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Seasonal Variation in Bee-Plant Interactions in an Inselberg in the Atlantic Forest in Southeastern Brazil

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Abstract

Studies on bee-plant interactions are relevant to the understanding of temporal patterns in neotropical communities. In isolated habitats such as inselbergs little is yet known about the temporal dynamics in the availability of floral resources and interacting bee. In the present study, the objective is to verify the effect of seasonality on the bee-plant interaction in an Atlantic Forest inselberg in southeastern Brazil. The bees were sampled monthly in the dry (April/2008-September/2008) and wet seasons (October/2008-March/2009) using an entomological net. A total of 322 bees of 33 species were captured on flowers of 34 species of plants during the year. Bees richness was similar between seasons (22 species in the wet season and 21 in the dry season), but abundance was higher in the wet season (60% of individuals) and higher diversity occurred in the dry season. Augochloropsis sp1 were the most abundant species and visited the largest number of plant species at each season. In the interaction network, plants with the highest degree were distinct between the seasons. The number of possible interactions was higher in the dry season compared to the wet season and connectance was similar; nestedness however varied between the seasons. The composition of plant and bees species was distinct between the seasons, as well as the interactions between them, mainly due to the alteration in the composition of the plant species and the change in the choice of the bees for the floral resources between the seasons.

Introduction

The fragmentation and degradation of natural and seminatural habitats and the consequent loss of plant species and pollinators are recurrent concerns in the literature (Moreira et al., 2015; Potts et al., 2016). Predicting how interactions between plants and pollinators change in the face of biotic and abiotic factors is an important step in attempting to preserve forest ecosystems (Sargent & Ackerly, 2008).

Inselbergs are single or multiple rock outcrops occurring isolated in the surrounding flat landscape and they are considered among the priority areas for conservation (Porembski & Barthlott, 2000). The different microhabitats resulting from a marked microclimatic variation favor the establishment of different species in these environments (Porembski et al., 1998), providing refuges for rare or endemic plant and animal species (Santos et al., 1999; Porembski & Barthlott, 2000; Silva, 2016). These ecosystems are subject to constant threats, including mineral extraction and wide agricultural practices in the surrounding areas (Silva, 2016). The forest formations in inselberg areas can be determined by a complex system of gradients related to altitude, soil depth, water availability, and climatic variation, contributing to vegetation characterized by rupicolous communities and dry or savanna-like forests (Gröger & Huber, 2007). Among the dry forests, the semi-deciduous seasonal forest in southeastern Brazil is one of the most threatened and fragmented ecosystems in the world, consisting of small scattered fragments (Santos et al., 2009; Pimenta et al., 2011). This fact raises the importance of studying the plantpollinator interactions in this ecosystem since it guarantees the reproduction of plants and promotes their genetic diversity and also provides resources for animals (Rech et al., 2014).



These mutualistic interactions between bees and plants may vary on different spatial and temporal scales, according to environmental conditions (such as temperature, relative humidity and light intensity), and also to intrinsic characteristics of bees (activity and foraging periods) and plants biology (flowering period) (Olesen et al., 2008; Kleinert et al., 2009; Burkle & Alarcón, 2011; Deprá & Gaglianone, 2018). In the studies of the composition and distribution of floral resources, the inselbergs constitute an excellent model due to the geographic isolation and the endemism of species. The environmental variables may be associated to the different patterns of occurrence and distribution of plant resources, especially in forests with seasonal climates such as inselbergs composed of deciduous or semi-deciduous forests (Morellato & Leitão-Filho, 1996; Nunes et al., 2005; Mauad et al., 2014).

The approach of ecological networks and their metrics emerge as a contribution to the understanding of patterns in the structures of interactions among species, the fragility of these interactions, the impact of the environmental and anthropic effects, and the temporal and spatial variation of the species (Memmott et al., 2004; Silva et al., 2007; Deprá & Gaglianone, 2018). This network approach contributes to the planning required for the conservation and management of threatened environments (Biesmeijer et al., 2005).

Studies on the evaluation of the community structure of bees and floral species in inselberg areas in Brazil have been carried by Aguiar and Zanella (2005) and Batalha-Filho et al. (2007) in Caatinga phytophysiognomies in the state of Bahia, Brazil. These authors approached the topic using traditional analytical tools of population and community studies. Studies on bee-plant interactions in a unique habitat such as the inselbergs, with rare and endemic species and with seasonal vegetation that varies floral resources along the year, can bring relevant results for the understanding of the temporal dynamics of plant-pollinators in the Atlantic Forest. In addition they can provide knowledge to be used in conservation programs of this ecosystem.

