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Article

Hummingbird-plant networks in rupestrian fields and riparian forests in altitudinal areas of the Serra da Canastra National Park, Minas Gerais, Brazil

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Abstract: Hummingbirds are specialized in consumption of nectar and play an important role in Neotropical plant communities acting as pollinator organisms. Despite the importance of this mutualistic interaction, studies about hummingbird-plant relationships remain scarce regarding the Cerrado domain (Brazilian savanna). In this study, we aimed to describe the interaction network between hummingbirds and plants in rupestrian fields and riparian forests located in altitudinal areas of the Serra da Canastra National Park. We established two transects in each phytophysiognomy, that were sampled monthly for four days, from November 2018 to October 2019. Flowering plants in each transect were observed each survey, and all the visiting hummingbirds were recorded. Networks were constructed using the R bipartite package, considering each phytophysiognomy type, and grouping data of both environments. From these three network arrangements, we extracted complementary metrics at the community level (modularity, nestedness, and network specialization index), and at the species level (species specialization index and species strength in the network). We recorded 647 interactions between 10 hummingbird species and 23 flowering plant species. The hummingbird Colibri serrirostris was responsible for most of observed bird-plant interactions and the plant Qualea cordata was the most visited. The general network was significantly modular, comprising four modules, and showed considerable high specialization and low nestedness. The interaction network in the rupestrian field showed a higher specialization, nestedness, and modularity index when compared to riparian forests, while the metrics of this ecosystem did not differ from those of the general network. However, the metrics at hummingbird species level did not differ significantly between phytophysiognomies. This study corroborated some findings about hummingbird-plant networks in other areas of the Cerrado domain, but also pointed idiosyncrasies in networks of the investigated phytophysiognomies, especially the rupestrian fields.

Keywords: *Cerrado; gallery forest; nectivory; pollination; rocky grassland.*

Redes de beija-flor-planta em campos rupestres e florestas ripárias em áreas de altitude do Parque Nacional da Serra da Canastra, Minas Gerais, Brasil

Resumo: Beija-flores são especializados no consumo de néctar e desempenham um papel importante em comunidades de plantas Neotropicais, agindo como organismos polinizadores. Apesar da importância dessa relação mutualística, estudos sobre a relação de plantas e beija-flores ainda são escassos no Cerrado. Neste estudo, objetivamos descrever a rede de interações entre beija-flores e plantas em campos rupestres e matas ripárias localizadas em áreas de altitude do Parque Nacional da Serra da Canastra. Estabelecemos dois transectos em cada fitofisionomia, os quais foram amostrados mensalmente durante quatro dias, de novembro de 2018 a outubro de 2019. Plantas em floração em cada transecto foram observadas em cada amostragem, e todos os beija-flores visitantes foram registrados. As redes de interação foram construídas utilizando o pacote bipartite do R, considerando cada fitofisionomia e agrupando os dados de ambos os ambientes. Destes três arranjos de rede, extraímos métricas complementares no nível de comunidade (modularidade, aninhamento e índice de especialização de rede) e no nível de espécies (índice de especialização da espécie e força da espécie na rede). Registramos 647 interações entre 10 espécies de beija-flores e 23 espécies de plantas. O beija-flor Colibri serrirostris foi o responsável pela maior parte das interações ave-planta observadas e a planta Qualea cordata foi a mais visitada. A rede geral foi significativamente modular com quatro módulos e apresentou considerável especialização e baixo aninhamento. A rede de interações no campo rupestre apresentou maior especialização, aninhamento e índice de modularidade quando comparada à mata ripária, enquanto as métricas deste ecossistema não foram diferentes da rede geral. Entretanto, as métricas no nível de espécies de beija-flores não apresentaram diferenças significativas entre as fitofisionomias. Este estudo corrobora alguns resultados de redes de beija-flores-plantas em outras áreas do domínio do Cerrado, mas também aponta idiossincrasias nas redes das fitofisionomias investigadas, especialmente os campos rupestres.

