting plant-hummingbird interaction frequencies~~. Sonne et al. (2020) proposed that morphological matching is a less important driver of plant-hummingbird interaction frequencies far from the equator. Biogeographical and evolutionary history has an important role in patterns of trait-matching in hummingbird–plant associations (Dalsgaard et al., 2021). North American hummingbird clades (Bees, Mountain Gems, and Emeralds) are less morphologically specialized than those of other clades in south America, such as the Hermits, Mangoes, and Patagonas, which have longer and more curved bills (Rodríguez-Flores et al., 2019).

A high degree of specialization in resource use produces modules (Dormann & Strauss, 2014). Our results indicate that hummingbird species' dominance status and plants' nectar volume were the main traits that explain the separation of species into modules. The top species in the dominance hierarchy fed mainly on *Agave inaequidens* flowers, which are among the most abundant at our study site flowering plant species, and forming flower patches with higher energy availability (López-Segoviano, Bribiesca & Arizmendi, 2018). Thus, the modules are aggregated in sets of interacting species, reflecting that these species are linked more tightly together than species in other modules (Olesen et al. 2007, Dormann & Strauss 2014). In Mexico, biogeographic origin is one of the main factors that separates hummingbird modules at the national scale (Martín González et al., 2018), and along an altitudinal gradient at regional scale the distribution of plant and hummingbird species separate modules (López-Segoviano et al., 2021).

Some studies propose that dominant ~~behaviour~~behavior can influence the preferences of hummingbird species for floral resources (Stiles & Wolf, 1970; Sandlin, 2000; Maglianesi et al., 2014; López-Segoviano, Bribiesca & Arizmendi, 2018), which can affect the rates of flower visitation that may be reflected in the hummingbird-plant network. Our study revealed that hummingbird species' specialization was related to their place in the dominance hierarchy of the hummingbird community, in contrast to the findings of Ramírez-Burbano et al. (2022), where the dominance hierarchy had a negligible effect on determining hummingbird specialization in the visitation network of feeders and plants in gardens. The authors attribute the lack of influence of the dominance hierarchy on specialization in that even non-dominant species can use the best food resources as territory intruders (Justino, Maruyama & Oliveira, 2012; Ramírez-Burbano et al., 2022). In addition, the hummingbird community of this study in Colombia is morphologically complex, with some non-territorial and specialized hermit species (Stiles, 1975; Feinsinger & Colwell, 1978). Consequently, morphological matching was the most important determinant of pairwise interactions (Ramírez-Burbano et al., 2022). It should be noted that in studies in the tropics, the non-territorial hermits were the most specialized species (Maglianesi et al., 2014, 2015). Hermits' complementary bill morphology allows them access to almost exclusive resources, at the same time as it provides plants the best vectors for their pollen (Stiles, 1975; Wolf & Stiles, 1989; Maruyama et al., 2014; Maglianesi et al., 2014). In the temperate forest in Mexico, hummingbird species do not have exclusive resources; rather, they defend the floral resources they depend on for energy (Sandlin 2000, Rodríguez-Flores & Arizmendi 2016, López-Segoviano et al. 2018b). Aggressive dominance allows the dominant species to access the best food resources (Stiles & Wolf, 1970; Wolf, Stiles & Hainsworth, 1976; Sandlin, 2000; Rodríguez-Flores & Arizmendi, 2016; López-Segoviano, Bribiesca & Arizmendi, 2018). Hence, the most dominant hummingbird species have the strongest interaction with the plant species whose flowers provided the highest energy floral reward, *A. inaequidens* (López-Segoviano et al. 2018b).