The present work aims to describe and analyze the seasonal variation in interactions between plants and bees in an Atlantic Forest inselberg. Our hypothesis is that the key plants can be substituted between the seasons in the semidecidual seasonal forest, resulting in the changing in the availability of foraging resources that affects the bee-plant interactions.

Material and Methods

Study area

The samplings were carried out on semideciduous seasonal forest area, Itaoca massif (21°48' S 41°26' W), a rocky outcrop of 900 ha at 420 m a.s.l., in southeastern Brazil. This inselberg is isolated amidst the surrounding flat landscape and flooded areas surrounded by pastures, sugarcane plantations, and rock exploration activity.

This area has a clear seasonal climate with low relative humidity comparing to other Atlantic Forest areas, and it is considered important for the floristic diversity of Rio de Janeiro state (Pessanha et al., 2014) as a hotspot within the Atlantic Forest (Murray-Smith et al., 2008). The climate of the region is classified as Aw (*sensu* Köppen, 1948), characterized by tropical hot and humid with a dry winter (April to September) and wet summer (October to March). In the studied period (2008 and 2009), the amplitude of the abiotic values for the dry and wet seasons were: temperature 21.6 to 26.6 °C and 24.6 to 28.5 °C, relative humidity 74 to 78% and 74 to 82%, and monthly rainfall 3.5 to 63.8 mm and 51.6 to 526.2 mm, respectively (Fig 1). Climatic data was obtained from the weather station of Campos/RJ of National Meteorological Institute (INMET, 2017).

Sampling

Samplings of the floral visiting bees were carried out in the dry (April/2008 to September/2008) and wet seasons (October/2008 to March/2009) in the semi-deciduous seasonal forest vegetation, every 30 days, except in December when sampling was not possible due to impassable roads caused by intense rain. The sampling of bees was performed by a collector using an entomological net, from 7 am to 4 pm. All flowering plants, mainly herbs and shrubs, were inspected for up to three minutes in search of their floral visitors in a trail called locally

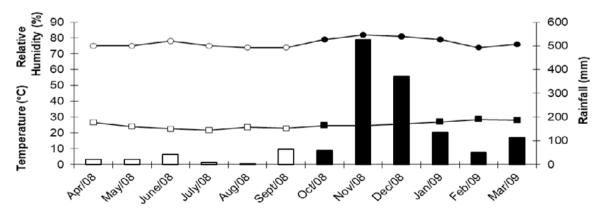


Fig 1. Climatic conditions between April 2008 and March 2009 at the Itaoca Inselberg in the Atlantic Forest in southeastern Brazil. Dry season: white color; Wet season: black color. Temperature: square; Relative Humidity: circles; Rainfall: bars.

"tower trail" with 3000 meters long. Arboreal plants were sampled using extensive netting up to 5 m in height.

After capture, the bees were killed in flasks containing ethyl acetate and separated according to time interval and plant. In the laboratory, the bees were mounted with entomological pins, labeled, identified and deposited in the entomological collection in the Setor de Ecologia Experimental of the Laboratório de Ciências Ambientais of the Universidade Estadual do Norte Fluminense Darcy Ribeiro, in Campos dos Goytacazes, RJ, Brazil. Identification of the plants was carried out by comparison with the reference material of the study area deposited in the Herbário UENF (HUENF) and confirmed by specialists. Classification of angiosperms followed the system proposed by APG III (2009).

Data analysis

The diversity of the flower-visiting community was assessed by the Shannon index (1-D) and dry and wet seasons were compared using the t-test diversity at the 5% level. Equitability was obtained by the Pielou index (J^c). These indices and tests were calculated using the PAST program 3.20 (Hammer et al., 2001).

From the data of visitation, adjacency matrices were constructed with the species of bees plotted on the rows and the plants in the columns, using the abundance of bees captured in each plant. Two matrices were constructed considering the community of bees and plants visited in dry and wet season. From these matrices a tripartite graph was constructed for visualization of interactions between bees and plants in the dry and wet seasons. Connectance, nestedness (NODF) and robustness (HL) network were analyzed using the Bipartite package of program R 3.3.2 (R Development Core Team, 2016), also used for the construction of networks. Connectance (C=100 I/M) is the percentage of actually observed interactions (observed interactions=I) with respect to the total possible number of interactions in the network (M=BP, where B and P are the number of interacting bees and plants in the network, respectively) (Jordano, 1987). The nestedness was based on overlap and decreasing fill - NODF and the higher value of this index means greater nestedness of the network (Almeida-Neto et al., 2008). Nestedness occurs when specialist species tend to interact with more generalist species and these last one interact with each other (Bascompte et al., 2003). The robustness HL was calculated to evaluate the resistance of the bees to secondary extinctions in relation to the random extinction of plants and this metrics calculates the area below the extinction curve generated by secondary extinctions (Memmott et al., 2004).