Palavras-chave: *Campo rupestre; cerrado; mata de galeria; nectivoria; polinização.*

Introduction

Interactions between plants and animals are present in all terrestrial ecosystems, and biotic pollination is estimated to occur in 94% of tropical plants (Ollerton et al. 2011). These mutualistic interactions create complex networks and the comprehension of patterns and processes that structure them can be used to predict the dynamics and stability of biological communities (Bascompte 2009, Thompson et al. 2012, Schleuning et al. 2015, Bartomeus et al. 2016; Tinoco et al. 2017). Recently, an increasing number of studies have been elucidated pollination relationships patterns and its architecture in the light of the network approach (e.g., Vizentin-Bugoni et al. 2014, Souza et al. 2018, Maruyama et al. 2019). However, networks remain under investigated in the tropics with a particular gap in central Neotropical savanna areas (Vizentin-Bugoni et al. 2018), especially in attitudinal environments and open vegetation.

The Cerrado is the second largest morphoclimatic and phytogeographic domain of Brazil and the most biodiverse savanna of the world (Ratter et al. 1997, Ribeiro & Walter 1998). It harbors diverse types of phytophysiognomies, that encompasses grasslands, savanic and forest formations, considered within the Cerrado *sensu lato* classification, and other singular ecosystems such as rupestrian environments and riparian forests (see Ribeiro & Walter 1998). The rupestrian fields, regionally called *campos rupestres,* are a montane vegetation complex that occurs over rock outcrops (Alves et al. 2014, Silveira et al. 2016). It is predominantly dominated by herbaceous and shrubby vegetation that have xeromorfic features (Alves et al. 2014, Conceição et al. 2016, Morellato & Silveira 2018). The riparian forests occur alongside waterbodies and, unlike the adjacent grassland vegetation, are little affected by water restriction (Ribeiro & Walter 1998, Coelho et al. 2007). This feature may have implications for the dynamics of interactions between animals and plants since the phenology of plant species is often associated with the water regime (Conceição et al. 2007). Additionally, animals can move between different habitats according to the availability of resources, preferences for habitats and behavioral characteristics (Maruyama et al. 2014, 2019, Rodrigues & Rodrigues 2015). Therefore, differences between phytophysiognomies may play an important role in structuring the plant-pollinator interaction networks, which is particularly evident among hummingbirds (e.g., Maruyama et al. 2014, 2019, Rodrigues & Rodrigues 2015).

Hummingbirds are highly specialized in nectar consumption and act as important pollinator agents in the Neotropics, in such an extent that many plant species have evolved adaptations to attract then (Jordano 1987, Cronk & Ojeda 2008). Interactions between hummingbirds and plants provide good models to explore the structure of mutualistic networks, due to high dependence of hummingbirds on nectar, convenient sampling, and wide distribution of hummingbird species across nearly the entirety of the Americas (McGuire et al. 2014, Vizentin-Bugoni et al. 2018). In this sense, several studies have addressed structural patterns in hummingbird-plant networks, such as considerable specialization (e.g., Maglianesi et al. 2014), modular structure (e.g., Maruyama et al. 2014) and usually low nestedness (e.g., Vizentin-Bugoni et al. 2014). In other words, hummingbird-plant networks are mainly characterized by: (1) few species have many partners and/or interactions, while most have just a few links (Bascompte et al. 2006); (2) modules of species that interact strongly with each other (Olesen et al. 2007); and (3) species with few interactions do not always form subgroups with species with many interactions (Bascompte et al. 2003). Despite these general patterns, hummingbird-plant networks can show considerable variability through different habitats (e.g., Maruyama et al. 2019).

In altitudinal areas inside the Cerrado domain, the riparian forests and open vegetation in rupestrian fields can occur in mosaics at landscape levels (IBAMA 2005, Fieker et al. 2014), creating an interesting situation in which hummingbirds can use floral resources from both ecosystem types. Thus, using the ecological network approach, we aimed to characterize the interactions between hummingbirds and their floral resources in the main plateau of the Serra da Canastra National Park (SCNP), a federal Conservation Unit in the state of Minas Gerais, Brazil, where, as far as we know, there are no surveys on mutualistic interactions between bird pollinators and the visited flower community. We investigated whether the interactions between hummingbirds and their floral resources differ between vegetation types, reflected in network topologies and specialization metrics.

