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Network of Bee-plant Interactions and Recognition of Key Species in Semideciduous Forest

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Abstract

Bees are the most effective pollinators of native plants, contributing to the maintenance of many ecosystems, including forests. Studies about networks of bee-plant interactions are critical for conservation and habitat management of native pollinators. This study aimed to determine the richness of flower-visiting bees in a fragment of the Semideciduous Forest (SF) in Uberlândia-MG, identify the plants visited by them and build the bee-plant interactions network in this fragment. The study was conducted between October 2010 and September 2011 along a transect of 200 meters on the edge of the forest, with monthly collections performed from 8:00 am to 2:30 pm. We yielded the bee-plant interaction networks and calculated the NODF index and betweenness centrality. We collected 70 bee species and 25 plant species. The network of interactions was nested (NODF = 10.97, $P = 0.03$). *Apis mellifera* Linnaeus and *Merremia macrocalyx* (Ruiz & Pav.) O'Donell showed the highest centrality. The nestedness of the bee-plant interaction confers stability to the network, demonstrating its importance for the fragment conservation. It is likely that *M. macrocalyx* is a key species in this network since this plant attracted the highest number of bee species and showed the highest centrality, contributing to network cohesion.

Introduction

The scanty information about species richness, diversity, taxonomy, distribution and population dynamics, along with the impact of human activities on most bee species represent the major environmental issues that hinder the conservation of native areas in Latin America (Freitas et al., 2009). Determining the diversity of both the fauna and flora of many ecosystems is the starting point for specific investigations, such as assessing the role of pollinators in maintaining the flora (Anacleto & Marchini, 2005). The importance of this matter arises therefrom.

Studies about networks of interactions between bees and plants are fundamental for the conservation and management of native pollinators habitat (Biesmeijer et al., 2005). Network approaches to ecological research emphasize the pattern of interactions among species, i.e., how the links (interactions) are systematized within the network, rather than only providing the identity of the species that constitute a community (Bascompte, 2009).

Thus, investigations of bee-plant interaction networks can provide relevant information about the community, such as the identification of key species (Martín Gonzalez et al., 2010) and coexistence and stability of species in the system (Bascompte & Jordano, 2007). Consequently, the identification of key species in a community can be helpful in setting priorities and conservation goals (Jordán, 2009).

Inventories of the bee fauna are crucial for the knowledge of composition, geographic distribution patterns and relationships between fauna and flora. Several factors influence the determination of the richness and abundance of local fauna of bees. For example, the amount of food and diversity of available food sources, which favor the existence of large populations and greater consumer species richness, respectively (Silveira et al., 2002). Several surveys of bee species have been conducted in the Cerrado (Carvalho & Bego, 1996; Andena et al., 2009; Siqueira et al., 2012). The conservation status of this biome is becoming increasingly alarming because its vegetation is being hastily replaced

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by pasture and crops (Freitas et al., 2009). About 50% of the 2 million km^2 of the Cerrado original biome have been transformed into agricultural areas and pastures, besides other types of use, such as planted forests and urban areas (Silva et al., 2006). As a result of this fragmentation process, plant and animal populations have been lost and extinctions may occur.

The Semideciduous Forests (SF) are among the most threatened and fragmented ecosystems in the world. The history of disturbance in Brazilian SF reduced these forests to small scattered fragments and, consequently, led to biodiversity loss in these environments (Santos et al., 2009). Few studies on bee communities have been conducted in SF and studies on bee-plant interactions are also rare in this phytophysiognomy.

Due to anthropic activities, such as habitat destruction for agriculture and excessive use of pesticides, bee populations have been drastically reduced (Michener, 2000). The impoverishment of pollinators in forest fragments can cause changes in gene flow within and among plant populations and directly affect natural regeneration (Engel et al., 1998). Bees are the main pollinators of most species of tropical forest trees (Michener, 2000), playing an important role in the conservation of plants and animals that depend on them.

This study aimed to deepen our knowledge about the richness and composition of flower-visiting bees in a fragment of semideciduous forest, analyzing the patterns of interactions between bees and visited plants.

Material and Methods

Study area

This study was conducted in a fragment of semideciduous forest (18º 51’ 36’’ S and 48º 13’ 53’’ W) located in the legal reserve of the “Fazenda São José”, in Uberlândia, Minas Gerais, Brazil. The fragment has 22 hectares. Its interior shows evidence of selective logging and cattle trails and the surrounding matrix is composed of monoculture eucalyptus plantations, annual crops and pastures (Prado Júnior et al., 2011).

