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Geographical Patterns in the Architecture of Neotropical Flower-visitor Networks of Hummingbirds and Insects

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Geographical variations in environmental factors can affect species diversity and consequently influence the structure of interspecific ecological interactions. Relationships between flowering plants and animal flower visitors are among the most important ecological interactions and can structure and maintain ecological diversity in different environments. Additionally, many animal and plant species participate in these interactions, which shape the specific characteristics of these communities, in terms of both the responses of the interacting species involved and environmental differences. Therefore, in the present study we investigated geographical and environmental effects on the architecture of Neotropical flower-visitor networks of vertebrates and invertebrates. To this end, we used data regarding interaction networks available in the literature and constructed binary interaction networks of plants and plant-visitors (hummingbirds and insects) and tested the effects of altitude, latitude, vegetation type and number of plant families on the structure of these networks. In total, we analyzed 55 networks of flower-visitor interactions with 746 species of flower-visiting animals and 1,185 species of plants, totaling 5,463 distinct plant-animal interactions. In general, the architecture of flower-visitor networks varied along latitudinal and altitudinal gradients, with more pronounced effects for flower-insect networks in which latitude influenced network size, modularity, and nestedness, and altitude influenced network size and connectance. Flower-hummingbird networks in open vegetation (grassland) were more modular than networks in other environments. The number of plant families positively influenced the size of insect and hummingbird networks, and positively affected connectance and nestedness and negatively affected modularity in the flower-insect networks. So, the patterns we found indicate that plant-visitor interactions in flower-insect and flower-hummingbird networks are differently affected by geographical and plant-related factors, possibly due to the differences in taxonomic and functional groups involved in these interactions.

Key words: Bees, Ecological services, Plant-animal interactions, Pollination, Tropical ecology.

BACKGROUND

Interactions between flowering plants and animal flower visitors represent one of the most important biological interactions and have fundamental consequences for the evolution and maintenance of ecological diversity (Senapathi et al. 2015). Studies indicate that about 300,000 species of angiosperm plants are pollinated by animals (Ollerton et al. 2011) and in tropical regions all plant species have some type of

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dependence on their flower visitors in some ecological communities (Rech et al. 2016). Therefore, ecological networks formed by flowering plants and their visitors in the Tropics have proven to be species rich and have very complex interactions among species (reviewed in Vizentin-Bugoni et al. 2018). The consensus in the literature is that plant-flower visitor interactions are very specialized in tropical communities, as discussed in recent thematic reviews (Ollerton 2017; Vizentin-Bugoni et al. 2018). In plant-flower visitor networks, species can be defined as specialists when they have a low number of interactions, while those with a high number of interactions are defined as generalists (Carstensen et al. 2018). Nevertheless, the hypothesis that plant-visitor interactions are more specialized at low latitudes has rarely been tested (Ollerton 2017), and the results of these tests have generally been contradictory due to the idiosyncrasy of the limited taxonomic groups tested (*e.g.*, Olesen and Jordano 2002; Ollerton and Cranmer 2002; Biesmeijer et al. 2005).

The hypothesis that latitude and altitude can influence interactions is derived from the latitudinal and altitudinal gradients observed for species diversity (review in Hillebrand 2004; McCain and Grytnes 2010). A recent meta-analytical review corroborates the well-known pattern that the number of species diminishes from the equator towards the poles (Kinlock et al. 2018). There is also a general consensus that richness decreases with increasing elevation (McCain and Grytnes 2010). Latitude is expected to influence plant-visitor interactions because, in very diverse communities, species tend to have more narrow ecological niches (Hillebrand 2004; Brown 2014). In this context, in tropical latitudes there is a general expectation that species of flower-visiting animals frequent a low number of flower species and that each flowering plant receives few flower visitors (Vizentin-Bugoni et al. 2018). This high average species specialization means that plant-visitor networks at low latitudes have a loosely connected and very modular topology (Trøjelsgaard and Olesen 2013). A similar pattern is found for the altitudinal gradient, since considerable evidence indicates that communities at low altitudes tend to be more diverse and contain more specialized species (Cuartas-Hernández and Medel 2015). Despite the apparently clear patterns for latitudinal and altitudinal gradients in species diversity, studies on the effects of latitude and altitude on the structure of plant-visitor networks present contrasting results, both confirming (Trøjelsgaard and Olesen 2013; Cuartas-Hernández and Medel 2015) and contradicting expectations (Biesmeijer et al. 2005; Schleuning et al. 2012).

Plant-animal interactions also can be influenced by plant-related factors such as vegetation type and plant taxonomic diversity. For other ecological interactions, such as plant-herbivore networks, evidence shows that forest vegetation and open vegetation can differ significantly in the network structure (Araújo et al. 2020), which is related to the negative effect that the sclerophylly of open vegetation has on the palatability of plants for herbivores (Neves et al. 2010). For interactions between flowering plants and their visitors, the effects of the vegetation type are expected because the higher level of environmental severity in the open vegetation can generate a greater environmental filter for plant diversity (Kissling et al. 2008; Fründ et al. 2010; Laliberté et al. 2014), such as types of flowers. These environmental filters can also act on animal characteristics and restrict many interactions within plant-animal networks (Araújo et al. 2020). The taxonomic diversity of plants can also affect the structure of plant-flower visitor networks because each plant taxon (*e.g.*, plant family) tends to have plant species with functionally and morphologically similar flowers (Albor et al. 2019). Thus, the greater the diversity of plant families in the network, the greater the diversity and specialization of the interactions of floral visitors must also be (Albor et al. 2019). Both types of vegetation and the taxonomic diversity of plants are expected to vary geographically, given that at low latitudes in the Neotropical region landscapes tend to be dominated by tropical rain forests that are extremely rich in plant species and families (Iwasa et al. 1995).