Material and Methods

1. *Study area*

This study was conducted in the SCNP, in the plateau known as *Chapadão da Canastra* (20°13’51.52”S, 46°29’11.39”W; Cunha et al. 2019) located in the southwestern portion of the Minas Gerais state, Brazil (IBAMA, 2005). The geographical limits comprise an area of 71,525 ha at 1,250 to 1,450 m of elevation (Cunha et al. 2019), harboring several phytophysiognomies of the Cerrado domain. The regional climate is characterized by a well-marked seasonality, with cold and dry winters (dry season) from April to September, and rainy summers (wet season) from October to March (IBAMA, 2005). Our fieldwork was carried out in two phytophysiognomies: the rupestrian fields (*campos rupestres*), characterized by open vegetation (grassland and open savanna) in gravelly/sandy soil with clumps of rocky outcrops in altitudinal mountaintops, and the riparian forests, composed by riverine forests alongside streams and rivers, and small patches of forests in hydromorphic soils, commonly associated to water sources and connected with gallery forests.

2. *Field methods*

From November 2018 to October 2019, we made 11 expeditions to the SCNP with an interval of 30 to 35 days. Each data collection comprised four days of observations in four different sites. Two transects were established in riparian forest (each of approximately 100 m) and two in the rupestrian fields (each of approximately 200 m) (see Silva 2021 for detailed information). The differences in the transect length between the two phytophysiognomies is due to the difficulty in going through the fragments of riparian forests. Each site was sampled monthly during morning and afternoon, from 8 am to 12 pm and later from 3 pm to 6 pm (approximately seven hours per site per month), totalizing 308 hours of sampling effort. Observations of hummingbird-plant interactions normally start at sunrise (Machado & Rocca 2010). However, we defined the observation time as mentioned above due to logistical difficulties to reach the study sites.

Flowering plants were observed for 30 minutes with direct visualization with the aid of binoculars (Nikon 8 x 42 mm). Whenever possible, more than one plant was observed simultaneously.

For each plant species, we recorded the number of visits by hummingbirds, considering as one visit the foraging performed within an uninterrupted flight regardless of the number of flowers visited (Las-Casas et al. 2012). A new visit was counted when the bird perched and returned to the floral resource or when it left the site and returned to forage on flowers again. Only legitimate visits were considered, that is, when the bird accesses the floral resource through the opening of the corolla and meets the reproductive structures of the flower.

Identification of the hummingbirds were confirmed with the help of a specialized guide when necessary (Grantsau 1989) and scientific nomenclature followed Piacentini et al. (2015). Samples from all plants visited were collected for identification to the highest possible taxonomic resolution and subsequently deposited at the herbarium of the Federal University of São Carlos (SPSC, acronym according to Thiers 2020).

3. *Data analysis*

To characterize and analyze hummingbird-plant network in the SCNP, we built interaction matrices weighted by the total number of visits observed between pairs of species. In these, three arrangements of interaction networks considering the entire period of study were considered: (1) general interaction network, in which all data collected in this study were grouped into a single matrix; (2) network of interactions in the rupestrian fields; (3) network of interactions in the riparian forests.

From these different network arrangements, we extracted three complementary metrics that describe different aspects of the network, namely: modularity, nestedness and network specialization index. The modularity in interaction networks allows the identification of subgroups (modules) of species that interact strongly with each other and with less intensity with species outside the module (Olesen et al. 2007). Here, we compute modularity through DIRTLPAwb+ algorithm (Beckett 2016). The modularity index ranges from 0 to 1, for the minimum modularity and maximum modularity, respectively. Nestedness was calculated using the weighted version of the metric NODF, the wNODF (Almeida-Neto & Ulrich 2011, Almeida-Neto et al. 2008). The wNODF index range is from 0 to 100, indicating, in this order, the minimum and maximum nestedness structure. The complementary specialization of the network was estimated using the metric H2'. This index is derived from Shannon entropy and describes the degree of specialization of a quantitative network (Blüthgen et al. 2006). Its variation is from 0 to 1, indicating the lowest and highest specialization, respectively.

The metrics of the observed networks described above were compared with the averages of the estimated metrics of 1.000 random null models, using Z tests. We consider the significance level of 0.05, so if test values ranged between -1.96 and 1.96, it is accepted the null hypothesis of equality of metrics observed at the expense of those expected at random. The null models were generated using the vaznull method (Vázquez et al. 2007). In this procedure, the observed network connectance is maintained and the totals of individual interactions are randomized. The analyzes were performed using the "bipartite" package (Dormann et al. 2008), with the metrics extracted by the function "networklevel" (Dormann et al. 2009).