The regional climate presents two distinct seasons, a rainy season that extends from October to March and a dry season, from April to September. The annual rainfall ranges from 1160 to 1460mm/year and the average annual temperature varies between 23 and 25°C, and is uniform throughout the year (Alves & Rosa, 2008).

Data collection

The study was conducted between October 2010 and September 2011, totalizing one year of sampling. Bees were collected with entomological nets during their visits to flowers, and eventually during flight, along a 200 metre transect at the forest edge, the most representative section in number of flowering plants. There were no collections within the fragment due to the difficulty in simultaneously observing and collecting, since the flowers were several feet high, preferably in the canopy.

Bees were collected from 8:00 to 14:30, the time of highest foraging activity. The collection effort involved the work of two collectors during 30 minutes every hour, totalizing 84 hours of sampling. At each time, the temperature and relative humidity were recorded using a digital thermo-hygrometer.

Only the composition of bee species was sampled. The abundance of these insects was not quantified. Bees were sacrificed in a chamber with ethyl acetate. After undergoing pinpricking, they were deposited in the “Coleção do Museu de Biodiversidade do Cerrado (MBC)”, located in the “Laboratório de Ecologia e Comportamento de Abelhas (LECA)” of the “Instituto de Biologia (INBIO)” at the “Universidade Federal de Uberlândia (UFU)”.

The plants visited by bees were marked, and three flowering branches of each type were collected and deposited in the “Herbarium Uberlandense (HUFU)” of UFU. Plants and bees were subsequently identified using identification keys. We had the help from experts, when necessary.

Data Analysis

To evaluate sampling sufficiency, we elaborated the rarefaction curve using the program EstimateS 8.2.0 (Colwell, 2006). The nonparametric estimator Jack 1 was used to verify if the species richness value found corresponded to the estimated value. This estimator was chosen because it is one of the most accurate richness estimators (Palmer, 1990; Krebs, 1999).

Bee-plant interactions were represented in a bipartite graph (network) generated by the bipartite package (Dormann et al., 2008) in R 3.0.1 software (R Development Core Team - http://www.r-project.org). The centrality of species was calculated by the program Pajek (Program for Large Network Analysis) (Batagelj & Mrvar, 1998).

The nestedness index NODF (Nestedness metric based on Overlap and Decreasing Fill) was calculated using Aninhado 3.0.3 software (Guimarães & Guimarães, 2006). We used a null model which assumes that probability of each cell being occupied is the average of probabilities of occupancy of its row and column. Biologically, this means that probability of drawing an interaction is proportional to the level of generalization (degree) of both the animal and the plant species (Bascompte et al., 2003). The higher the value of this index, the greater the nestedness network (Almeida-Neto et al., 2008). Nested networks are characterized by interactions between generalists, specialists interacting with generalists and absent or rare interactions between specialists (Guimarães et al., 2006).

For the calculation of centrality, the Index of Betweenness Centrality was chosen. This index shows the importance of a species as a connector between different parts of the network and evaluates the contribution of each species to its cohesion (Borgatti & Everrett, 2006).

Results

Throughout the study period, 74 bee species distributed in five families were collected (Table 1). Four species were caught only in flight (*Anthidioctes megachiloides, Augochlora* sp.5*, Eulaema nigrita* and *Lorocanthidium* sp.). Apidae was the most represented family with 48 species, followed by Halictidae and Megachilidae. Andrenidae and Colletidae were the less representative families. Meliponina was the group with the highest richness, with 15 species sampled. The rarefaction curve showed no tendency to stabilization. The value found for the richness estimator Jack 1 was 114.51, suggesting that approximately 65% of the species in the area were sampled (Figure 1).

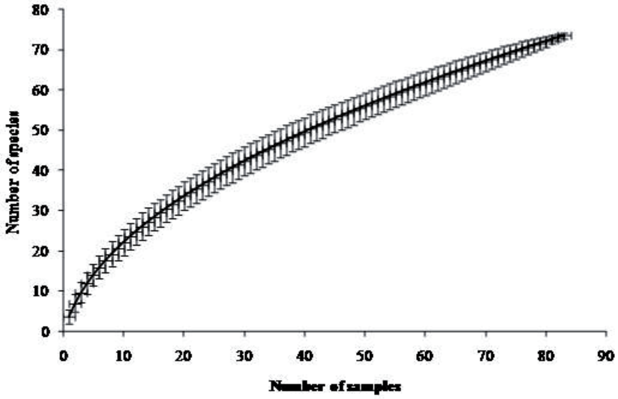

Fig 1. Rarefaction curve representing the cumulative number of species sampled in function of the quantity of samples in Semideciduous Forest of "Fazenda São José", Uberlândia-MG, in 2010 and 2011.