Various groups of vertebrates and invertebrates act as flower visitors and pollinating agents in Neotropical environments (Vizentin-Bugoni et al. 2018). Insects, especially Lepidoptera (butterflies and moths) and Hymenoptera (bees), are the most diverse invertebrates that visit flowers in the Neotropical region, and indeed worldwide (Ollerton 2017). Estimates suggest that Brazil alone contains more than 26,000 species of lepidopterans and 3,000 species of bees (Lewinsohn et al. 2005). Among vertebrates, the most important group is birds, mainly the hummingbird family (Trochilidae), which host the largest number of Neotropical flower visitors (Ollerton 2017), with 86 species recorded in Brazilian territory (Ficher et al. 2014). In the literature regarding flower-visitor interaction networks, studies comparing different taxonomic groups of visiting animals at the macroecological scale are scarce (*e.g.*, Zanata et al. 2017) and no study has focused on vertebrates and invertebrates simultaneously.

In the present study, we investigated the geographical and environmental effects on the architecture of Neotropical flower-visitor networks of vertebrates and invertebrates. Thus, we compiled the interactions between flowers and their visitors in communities composed of hummingbirds and insects. We characterized the plant-visitor networks using the topological descriptors network size, connectance, modularity, and nestedness (Dormann et al. 2009). Network size is a measure of the number of species interacting in the network, and the connectance is a descriptor of the level of connectivity (*i.e.*, specialization) among these species (Antoniazzi et al. 2018). In turn, modularity and nestedness are measures of the modular (*i.e.*, occurrence of specialized subsets of interacting animals and plants) or nested (*i.e.*, species forming a single dense nest of interactions) arrangement of interactions between species within the network (Lewinsohn et al. 2006). Thus, we tested the following hypotheses: 1) plant-flower visitor networks are larger, less connected, more modular, and less nested at low latitudes; 2) altitude has a negative effect on network size and modularity and a positive effect on connectance and nestedness of plant-visitor networks; 3) plant-flower visitor networks of open vegetation are more specialized (*i.e.*, more diverse, less connected, less nested and more modular) than networks of forest vegetation; 4) plant taxonomic diversity has a positive effect on network size and modularity and a negative effect on connectance and nestedness of the networks; 5) plant-visitor networks composed of hummingbirds and insects have different response patterns because insects are more diverse in species and functional groups, and are expected to better reflect geographical and plant-related factors.

MATERIALS AND METHODS

Data collection

We compiled a comprehensive set of interaction data between flowering plants and their visitors in the Neotropics (Table S1). We used data from interaction networks available on the Interaction Web Database of the National Center for Ecological Analysis and Synthesis (www.nceas.ucsb.edu/interactionweb). Additional data were retrieved from the Google Scholar and Scopus databases using the following keywords: (plant*) AND (pollinator*) AND (floral visitors) AND (network* OR interaction*) AND (search OR list). The data search was carried out in December 2018 and all data available to date were included. We also carried out a search of the literature cited in macroecological studies on the flower-visitor interactions involving insects (Biesmeijer et al. 2005) and birds (Zanata et al. 2017).

The following criteria were adopted when determining which studies to include: (1) provision of at least a basic description of the study area, containing a geographical coordinate; (2) indication of the species (or morphospecies) of visitors to each species (or morphospecies) of plant; (3) the network had at least five species of plants and five species of flower visitors, totaling at least 10 species; and (4) at least 80% of the visitors were identified to the species level. The following data were extracted from the selected studies: geographical coordinates, altitude, country, type of vegetation and number of plant families.

Network measures

The compiled interaction data were used to build binary bipartite networks between flowering plant species and their visitor species (Figs. 1, 2). We did not use quantitative data regarding interactions because this information was missing for many networks. In order to describe the structure of flower-visitor networks, we used the following network descriptors: network size, connectance, modularity and nestedness. These network descriptors were adopted because they are commonly indicated to describe the architecture of binary bipartite networks (reviewed in Dormann et al. 2009) and they have been used in several recent studies investigating flower-visitor interaction networks (Cuartas-Hernández and Medel 2015; Zanata et al. 2017; Traveset et al. 2018; Zhao et al. 2019).

We calculated the network size by counting the total number of plants and animal species in each network (*i.e.*, the species richness). Network connectance was calculated as the ratio between the number of observed interactions and the number of possible interactions within the network (Dunne et al. 2002; Dormann et al. 2008). Connectance is an inverse measure of network specialization, and therefore greater connectance values imply lower network specialization (Araújo et al. 2015). To compute the network modularity, we used the bipartite modularity index Q (Barber 2007) through the DIRTLPAwb+ algorithm to detect network modules (Beckett 2016). Network nestedness was calculated using the Nestedness metric based on Overlap and Decreasing Fill (NODF) (Almeida-Neto et al. 2008). NODF accounts for the paired overlap and the decreasing fill of the matrix representing an interaction network, and its values range from 0 (perfectly non-nested) and 100 (perfectly nested). All networks were built and analyzed using the bipartite package in R (Dormann et al. 2008).