Regarding the species level network metrics, we consider only the metrics related to hummingbirds, as the plants may have other pollinators that were not identified here. The estimated metrics were: (1) species specialization by the d' index and (2) species strength in the network. The first metric calculates how much a species deviates from a random sample of available interaction partners (Blüthgen et al. 2006). Its variation occurs from 0 to 1, in a minimum and maximum specialization scale, respectively. The last one estimates the sum of the dependencies of each species (Bascompte et al. 2006). We obtained these metrics also through the "bipartite" package, using the function "specieslevel" (Dormann 2011). All analyzes were performed in the computational environment R Core Team (2020).

Results

We recorded 647 interactions from 10 hummingbird species (Table 1) on 23 flowering plant species distributed in 14 plant families (Table 2). Seven species of hummingbirds visited 12 plant species in rupestrian fields and nine hummingbird species visited 13 species in riparian vegetation (see Figure 1). Only two plant species were recorded in both phytophysiognomies: *Psittacanthus robustus* and *Hololepis pedunculata*. Six bird species were observed interacting with plants in both vegetation types, while *Calliphlox amethystina* used nectar resources only in rupestrian fields, and *Amazilia fimbriata*, *Anthracothorax nigricollis*, and *Heliomaster squammosus* interacted with flowering plants only in riparian forests.

Table 1. Hummingbird assemblage (Aves: Trochilidae) recorded visiting plant species in riparian forests and rupestrian fields in the Serra da Canastra National Park, MG, southeastern Brazil, from Nov/2018 to Oct/2019. NI = number of interactions recorded; ss = species strength in the network; d' = species specialization.

Species	Rupestrian fields			Riparian forests			General network		
	NI	ss	d'	NI	ss	d'	NI	ss	d'
Phaethornis pretrei (Lesson & Delattre, 1839)	2	0.0329	---	29	1.5443	0.4948	31	1.4737	0.4756
Eupetomena macroura (Gmelin, 1788)	56	1.3011	0.7252	51	0.9211	0.2615	107	1.6659	0.4548
Colibri serrirostris (Vieillot, 1816)	152	9.2305	0.6234	207	4.8778	0.5947	359	13.2649	0.6
Anthracothorax nigricollis (Vieillot, 1817)	---	---	---	2	0.2857	0.7374	2	0.2857	0.7483
Chlorostilbon lucidus (Shaw, 1812)	18	0.8687	0.2917	84	3.1769	0.1335	102	3.6593	0.1729
Thalurania furcata (Gmelin, 1788)	2	0.0294	0.1427	23	0.7204	0.5017	25	0.7119	0.4759
Amazilia fimbriata (Gmelin, 1788)	---	---	---	4	0.0889	0.4368	4	0.0354	0.2839
Amazilia lactea (Lesson, 1832)	2	0.0941	0.2192	8	0.3627	0.1619	10	0.4569	0.2027
Heliomaster squamosus (Temminck, 1823)	---	---	---	3	1.0222	0.7155	3	1.0088	0.6705
Calliphlox amethystina (Boddaert, 1783)	4	0.4433	0.5613	---	---	---	4	0.4374	0.6105

Table 2. Plants visited by hummingbirds in riparian forests and rupestrian fields of the Serra da Canastra National Park, MG, southern Brazil, from Nov/2018 to Oct/2019. ● Plants with ornithophilous syndrome; N.V = Number of visits. D = Degree of visits by hummingbirds.