The differences in the networks between the seasons were quantified by the Jaccard beta diversity index (Jaccard Beta Diversity-JBD), which is defined as the turnover of the interactions between the networks (following Novotny, 2009 and Kemp et al., 2017). JBD is partitioned into the effects of the turnover of plant species (Bp), floral visitor species (Bh), both plant and floral visitor species (Bph), and choices of floral visitor by plant species (Bo) between the seasons. This index was calculated in program R 3.3.2 (R Development Core Team, 2016).

Results

In total, 322 bees from 33 species of the families Apidae (18 species), Halictidae (8), and Megachilidae (7) were captured (Table 1). The richness of bees was similar between the seasons, presenting 22 species of bees in the wet season and 21 in the dry season and among these, 10 species were sampled on flowers in both seasons. However, abundance was higher in the wet season (60% of individuals) compared to the dry season (40%).

The bee diversity was higher in the dry season (H = 2.36) compared to the wet season (H = 2.08), and these values differ statistically (Diversity H' t-test: t = 2.068, p = 0.035). The equitability index was higher in the dry season (dry season J': 0.77; wet season J': 0.67) (Table 3).

The plants visited by these bees consisted of 34 species belonging to Fabaceae (8 species), Asteraceae (5), Solanaceae (4), and Malvaceae (2), in addition to 15 other families, each visited by one species (Table 2). A total of 47% of the plant species were visited exclusively in the dry season, 29% exclusively in the wet season, and 24% were visited in both seasons.

Augochloropsis sp1, Plebeia droryana (Friese) and Plebeia lucii Moure were the most abundant bee species and occurred in both seasons. Augochloropsis sp1 was particularly abundant in the wet season and interacted with a largest number of plant species in the dry season (5 in dry season, 8 in wet season and 10 in total). The second floral visitor most abundant and interacted with a largest number of plant in the dry season (6 in dry season, 3 in wet season and 8 in total) was *P. droryana*. In the wet season, *P. lucii* was the most abundant floral visitor and interacted with six plant species in total (2 in dry season and 4 in wet season).

The plants with the highest degree were distinct between the seasons; *Austroeupatorium* sp. and *Spermacoce verticillata* L. showed the highest number of links during the wet season. *Crotalaria* sp. and *Solanum hexandrum* Vell. were the most connected plants in the dry season.

The number of possible interactions was higher in the dry season, 504 interactions (48 interactions observed), than in the wet season, 396 interactions (40 interactions observed) (Fig 2). The connectance was similar between the both seasons (dry season: 0.095; wet season: 0.101).

A higher nestedness was observed in the wet season (11.588) when compared to the dry season (3.933). The value of the robustness (HL) in the dry season was similar (0.617) to the wet season value (0.580) (Table 3). Rare interactions occurred in both seasons; 10 and 12 species of bees interacting with only one plant species each in the dry and wet seasons, respectively.

Table 1. Species composition (and acronyms) and relative abundance (%) of the bees captured in flowers in the dry and wet seasons on the Itaoca Inselberg in the Atlantic Forest in southeastern Brazil.