Data analyses

In addition to latitude and altitude, we used the number of plant families and type of vegetation as explanatory variables for the flower-visitor network descriptors. We used the number of plant families as a measure of taxonomic diversity. The number of plant families also is an indirect measure of sampling effort (because, to obtain networks with many plant families, more time and more sampling effort are required) and a proxy for the phylogenetic diversity in the network (since a positive correlation between the number of families and the phylogenetic diversity of plants is expected). Vegetation type was determined for each network according to the description given by the authors of the original studies. We categorized vegetation into three types based on the structure of the vegetation: grassland (vegetation predominantly composed of grasses and herbs, without canopy), savanna (vegetation with few trees, with open canopy) and forest (tree vegetation, with closed canopy).

We used generalized linear models followed by ANOVA to test the effects of latitude, altitude, type of vegetation and number of plant families on the descriptors of network structure (network size, connectance, modularity and nestedness). In order to control possible effects of network size on the network topology, we used network size as an explanatory variable in the models for connectance, modularity and nestedness (Dormann et al. 2017). Additionally, we performed post-hoc contrast tests to highlight the differences in the network descriptors among types of vegetation. We built different models for network descriptors of flower-hummingbird and flower-insect networks. The error distribution was assumed to be normal (Gaussian distribution) for all of the models. All statistical analyses were performed in R software (R Development Core Team 2020).

RESULTS

In total, we analyzed 55 networks of flower-visitor interactions (Fig. 1; Table S2) with 746 species of floral visiting animals and 1,185 species of plants, totaling 5,463 distinct plant-animal interactions. Of these, 28 networks were based on hummingbirds with 429 plant species, 57 animal species and 1,411 distinct interactions. There were 27 insect-based networks in total, comprising 787 plant species, 689 visitor species and 4,052 distinct interactions. Flower-hummingbird networks ranged from 12 to 774 interactions (128.5 mean ± 157.2 SD), while flower-insect networks ranged from 12 to 328 interactions (68.3 mean ± 77.6 SD). Among hummingbirds, the species that interacted with the largest number of plant species were *Chlorostilbon*

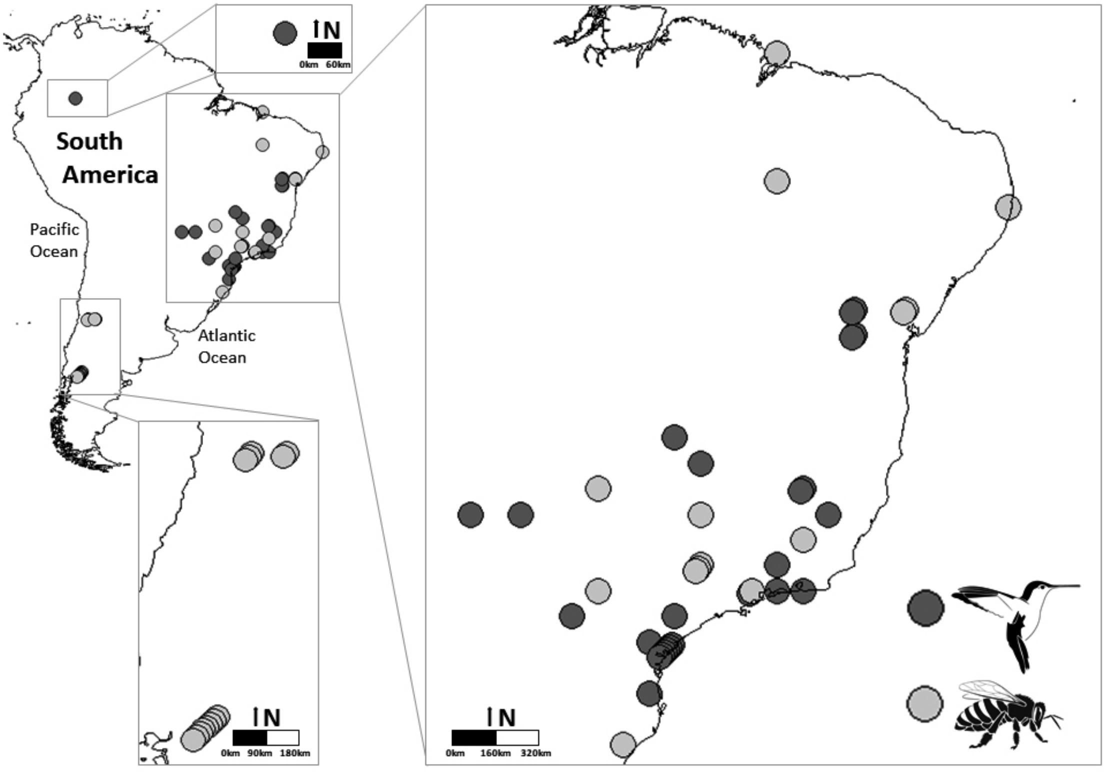

Fig. 1. Distribution of the 55 flower-visitor networks analyzed in this study. Dark gray circles represent flower-hummingbird networks and light gray circles the flower-insect networks. At this map scale, some flower-visitor networks are located so close together that they are indistinguishable.

lucidus Shaw, 1812 (n = 112); *Thalurania glaucopis* Gmelin, 1788 (n = 86); and *Colibri serrirostris* Vieillot, 1816 (n = 83). Regarding insects, nine orders of flower visitors were recorded (Coleoptera, Diptera, Hemiptera, Hymenoptera, Lepidoptera, Odonata, Orthoptera, and Thysanoptera). Bees interacted with the most plants of any insect group (Hymenoptera: Apidae), specifically *Apis mellifera* Linnaeus, 1758 (n = 343); *Trigona spinipes* Fabricius, 1793 (n = 262); and *Paratrigona subnuda* Schwarz, 1938 (n = 114).