Family/Species	Habitat	N.V	D
Acanthaceae			
Justicia monticola (Ness) Profice ●	riparian forest	75	4
Amaryllidaceae			
Hippeastrum cipoanum (Ravenna) Meerow ●	rupestrian field	1	1
Asteraceae			
Asteraceae sp.1	riparian forest	2	1
Lessingianthus sp.	rupestrian field	5	2
Eremanthus sp.	rupestrian field	3	1
Hololepis pedunculata (DC. ex Pers.) DC. ●	riparian forest - rupestrian field	55-26	5-3
Lychnophora sp.	rupestrian field	7	2
Wunderlichia mirabilis Riedel ex Baker	rupestrian field	4	2
Bignoniaceae			
Pyrostegia venusta (Ker Gawl.) Miers ●	riparian forest	6	1
Bromeliaceae			
Aechmea bromeliifolia (Rudge) Baker ●	riparian forest	7	3
Dyckia minarum Mez ●	rupestrian field	14	2
Vriesea friburguensis Mez ●	riparian forest	6	3
Ericaceae			
Gaylussacia brasiliensis (Spreng.) Meisn. ●	riparian forest	38	3
Gaylussacia pseudogaultheria Cham. & Schltdl ●	rupestrian field	44	3
Gaylussacia reticulata Mart. ex Meisn. ●	rupestrian field	3	1
Lamiaceae			
Hypenia reticulata (Mart. ex Benth.) Harley	rupestrian field	2	1
Loganiaceae			
Spigelia sellowiana Cham. & Schltdl. ●	riparian forest	2	1
Loranthaceae			
Psittacanthus robustus (Mart.) Mart. ●	riparian forest -rupestrian field	68-45	5-6
Orobanchaceae			
Esterhazya splendida J.C.Mikan ●	riparian forest	6	3
Sapindaceae			
Serjania erecta Radlk	riparian forest	5	2
Theaceae			
Laplacea fruticosa (Schrad.) Kobuski	riparian forest	7	2
Velloziaceae			
Barbacenia lymansmithii Mello-Silva & N.L.Menezes	rupestrian field	30	1
Vochysiaceae			
Qualea cordata Spreng.	riparian forest	186	4