Bee family	Species	Acronym	Dry Season	Wet Season
Apidae	Apis mellifera Linnaeus	Ap_me	-	0.5
	Bombus morio (Swederus)	Bo_mo	4.7	-
	Centris flavifrons (Fabricius)	Ce_fl	0.8	-
	Epicharis flava Friese	Ep_fl	0.8	-
	Eufriesea surinamensis (Linnaeus)	Eu_su	-	0.5
	Euglossa sp.	Eu_sp	-	1.0
	Eulaema cingulata (Fabricius)	Eu_ci	1.6	-
	Eulaema nigrita Lepeletier	Eu_ni	0.8	-
	Exomalopsis analis Spinola	Ex_an	-	0.5
	Melissodes sp.	Me_sp	-	3.2
	Oxaea flavescens Klug	Ox_fl	3.1	-
	Paratetrapedia fervida (Smith)	Pa_fe	3.9	1.0
	Plebeia droryana (Friese)	Pl_dr	33.6	11.9
	Plebeia lucii Moure	Pl_lu	7.0	16.1
	Trigona spinipes (Fabricius)	Tr_sp	3.1	1.0
	Xylocopa frontalis (Olivier)	Xy_fr	1.6	-
	Xylocopa nigrocincta Smith	Xy_ni	0.8	-
	Xylocopa ordinaria Smith	Xy_or	0.8	-
Halictidae	Ariphanarthra palpalis Moure	Ar_pa	-	0.5
	Augochlora sp.	Aa_sp	-	0.5
	Augochlorella sp.	Ae_sp	9.4	13.0
	Augochloropsis sparsilis (Vachal)	Au_sp	-	2.7
	Augochloropsis spl	Au_sp1	12.5	37.2
	Augochloropsis sp2	Au_sp2	0.8	3.2
	Dialictus sp.	Di_sp	0.8	-
	Pseudaugochlora graminea (Fabricius)	Ps_gr	1.6	-
Megachilidae	Coelioxys sp.	Co_sp	-	0.5
	Hypanthidium divaricatum (Smith)	Hy_di	3.1	0.5
	Hypanthidium foveolatum (Alfken)	Hy_fo	2.2	3.7
	Megachile nudiventris Smith	Me_nu	7.0	1.5
	Megachile pseudanthidioides Moure	Me_ps	-	0.5
	Megachile sp1	Me_sp1	-	0.5
	<i>Megachile</i> sp2	Me_sp2	-	0.5

The species composition of bees and plants was distinct between the seasons, as well as the interactions between them. Jaccard beta diversity (JBD) between wet and dry seasons networks was JBD=0.90. It was generated mostly by the turnover in plant species only (Bp=0.30) and the changes in bees choices between the seasons (Bo=0.26). The turnover of bees species only (Bh=0.17) and the turnover of plant and bee species (Bph=0.17) were less important.

Plant family	Species	Acronym	Dry Season	Wet Season
Apocynaceae	Asclepias curassavica L.	As_cu	1.6	-
Asteraceae	Austroeupatorium sp.	Au_sp	7.0	41.8
	Bidens pilosa L.	Bi_pi	1.6	-
	<i>Conyza</i> sp.	Cn_sp	0.8	-
	Emilia sonchifolia (L.) DC. ex Wight	Em_so	-	2.1
	Vernonanthura phosphorica (Vell.) H.Rob.	Ve_ph	0.8	2.1
Boraginaceae	<i>Cordia</i> sp.	Co_sp	2.2	-
Commelinaceae	Commelina benghalensis L.	Co_be	-	0.5
Convolvulaceae	Jacquemontia aff. confusa Meisn.	Ja_co	2.2	-
Cucurbitaceae	Momordica charantia L.	Mo_ch	-	1.0
Euphorbiaceae	Croton sp.	Cr_sp	10.9	-
Fabaceae	Centrosema sp.	Ce_sp	-	0.5
	Chamaecrista sp.	Ch_sp	0.8	-
	Crotalaria sp.	Ct_sp	8.6	-
	Fabaceae Caesalpinoideae sp1	Fa_ca1	3.9	-
	Fabaceae Caesalpinoideae sp2	Fa_ca2	-	5.2
	Fabaceae Caesalpinoideae sp3	Fa_ca3	-	1.5
	Inga laurina (Sw.) Willd.	In_la	-	6.2
	Piptadenia gonoacantha (Mart.) J.F.Macbr.	Pi_go	0.8	-
Lamiaceae	Ocimum basilicum L.	Oc_ba	5.5	-
Lecythidaceae	Lecythis sp.	Le_sp	3.1	-
Malpighiaceae	Amorimia maritima (A.Juss) W.R.Anderson	Am_ma	-	4.6
Malvaceae	Pavonia sidifolia Kunth	Pa_si	10.9	-
	Sida rhombifolia L.	Si_rh	7.8	1.0
Melastomataceae	Tibouchina sp.	Ti_sp	-	0.5
Musaceae	Musa paradisiaca L.	Mu_pa	3.1	1.0
Myrtaceae	Psidium sp.	Ps_sp	6.3	-
Piperaceae	Peperomia rubricaulis (Nees) A.Dietr.	Pe_ru	-	4.6
Rubiaceae	Spermacoce verticillata L.	Sp_ve	7.0	22.7
Solanaceae	Aureliana fasciculata (Vell.) Sendtn.	Au_fa	1.0	-
	Solanum cordifolium Dunal	So_co	3.1	-
	Solanum hexandrum Vell.	So_he	6.3	0.5
	Solanum sp1	So_sp1	3.1	1.0
Verbenaceae	Stachytarpheta cayennensis (Rich.) Vahl	St_ca	1.6	3.2

Table 2. Species composition (and acronyms) of the plants visited by bees and relative abundance of their visitors in the dry and wet seasons on the Itaoca Inselberg in the Atlantic Forest in southeastern Brazil.