The ranges of both latitude (0.04°S to 41.00°S) and altitude (5 to 3400 m) varied greatly between the networks analyzed. Likewise, different types of vegetation (grasslands, savannas, and forests) and a wide range of host plant families (1 to 56) were sampled in the compiled studies. The size of flower-hummingbird networks was positively affected by altitude (Fig. 3a), contrary to our expectations, and number of plant families (Fig. 3b), confirming our expectations (Table 1). As expected, the size of flower-insect networks was negatively affected by latitude (Fig. 3c, Table 2). On the other hand, the size of flower-insect networks was positively influenced by altitude (Fig. 3d) and number of plant families (Fig. 3e) (Table 2). The connectance of flower-hummingbird networks was not affected by any of the explanatory variables (Table 1), but the connectance of flower-insect networks was negatively influenced by altitude (Fig. 4a) and positively influenced by number of plant families (Fig. 4b) (Table 2), partially corroborating our hypothesis. Modularity in flower-hummingbird networks was affected only by vegetation type (Table 1). As expected, the networks of open habitats (grassland) were more modular than networks of other environments (Fig. 5a, Table 1). For insects, the network modularity had a positive relationship with latitude (Fig. 5b), and a negative relationship with number of plant families (Fig. 5c) (Table 2), contrary to our expectations. Concerning network nestedness, flower-hummingbird networks were not affected by any of the explanatory variables (Table 1), but flower-insect networks were negatively influenced by latitude (Fig. 6a) and positively influenced by number of plant families (Fig. 6b) (Table 2).

DISCUSSION

Our results reveal that the effects of latitude and altitude were more pronounced for flower-insect networks. The latitude negatively influenced network size, positively influenced modularity and negatively influenced nestedness, while altitude positively affected

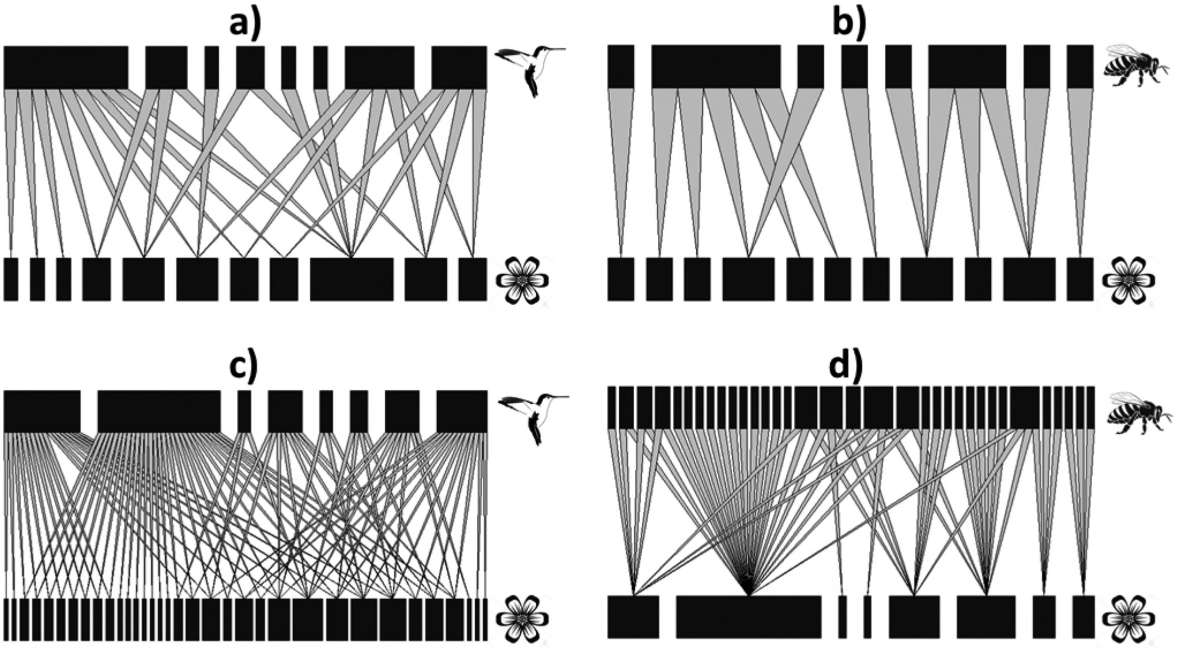

Fig. 2. Bipartite graphs showing the topological structure of examples of flower-visitor networks analyzed in this study. For each network, upper bars represent visitor species and lower bars represent flowering plant species. Bar thickness is proportional to the number of interactions of each species (drawn at different scales). a) flower-hummingbird network of Machado (2014); b) flower-insect network of Clemente et al. (2017); c) flower-hummingbird network of Lasprilla (2003); d) flower-insect network of Vázquez and Simberloff (2002) (network 5). Networks a and b have the same total number of species (network size) and the same number of species at each trophic level (plants and animals). Networks c and d have the same network size, although they have different numbers of species of plants and animals.

network size and negatively affected connectance for insects. These results corroborate recent studies indicating the geographical effects on the structure of plant-insect visitor networks (Cuartas-Hernández and Medel 2015; Kelly and Elle 2020). For flower-hummingbird networks, the only effect that we observed was the unexpected positive relationship between network size and altitude. In this context, the results observed in our study point in the opposite direction to what was expected, with lower network specialization at low latitudes and high altitudes. However, the patterns found indicate that plant-visitor interactions in flower-insect and flower-hummingbird networks are differently organized along latitudinal and altitudinal ranges. We also found that the taxonomic diversity of plants positively affected size, connectance and nestedness and negatively affected the modularity of flower-insect networks. On the other hand, flower-hummingbird network size was positively related to the taxonomic diversity of plants and was more modular in open habitats (grassland) than in the other vegetation.