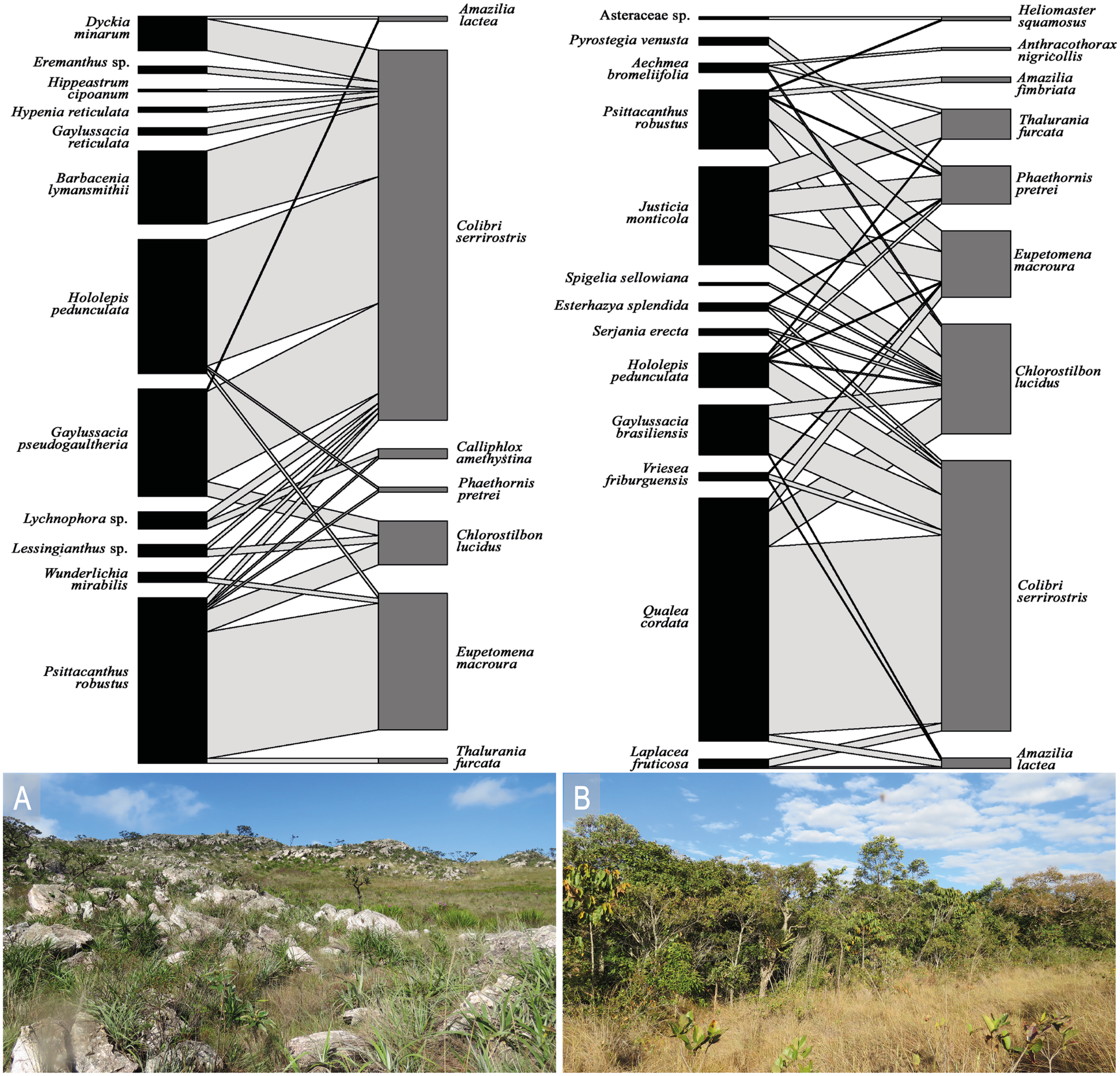

Figure 1. Plant-hummingbird network in (A) rupestrian fields and (B) riparian forests of the Serra da Canastra National Park, from Nov/2018 to Oct/2019. Plant species are represented by black and hummingbirds by gray polygons.

Colibri serrirostris was responsible for most of observed bird-plant interactions (55.49%), followed by *Eupetomena macroura* (16.54%) and *Chlorostilbon lucidus* (15.76%). The high number of interactions observed for *C. serrirostris* was mainly attributed to visits to the entomophilous species *Qualea cordata* during massive flowering events, representing 22.27% of all observed interactions, which made this plant the most visited in the study area. The ornithophilous species *Psittacanthus robustus*, *Hololepis pedunculata* and *Justicia monticola* also received a high number of visits, however, from more species of hummingbirds (Figure 1 and Table 2).

The overall hummingbird-plant network was significantly modular (Qobs = 0.36, Qd = 0.24, z-score = 17.58, p-value < 0.0005), comprising four modules of interacting species (Figure 2). Of those, two modules were composed of a single interacting pair, *Heliomaster squamosus* grouped with Asteraceae sp.1 and *Calliphlox amethystina* with *Lychnophora* sp. The hummingbirds *C. serrirostris* and *Amazilia lactea* were arranged in a single module with 14 plant species. The module with the highest number of hummingbird species, namely, *Amazilia fimbriata*, *Antrhacothorax nigricollis*, *Chlorostilbon lucidus*, *Eupetomena macroura*, *Thalurania furcata* and the only hermit species in the community, *Phaethornis pretrei*, has been associated with eight plant species, as shown in Figure 2. The network also indicated a considerable specialization (H2obs = 0.44, H2d = 0.32, z-score = 17.12, p-value < 0.0005) and low nestedness (wNODFobs = 33.49, wNODFd = -17.08, z-score = -3.72, p-value < 0.0005).