It has been reported that hummingbirds' bill traits influence their degree of specialization in the hummingbird-plant interaction networks (Dalsgaard et al., 2009; Maglianesi et al., 2014, 2015; Tinoco et al., 2017; Sonne et al., 2019; López-Segoviano et al., 2021). Our results showed that hummingbirds' d' was related to bill length but not bill curvature. ~~This is contrary to the findings of~~ Maglianesi et al. (2014a) in Costa Rica~~,~~ found~~where~~ that bill curvature has an important influence on hummingbirds' degree of specialization as well as resource use and niche partitioning in hummingbird assemblages (Maglianesi et al., 2014, 2015). However, in Northwestern Mexico, the bill curvature of the hummingbird community is less than in tropical regions. For example, in this study, Mexican violetear had the greatest curvature, which can be very low compared to some species in tropical regions (i.e., Hermits). Meanwhile, in our study the longer-billed and more specialized hummingbird species (Rivoli's Hummingbird and Blue-throated Mountain-gem) preferred to feed on *A. inaequidens* flowers. These flowers have generalized floral traits with a small and straight corolla that is morphologically accessible to all hummingbird species at the study site. Morphologically specialized hummingbirds should avoid visiting plants with generalized floral morphologies (i.e. short, straight floral corollas) to prevent competition with hummingbirds with generalized morphologies (Maglianesi et al., 2015; Sonne et al., 2019). In our study, the dominant species took the best resources by aggressively competing for them, regardless of floral traits. It seems that in this case, it is more important for hummingbirds to forage on flowers with high nectar volume than flowers with well-matched morphology (Stiles, 1976).

Our results showed that the core generalist species (White-eared and Rufous hummingbirds) were the less dominant hummingbird species. Contrary to what was described in an ant-plant network (Dáttilo, Díaz-Castelazo & Rico-Gray, 2014), in which the central core ants are generalists and are competitively superior to peripheral and submissive ant species. White-eared and Rufous hummingbirds had a medium bills and were the most abundant hummingbird in the region (López-Segoviano et al., 2018). In other hummingbird-plant networks, the hummingbird species' generalization was described as~~in~~ related~~ion~~ to their abundance (Simmons et al., 2019; Arizmendi et al., 2021; López-Segoviano et al., 2021). Likewise, the core generalist species are mainly associated with the abundance of the species (Miele, Ramos-Jiliberto & Vázquez, 2020; Vitorino et al., 2022).

Although dominance hierarchy shows some associations with assemblages between plants and hummingbirds (López-Segoviano, Bribiesca & Arizmendi, 2018), this pattern does not reflect in the interaction frequencies. The plant-hummingbird interaction frequencies were driven by abundance-based processes (neutral hypothesis; Vázquez et al. 2009a), and dominance hierarchy may act as forbidden links. In this sense, Sazatornil et al. (2016) propose that the role of niche-based processes that structure interactions between mutualistic partners can be much more complex than previously established. In the study region, the three plant species in which the interactions are concentrated were also the more abundant. Therefore, many of the interactions were focused on these plant species, and even the two more abundant hummingbird species (with lower dominance~~ species~~) visit the more abundant plant species with low caloric content. Future studies will help to clarify the contributions of the dominance hierarchy to the structure and assembly of hummingbird-plant communities by incorporating data from other sites and communities.

It is essential to highlight that this study includes a temporal window of hummingbirds and plants' possible interactions. The ecological conditions, such as forage availability and predation risk, can be ~~as ~~variable in time and~~s they are~~ across space (Mayor et al., 2009). Although we were able to record all of the hummingbird species that have been reported in the region (López Segoviano, 2018; López-Segoviano et al., 2021), the feeding behavior of hummingbirds and the structure of the network may change throughout the year (Márquez-Luna et al., 2018; Bustamante-Castillo, Hernández-Baños & Arizmendi, 2020), and the aggressive organization and specialization level of hummingbirds can vary depending on resource availability (Justino, Maruyama & Oliveira, 2012; Rodríguez-Flores & Arizmendi, 2016; Tinoco et al., 2017).

CONCLUSIONS

Species abundance was the main driver of interactions in the plant-hummingbird assemblage (in accordance with the neutrality hypothesis). This may be explained by the sampling period restricted the appearance of forbidden links and did not reflect the importance of phenological overlap. Within this network, aggressive dominance of hummingbird species determines the separation into three different interaction modules. Thus, the relationship between hummingbird species, and their level of aggressive dominance determine niche partitioning among species (López-Segoviano, Bribiesca & Arizmendi, 2018) and was reflected in the hummingbird-plant assemblages. Our results suggested that feeding behavior may play an important role in North America's hummingbird-plant networks. Aggressive dominance and bill length of hummingbird species seems to be determinants of the hummingbird specialization of the hummingbird-plant network. Further studies are needed in more diverse communities and throughout the year, including the role of feeding behavior as a variable in the hummingbird-plant network (i.e. Ramírez-Burbano et al. 2022). This study helps us understanding the importance of aggressive hummingbird behavior and the abundance of floral resources in the network of hummingbird-plant interactions.

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