Topological descriptors of flower-insect networks changed considerably with increasing latitude. The size of the networks (*i.e.*, the richness of animals and plants in the community) was negatively affected by latitude in the flower-insect networks. This finding is

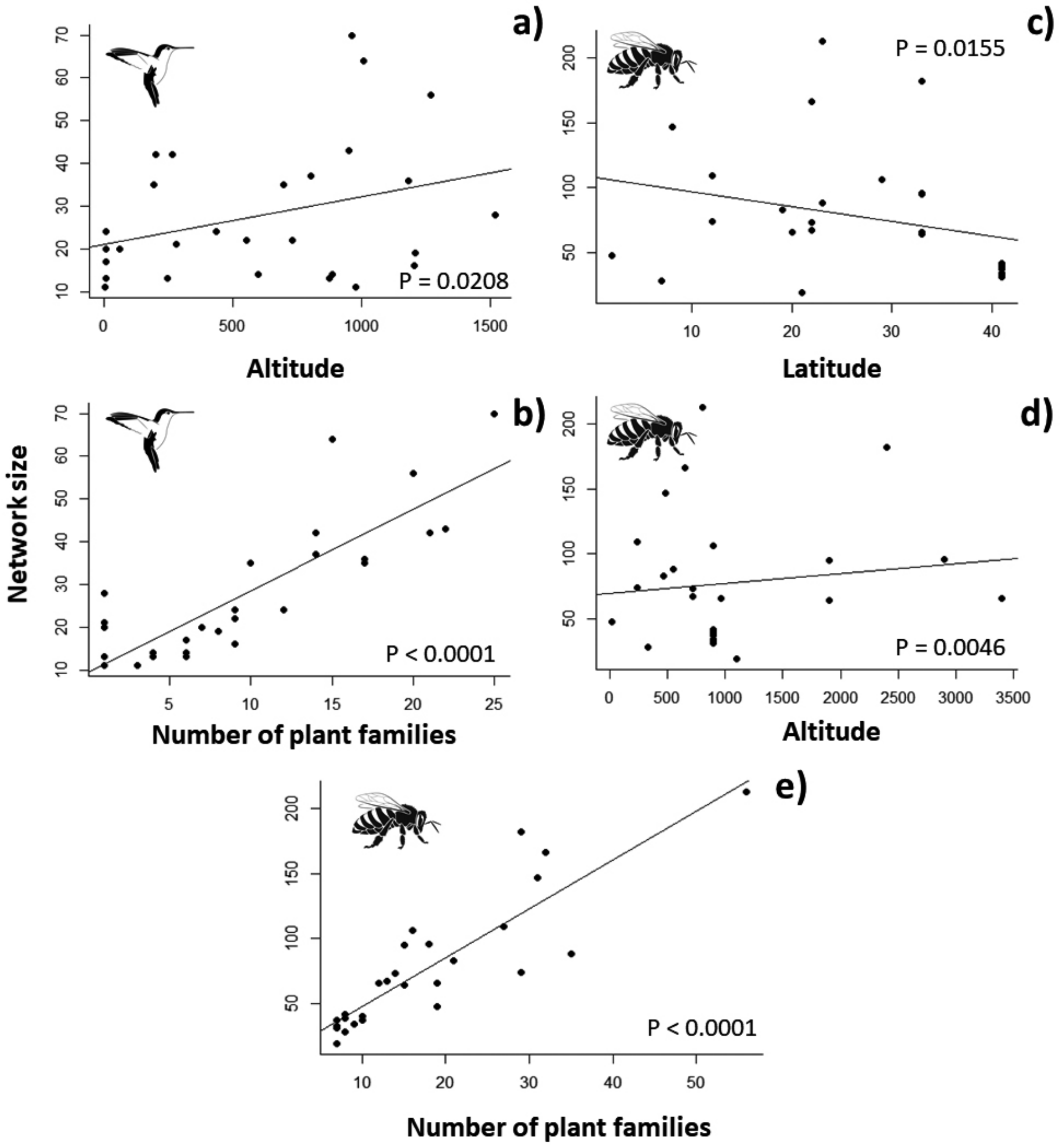

Fig. 3. Factors influencing the network size of flower-hummingbird and flower-insect networks.

in line with the well-documented pattern that species diversity decreases from the equator towards the poles (reviewed in Kinlock et al. 2017). However, latitude influenced modularity positively and nestedness negatively, contrary to our expectations and the pattern found in many previous studies (Olesen and Jordano 2002; Trøjelsgaard and Olesen 2013; Zanata et al. 2017). It is important to note that these results are not due to the dependence of modularity and nestedness on the size or connectance of the networks, as observed in other studies (Dunne et al. 2002; González et al. 2015), since in our study these parameters displayed the