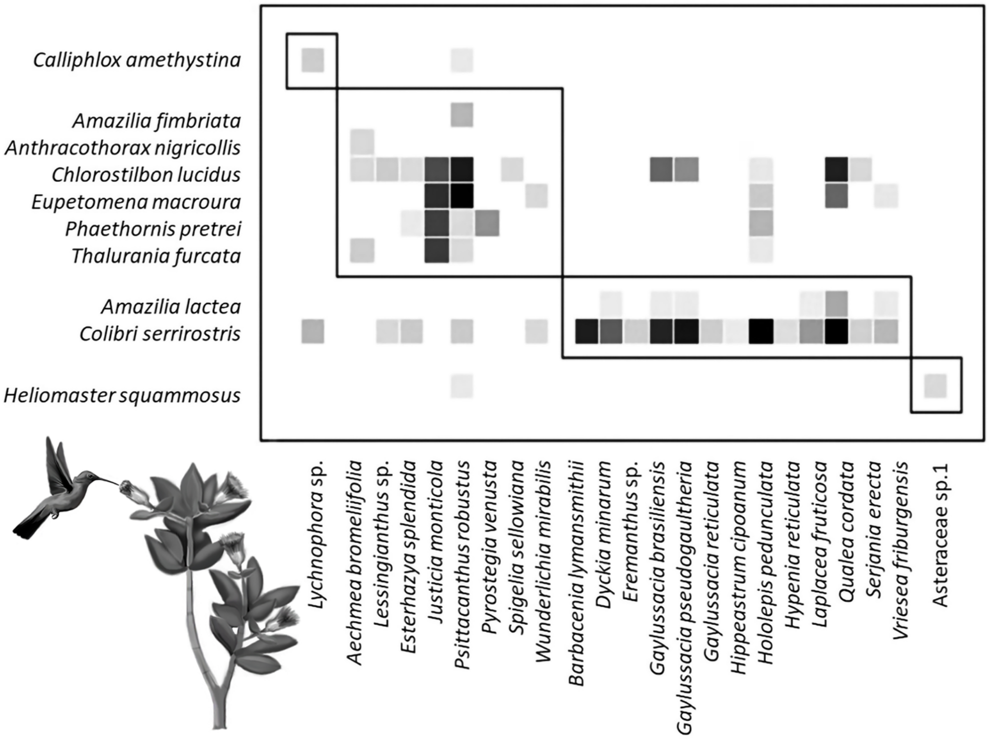

Figure 2. Plant-pollinator community in the main plateau of the Serra da Canastra National Park with indication of interaction abundance (darker tones represent a greater number of records) and the four identified modules of interactions. Data collected from Nov/2018 to Oct/2019.

Regarding to the species level network, the highest values of species strength index were registered to *C. serrirostris* (s.s = 13.2649) and *C. lucidus* (s.s = 3.6593). The lowest values of species strength were attributed to the hummingbird species *A. fimbriata* (s.s = 0.0354) and *A. nigricollis* (s.s = 0.2857). On the other hand, *C. lucidus* obtained the lowest values of d' index (d' = 0.1729), indicating to be a generalized pollinator, while *C. serrirostris* was moderately generalized to specialized according to the metric (d' = 0.6). The species that had d' indexes above that observed for *C. serrirostris* were *A. nigricollis*, *H. squamosus* and *C. amethystina* (Table 1). These hummingbirds visited one or two plant species, while *C. serrirostris* obtained the highest degree from the community, interacting with 18 plant species, of which it was the exclusive visitor of five plants, including *Barbacenia lymansmithii*, an endemic species only recorded in grasslands and rupestrian fields of the SCNP (Mello-Silva & Menezes 1999).

When considering networks for the two sampled physiognomies, we observed some idiosyncrasies between the environments and in relation to the completeness network. The network of the rupestrian fields showed higher specialization (H2obs = 0.55, H2d = 0.4, z-score = 9.29, p-value < 0.0005) and low nestedness, but obtained the highest wNODF of comparisons (wNODFobs = 44.64, wNODFd = -8.01, z-score = -1.23, p-value > 0.05) and a higher modularity index (Qobs = 0.38, Qd = 0.26, z-score = 9.85, p-value < 0.0005). The estimated network metrics for riparian forest were similar to those observed for the overall community network, therefore, also considerably specialized (H2obs = 0.41, H2d = 0.32, z-score = 15.01, p-value < 0.0005), but with the lowest estimated nestedness of the analyzes (wNODFobs= 24.02, wNODFd = -32.39, z-score = -5.12, p-value < 0.0005) and the same observed modularity index of the general network (Qobs = 0.36, Qd = 0.23, z-score = 15.86, p-value < 0.0005). The hummingbird species level metrics separated by phytophysiognomies did not differ significantly from each other (dfd' = 11.54, p-value = 0.53; W species strength = 23, p-value = 0.41).

Discussion

Studies on hummingbird-plant networks have revealed structural patterns characterized by heterogeneity in the distribution of interactions between species (Rodríguez-Flores et al. 2019), considerable specialization (Maglianesi et al. 2014), modular structure (Maruyama et al. 2014), and low nestedness (Vizentin-Bugoni et al. 2014). These patterns were also detected in this study, considering the complete network and its arrangements for the two phytophysiognomic types sampled (rupestrian fields and riparian forests). However, when comparing the hummingbird-plant interactions network of the rupestrian field and riparian forest, the rupestrian field network was more specialized and nested than the riparian forest network. The structure of the hummingbird-plant interactions network can be influenced, among other factors, by the animals' habitat preference for forest or open vegetation (Maruyama 2014, 2019). In this sense, the preference for open habitats of the hummingbird with the highest degree and number of interactions in SCNP seems to lead to differences in network topology between the two phytophysiognomies sampled in this study, as discussed below.

In view of the high topographic heterogeneity, a common feature in the rupestrian ecosystems (Alves et al. 2014), a high spatial turnover in interactions between pollinators and plants can be detected, which are more linked to variations in floristic composition than to differences in pollinator species between sites (see Carstensen et al. 2014).