Discussion

The bee-plant interactions differ between the dry and wet seasons, mainly due to the alteration in the composition of the plant species and the change in the choice of the bees for the floral resources. Changes in abundance and composition of flower resources between the seasons influenced the choices of plants by the bees. *Augochloropsis* sp1 visited mainly flowers of *Austroeupatorium* sp. in the wet season, and flowers of *S. verticillata* in the dry season, even when the two plants flowered in both seasons. In the wet season, *P. droryana* most

frequently visited *Inga laurina* (Sw.). Willd flowers and in the dry season, *Croton* sp. and *Pavonia sidifolia* Kunth. Kaiser-Bunbury et al. (2014) studying interactions in an inselberg also verified the importance of floristic composition in the structure of the bee-plant networks, similar to observed in this study.

Besides that, *forbidden links* need to be also considered in the discussion about the changes of interactions between the seasons. *Forbidden links* are made up of links that do not occur due to phenotypic or temporal variation of the species in which, put simply, the species of bees and plants are not found together in time or space (Jordano et al., 2003).

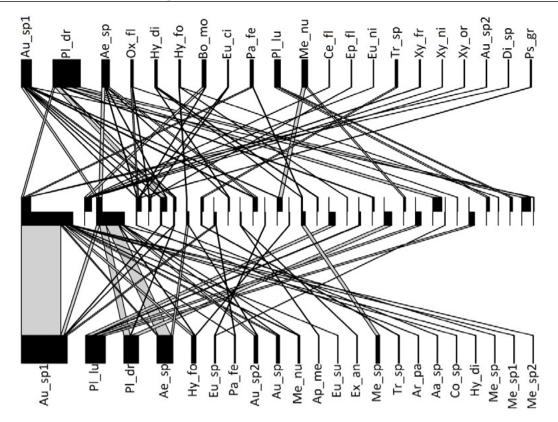


Fig 2. Bee-plant interactions in tropical Atlantic Forest at Itaoca Inselberg, southeastern Brazil. The species are represented by bars: plant species in the center and bee species on bottom (wet season) and top (dry season). The size of links indicates the number of interactions. The acronyms of plants from left to right are: Au_sp, Ct_sp, Sp_ve, So_he, So_co, Si_rh, So_sp1, Ve_ph, Mu_pa, Em_so, Bi_pi, Mo_ch, Oc_ba, Co_be, Ps_sp, Ce_sp, St_ca, As_cu, Fa_ca2, Cn_sp, Fa_ca3, Co_sp, In_la, Ja_co, Am_ma, Cr_sp, Ti_sp, Ch_sp, Pe_ru, Fa_ca1, Pi_go, Le_sp, Pa_si, Au_fa. The acronyms are according to Tables 1 and 2.

The interactions between bees and plants can vary on different spatial and temporal scales, influenced by several factors such as the flowering period of the plants, the activity period of the bees and competition (Olesen et al., 2008; Carstensen et al., 2014).

The high diversity of bees found in the dry season reflects the greater uniformity in the distribution of abundance, since the richness was similar between the seasons and the

Table 3. Metrics of interaction networks between bees and plants in the dry and wet seasons at Itaoca Inselberg in the Atlantic Forest in southeastern Brazil.

Network Metrics	Seasonal Sampling		
Network Metrics	Dry	Wet	
Richness	21 bees-24 plants	22 bees-18 plants	
Degree of bees (min-max)	1-8	1-5	
Degree of plants (min-max)	1-6	1-11	
Nº possible interactions	504	396	
Nº observed interactions	48	40	
Connectance	0.095 (9%)	0.101 (10%)	
Nestedness (NODF)	3.933	11.588	
Robustness (HL)	0.617	0.580	

abundance of bees was higher in the wet season. In this time, *Augochloropsis* sp1 was responsible for 37% of visits on flowers, mainly *Austroeupatorium* sp. (32%), and the dominance of this bee species and also of *P. droryana* and *Augochlorella* sp. may explain the low diversity in the wet season. The composition of the bees and mainly of the plants varied strongly between the seasons, indicating that the majority of bee and plant species were replaced seasonally. The availability of flowering plants and the choice by the visitors influenced the temporal variation in their interactions.