Table 1. Generalized linear models of the effects of latitude, altitude, type of vegetation and number of plant families on the size, connectance, modularity and nestedness of Neotropical flower-hummingbird networks

Response variable	Explanatory variable	Df	Resid. Dev.	*F*-value	*P*-value
Network size	Latitude	23	6310.8	1.319	0.2650
	Altitude	22	5851.9	6.360	0.0208
	Vegetation type	20	5656.2	1.357	0.2814
	Number of plant families	19	1370.9	59.393	< 0.0001
Network connectance	Latitude	23	0.0842	0.2664	0.6121
	Altitude	22	0.0807	0.9742	0.3367
	Vegetation type	20	0.0763	0.5993	0.5598
	Number of plant families	19	0.0729	0.9139	0.3517
	Network size	18	0.0659	1.9336	0.1813
Network modularity	Latitude	23	0.1796	1.437	0.2462
	Altitude	22	0.1578	3.9513	0.0623
	Vegetation type	20	0.1049	4.7872	0.0215
	Number of plant families	19	0.1010	0.7118	0.4099
	Network size	18	0.0993	0.2992	0.5911
Network nestedness	Latitude	23	5366.3	2.9975	0.1005
	Altitude	22	5047.5	1.5176	0.2338
	Vegetation type	20	4273.8	1.8414	0.1873
	Number of plant families	19	4040.1	1.1128	0.3054
	Network size	18	3781.2	1.2321	0.2816

Table 2. Generalized linear models of the effects of latitude, altitude, type of vegetation and number of plant families on the size, connectance, modularity and nestedness of Neotropical flower-insect networks

Response variable	Explanatory variable	Df	Resid. Dev.	*F*-value	*P*-value
Network size	Latitude	24	53100.0	7.009	0.0155
	Altitude	23	47237.0	10.196	0.0046
	Vegetation type	21	43330.0	3.398	0.0537
	Number of plant families	20	11501.0	55.348	< 0.0001
Network connectance	Latitude	24	0.1164	0.2857	0.5992
	Altitude	23	0.0936	8.2197	0.0099
	Vegetation type	21	0.0923	0.2329	0.7944
	Number of plant families	20	0.0723	7.2036	0.0147
	Network size	19	0.0528	7.0064	0.0159
Network modularity	Latitude	24	0.2992	7.3854	0.0137
	Altitude	23	0.2938	0.6468	0.4312
	Vegetation type	21	0.2646	1.7285	0.2043
	Number of plant families	20	0.1610	12.2859	0.0024
	Network size	19	0.1602	0.0863	0.7721
Network nestedness	Latitude	24	4757.5	10.0281	0.0051
	Altitude	23	4294.9	4.0142	0.0596
	Vegetation type	21	3939.8	1.5406	0.2398
	Number of plant families	20	3180.9	6.5863	0.0189
	Network size	19	2189.4	8.6051	0.0085

opposite pattern or did not vary, respectively. On the other hand, our results corroborate the patterns found by Schleuning et al. (2012) of pollination networks and Dalsgaard et al. (2017) of dispersal networks, showing that specialization decreases toward tropical latitudes. These finding suggest that high tropical diversity can often generate less specialized topological patterns in ecological networks.

Altitude positively affected network size (species richness) in both flower-insect and flower-hummingbird networks, contrary to our expectations. In addition, we observed that altitude had a negative effect on the connectance of flower-insect networks, also contradicting our hypothesis. We observed that the largest networks were located in a range that extends from 1000 to 2500 m in altitude (see Fig. 3). Considering that altitudes in our study reached as high as 3400 meters, our results indicate a peak of species richness (animals and plants) in intermediate to high altitudes. Our observations agree with Rahbek (1995), who, in a thorough review of the literature, showed that in tropical communities higher species diversity is very frequently reported at intermediate altitudes. This pattern is probably due to the intermediate altitudes having mixed environmental conditions that allow the occurrence of species typical to both high- and low-