Similarly, we observed noteworthy differences in the floristic composition, even between the same phytophysiognomy sampled in different areas, while the composition of hummingbird species was similar between the sampling sites. In fact, given the high mobility of hummingbirds and frequent generalized choice of floral resources (Stiles 1981; Wolf et al. 1976), it is expected a more homogeneous distribution of hummingbird species between different sites of the same region.Conversely, considering explicit variations in the vegetation landscape, such as forest patches immersed in open grasslands, the preference for habitat and/or the restriction on the occurrence of certain species before another hierarchically dominant species can emerge as a structuring pattern for interactions (Dupont et al. 2009, Morales & Vázquez, 2008). In this sense, the network topologies were consistently different between environments, with the greatest specialization and nestedness in the rupestrian fields.

The formation of subgroups of species that interact more strongly with each other than with species outside the group, that is, the modular arrangement of interactions (Olesen et al. 2007), supported the findings about the differences in network topologies between phytophysiognomies. The module with the highest number of hummingbird species was, above all, associated with the plant species observed in forest patches. Interestingly, this module also included the long-billed hummingbird, *Phaethornis pretrei*, the only recorded species of the hermit clade, which is capable of travelling long distances using the trapline foraging behavior (McGuire et al. 2014). This result contrasts with other studies also developed in the Cerrado domain, in which *P. pretrei* has been separated from the other hummingbirds in a single module (Maruyama et al. 2014, Queiroz 2018), what can be expected given the frequent association of hermit hummingbirds with morphologically specialized flowers of the ornithophilous plants (Feinsinger & Colwell 1978, Maglianesi et al. 2014, Maruyama et al. 2014). However, this particularity reported here for the interactions between hummingbirds and plants in forest patches does not seem to be associated with greater generalization in the choice of *P. pretrei*, but the greater frequency of visitation to ornithophilous plant species by hummingbirds belonging to other clades.

While the module formed by the largest number of hummingbird species was mostly composed of plant species from forest patches, another module with only two hummingbird species, *Colibri serrirostris* and *Amazilia lactea*, was associated with more than half of the plant species registered in the entire community, mainly with flowering species observed in the rupestrian fields. Similarly, the arrangement of *Colibri serrirostris* and *Amazilia lactea* in the same module closely related to plant species in open landscapes of the Cerrado domain was detected in another study (Maruyama et al. 2013). The hummingbird *C. serrirostris* interacted not only with all plant species in the module, but with all plants recorded in the rupestrian fields. The high degree of visitation performed by this hummingbird indicated its connecting role in the network of rupestrian fields, which is in line with his preference for open vegetation types (Sick 2001). In the forest patches, the role as connector species, according to the degree distribution to the plant species visited, was played by *Chlorostilbon lucidus*.

As pointed out by the modular structure of the network, we found that the interaction network in the rupestrian fields is more specialized and, still, nested than the network in forest patches. These variations in the network topology are probably related to the preference of habitats of the main interacting hummingbird species in each phytophysiognomy. The greater abundance in the rupestrian fields of a hummingbird known to be territorialist (Jacobi & Antonini 2008, Justino et al. 2012) seems to be associated with the greater exclusivity of the interactions in these environments. In this context, *C. serrirostris* was the exclusive visitor of five plant species in the rupestrian field, including the species *Barbacenia lymansmithii*, endemic to the SCNP (Mello-Silva & Menezes 1999). In other study, carried out in rupestrian ecosystems, the main visitor was *C. lucidus* (Rodrigues & Rodrigues 2014), but in this study, it showed the highest degree of visitation in forest patches. The larger body size and high abundance of *C. serrirostris*, coupled with its preference for open habitats, seems to lead *C. lucidus* to forage preferentially in forest environments in the SCNP.

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Monique Maianne and Carolline Zatta Fieker: contribution in the concept and design of the study; data collection in the field; data analysis and interpretation; and manuscript preparation.

Manoel Martins Dias: contribution in the concept and design of the study; and manuscript preparation.

Matheus Gonçalves dos Reis: contribution in the data analysis and interpretation; contribution to critical review adding intellectual content; and manuscript preparation.

Conflicts of Interest

The authors declare that they have no conflict of interest related to the publication of this manuscript.

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