Despite the distinct composition of bees and plants observed between the seasons, the values of the network metrics, such as connectivity and robustness, were not discrepant between them, which may indicate relative stability of the network topology. Studies on network interactions of bees and plants point out that the topological metrics of the networks can remain stable despite variations in the composition of the species (Olesen et al., 2008; Petanidou et al., 2008; Dupont et al., 2009), where the existing species may be replaced by other topologically similar species (Dupont et al., 2009). On the other hand, o nestedness (NODF) differed between the seasons, demonstrating greater cohesion and resilience in wet season, despite both values were relatively low. In areas with marked seasonality, such as the studied area, these topological metrics were observed to be different between dry and wet seasons (Santos et al., 2014), probably influenced by the seasonal character of the vegetation. Especially the distinction in nestedness is probably related to different abundances of interactions between the seasons. The most nested network of the wet season was characterized by more generalist interactions composing the core of the network. In inselberg areas in Mahe, the largest granitic island of the Seychelles (Indian Ocean), the composition of the species and their abundance in the communities were the main determinants for the network architecture (Kaiser-Bunbury et al., 2014). Those authors emphasized that the floral composition determined the major changes in the patterns of network interactions and was mainly explained by the temporal variation.

The most abundant species in both seasons was *Augochloropsis* sp1 associated with its generalist behavior in the interaction with the largest number of plant species visited in both seasons, mainly in Asteraceae. Most species of this genus occur throughout the year and exhibit polylectic behavior, most frequently in species of Asteraceae (Mouga & Krug, 2010; Dec & Mouga, 2014).

Other bee species common to the two seasons, *P. droryana* and *P. lucii*, were abundant and generalist in use of floral resources. This amplitude of the food niche, the activity throughout the year, and the greater abundance may be related to eusocial behavior of these stingless bees, besides colony permanence, and recruitment foraging habits (Roubik, 1989). Despite the similar behavior and corporal size, these two bee species presented differences in the visited plant species. This behavior would avoid competition in resource use, that can be an important factor for the coexistence of eussocial species.

The bees of the *Xylocopa* genus sampled in this study were observed only in the dry season in flowers of *Crotalaria* sp. Data obtained by Bernardino and Gaglianone (2008) in a coastal area in the same region also pointed out *Xylocopa* bees is higher numbers in the dry season. Flowers of *Crotalaria* are considered important resources for bees due to their high concentration of nectar and availability of pollen from the anthesis to the total wilt of the flower (Marques et al., 2013), both resources collected by females of *Xylocopa*.

The most abundant Megachilidae species, *Hypanthidium divaricatum* (Smith), *Hypanthidium foveolatum* (Alfken) and *Megachile nudiventris* Smith, have been observed in the two seasons, mainly on flowers of Asteraceae, Convolvulaceae and Myrtaceae. The species of Megachilidae with smaller abundance were sampled only in the wet season. Other studies in semi-deciduous seasonal forests in the state of Rio de Janeiro emphasized the nesting preference of these bees during the wet season (Marques & Gaglianone, 2008; Teixeira et al., 2011).

Euglossina bees were sampled in both seasons, mainly *Euglossa* and *Eufriesea* in the wet season and *Eulaema* in the dry season. Aguiar and Gaglianone (2011) sampled

abundance peaks in both seasons to Euglossina captured with aromatic baits in the same study area. The explanation for this could be related to flowering peaks, nesting activities and adult emergence (Roubik & Hanson, 2004). *Eufriesea surinamensis* (Linnaeus) is a seasonal species, with adult activity restricted to the wet season in the study area and in other semideciduous seasonal forests (Aguiar & Gaglianone, 2011).

Species of bees unique to the dry season or the wet season demonstrated specialist behavior, visiting only one or two plant species. Most of these bee species were observed in plants that were common to both seasons, mainly *Austroeupatorium* sp. and *S. hexandrum*. This is expected considering the model preferential attachment, since a new species is more likely to interact with species that already has many links in the network (Barabási & Albert, 1999; Olesen et al., 2008).

These seasonal variations of the interaction network may occur in accordance with natural cycles and fluctuations in flowering patterns of plants and in populations of floral visitors and can also be influenced by environmental conditions. Future studies should investigate the causes of temporal variations in interactions between plants and pollinators, especially those that may be related to conservation of priority areas such as inselbergs, in order to identify actions that can minimize human impact and support conservation initiatives in these threatened ecosystem.

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