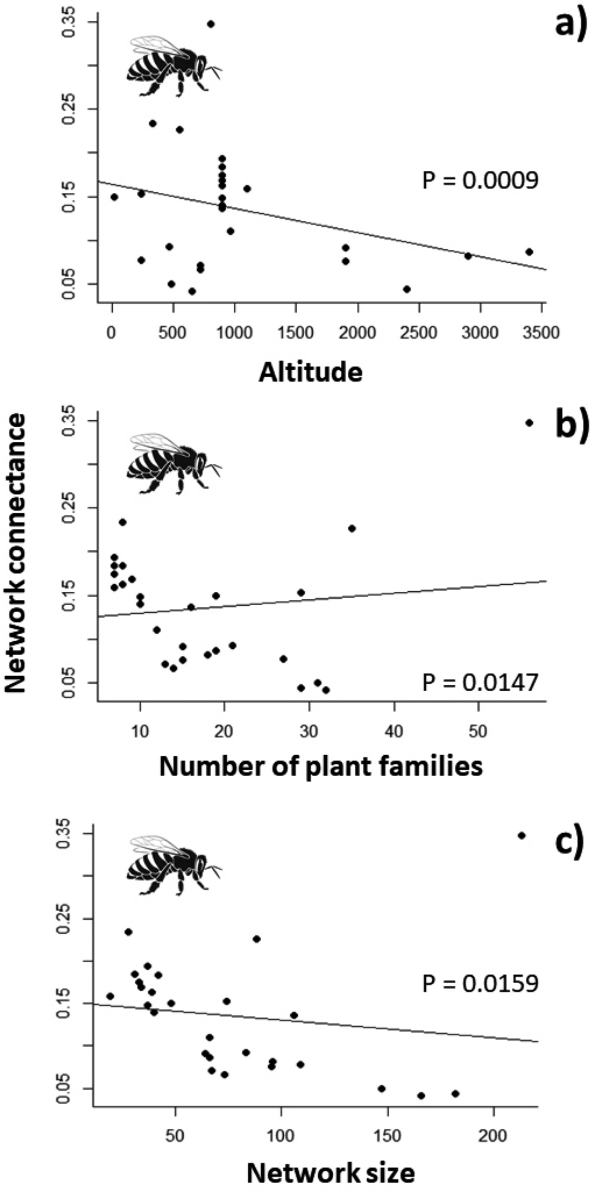

Fig. 4. Factors influencing the network connectance of flower-insect networks.

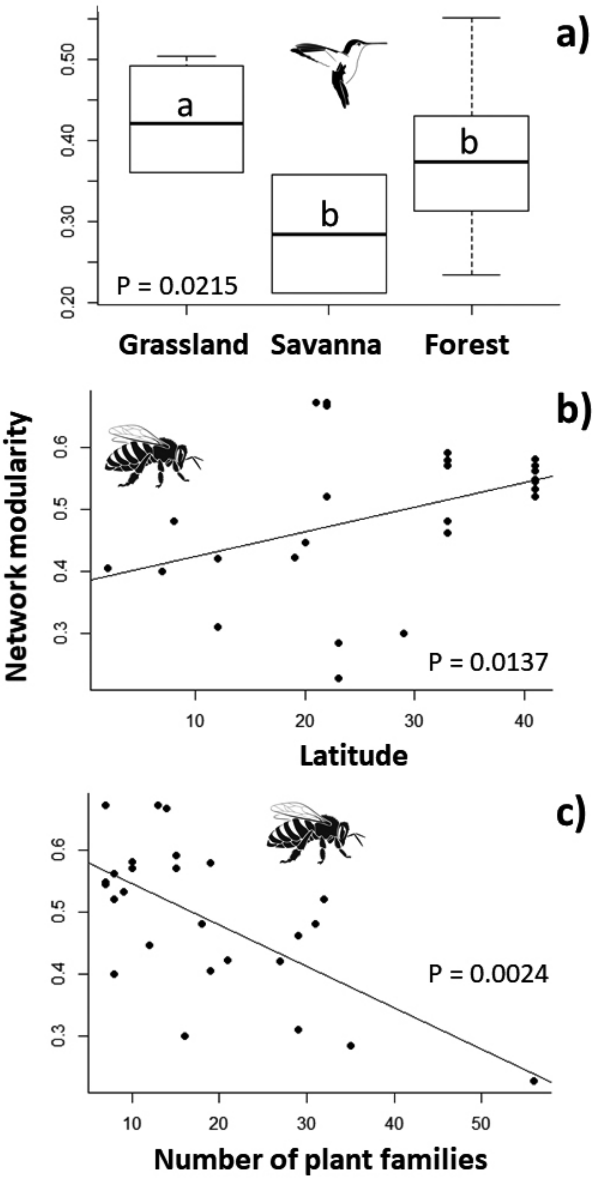

Fig. 5. Factors influencing the network modularity of flower-hummingbird and flower-insect networks.

altitude environments (Rahbek 1995). Although these are rare, some studies showed a positive correlation between altitude and species richness, as documented by Rohde (1992) for tropical birds. Similarly, Hortal et al. (2013) showed a positive hump-shaped relationship between elevation and bird species richness in Spain, which can be attributed to the greater diversity of habitats at intermediate elevations. In this context, another factor that may explain the larger species richness of the networks at intermediate and high altitudes is the conservation status of these habitats, which in general tends to be much better preserved against human interventions (Paudel and Šipoš 2014).

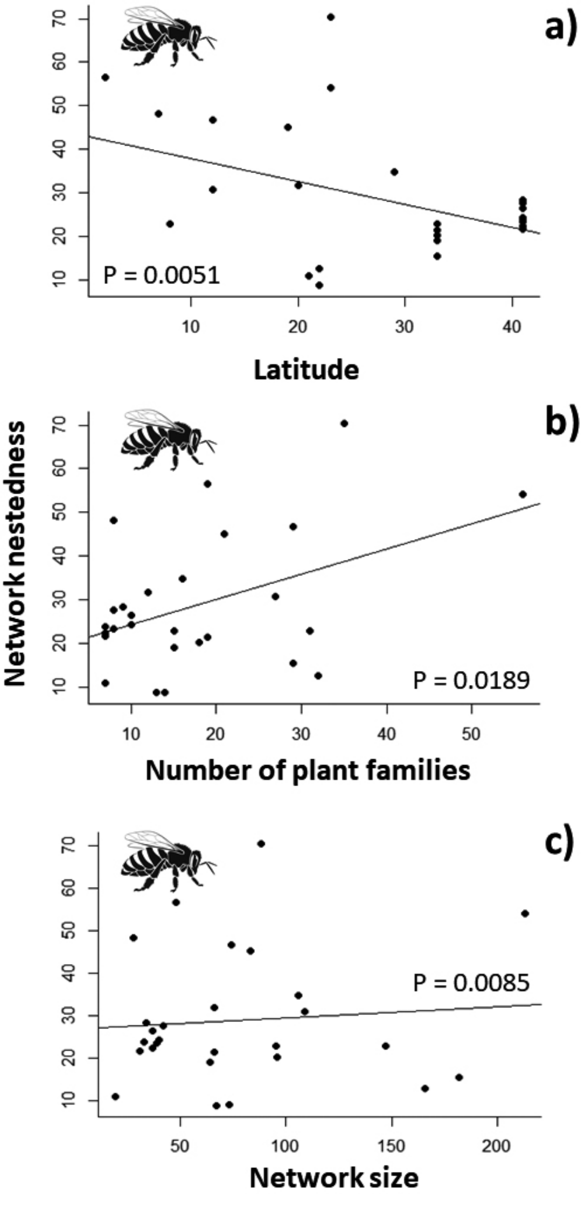

Fig. 6. Factors influencing the network nestedness of flower-insect networks.

For connectance of flower-insect networks, which decreases with altitude, we believe that the observed pattern is a reflection of the size of the networks. Corroborating this, we found a negative correlation between the size and connectance of flower-insect networks, as expected. This finding corroborates previous studies with ecological networks (*e.g.*, Dunne et al. 2002; Dormann et al. 2009; Araújo et al. 2015), and can be explained by the number of possible interactions increasing much faster (*i.e.*, geometric progression) with the size of the networks than the number of observed interactions (*i.e.*, arithmetic progression) (Dunne et al. 2002).

The architecture of Neotropical flower-visitor networks featuring both hummingbirds and insects showed some very interesting differences in responses to geographical and environmental variations. Flower-insect networks were much more variable along the latitudinal and altitudinal gradients (network size, connectance, modularity and nestedness) whereas flower-hummingbird networks varied only in network size. We believe that these differences can be attributed to the intrinsic characteristics of these networks. For example, networks compiled in our dataset of flower visiting insects were characterized by different groups of animals (*e.g.*, bees, butterflies and others) (Rech et al. 2014). This great diversity of taxonomic and functional groups within flower-insect networks can generate more variable responses along the geographic gradient (Adedoja et al. 2018). On the other hand, flower-hummingbird networks are made up of a single animal group, which results in strongly phylogenetically-structured interactions (González et al. 2015). This pattern suggests that, due to phylogenetic restrictions, flower-hummingbird networks tend to be structured independently of latitude and altitude, because we did not find any variation in the connectivity or in the arrangement of their interactions. Another factor may be the breadth of geographic distribution of the studies considered, because flower-insect networks were distributed over a wider latitudinal range (see Fig. 1), which allows for greater plasticity in responses. This observation indicates the need for further studies on interactions between flowering plants and hummingbirds (and other floral visiting vertebrates, such as other birds and bats) in Neotropical areas of higher altitudes and latitudes.

By using vegetation type and the number of plant families as explanatory variables in our analyses, we tested the possible plant-related effects related to the characteristics of the habitats and the taxonomic diversity (a proxy for sampling effort) of the studies, respectively. Vegetation type influenced flower-hummingbird network modularity with networks of grassland habitats being more modular than that of other environments. As expected, this pattern was likely found because the hummingbird species that occur in open vegetation have more diverse and specialized diets as a consequence of the severe environmental filters acting on plant-animal interactions (Araújo et al. 2020). Our finding is in concordance with Rodrigues and Rodrigues (2015) who, although their study was performed on a local scale, points out differences in hummingbird diversity between forest patches and the open rocky field in Brazil. The number of plant families positively influenced network size for both flower-insect and flower-hummingbird networks. Exclusively for flower-insect networks, the number of plant families affected connectance and nestedness positively and modularity negatively. These results indicate that the higher the taxonomic diversity (a proxy for the level of taxonomic inclusion), the greater the diversity of species and the generality of interactions recorded in the network. Contrary to expectations, our results point to a less specialized (that is, more connected and less modular) topology in networks with more plant families. One possible explanation for this pattern is that there is a high overlap in the floral visiting insects between different plant families so that, when the number of botanical families increases, the connectance and the nestedness of the interactions increase. Our study corroborates previous studies indicating that taxonomic and sampling amplitudes are important factors influencing the topology of ecological networks (Nielsen and Bascompte 2007; Trøjelsgaard and Olesen 2013; Araújo et al. 2015).

CONCLUSIONS

Our findings revealed interesting and contrasting geographical patterns of Neotropical flower-visitor networks composed of insects and hummingbirds. Our results indicated that flower-insect networks vary geographically in both species richness and network architecture, but contrary to expectations, topological descriptors showed lower network specialization near the equator. Although unexpected, these results corroborate some studies showing that network specialization decreases toward tropical latitudes (Schleuning et al. 2012; Dalsgaard et al. 2017). Flower-hummingbird networks, on the other hand, varied in species richness, but the network structure remained unchanged along the latitudinal and altitudinal gradients. In conclusion, our results suggest that relations between geography and interaction specialization in Neotropical flower-visitor communities are very complex and can vary between taxonomic and functional zoological groups.

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

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Supplementary materials

Table S1. References of the 55 flower-visitor networks used in the present study. (download)

Table S2. Characteristics of the 55 flower-visitor networks used in the present study. References for the original studies are listed in the table S1. (download)