Table 1. Bee species collected on the edge of the Semideciduous Forest of "Fazenda São José", Uberlândia-MG, in 2010 and 2011. Classification based on Silveira et al. (2002).

Family	Subfamily	Tribe	Subtribe	Species	Voucher Number
Andrenidae	Oxeinae			*Oxaea flavescens* Klug	MBC-372
	Panurginae	Calliopsini		*Acamptopoeum prinii* (Holmberg)	MBC-361
		Protandrenini		*Cephalurgus anomalus* Moure & Lucas de Oliveira	MBC-230
Apidae	Apinae	Apini	Apina	*Apis mellifera* Linnaeus	MBC-70
			Bombina	*Bombus morio* (Swederus)	MBC-653
			Euglossina	*Euglossa* (*Euglossa*) sp.	MBC-284
				Euglossa imperialis Cockerell	MBC-286
				Euglossa pleosticta Dressler	MBC-285
				Eulaema nigrita Lepeletier	MBC-288
			Meliponina	*Cephalotrigona capitata* (Smith)	MBC-337
				Leurotrigona muelleri (Friese)	378
				Melipona rufiventris Lepeletier	MBC-228
				Oxytrigona cf. *tataira* Smith	MBC-01
				Paratrigona lineata (Lepeletier)	MBC-340
				Partamona ailyae Camargo	440
				Partamona combinata Pedro & Camargo	317
				Plebeia droryana (Friese)	231
				Scaptotrigona aff. *depilis* (Moure)	MBC-139
				Scaptotrigona sp.	459
				Tetragona clavipes (Fabricius)	MBC-174
				Tetragonisca angustula (Latreille)	MBC-199
				Trigona cilipes (Fabricius)	463
				Trigona hyalinata (Lepeletier)	MBC-57
				Trigona spinipes (Fabricius)	MBC-111
		Centridini		*Centris* (*Centris*) *aenea* Lepeletier	434
				Centris (*Melacentris*) *collaris* Lepeletier	MBC-274
				Centris (*Trachina*) sp.	MBC-371
				Centris tarsata Smith	MBC-370
				Epicharis (*Hoplepicharis*) affinis	MBC-271
				Epicharis (*Epicharana*) *flava* (Friese)	MBC-262

Table 1. Bee species collected on the edge of the Semideciduous Forest of "Fazenda São José", Uberlândia-MG, in 2010 and 2011. Classification based on Silveira et al. (2002) (Continuation).

Family	**Subfamily**	**Tribe**	**Subtribe**	**Species**	**Voucher Number**
Apidae	Apinae	Emphorini		*Ancyloscelis apiformis* (Fabricius)	395
		Exomalopsini		*Exomalopsis auropilosa* Spinola	260
				Exomalopsis fulvofasciata Smith	MBC-275
		Tapinotaspidini		*Chalepogenus* sp.	MBC-295
				Monoeca cf. *brasiliensis* Lepeletier & Serville	MBC-315
				Monoeca planaltina Aguiar	423
				Monoeca sp.	460
				Paratetrapedia cf. *flaveola* Aguiar & Melo	MBC-289
				Paratetrapedia cf. *lugubris* (Cresson)	MBC-304
				Paratetrapedia connexa (Vachal)	176
				Paratetrapedia punctata Aguiar & Melo	MBC-313
				Tropidopedia flavolineata Aguiar & Melo	MBC-871
		Tetrapediini		*Tetrapedia* cf. *diversipes* Klug	MBC-310
				Tetrapedia cf. *ornata* (Spinola)	418
				Tetrapedia sp.	414
	Xylocopinae	Ceratinini		*Ceratina* (*Calloceratina*) *chloris* (Fabricius)	217
				Ceratina (*Crewella*) sp.1	MBC-650
				Ceratina (*Crewella*) sp.2	242
				Ceratina (*Crewella*) sp.3	223
				Ceratina sp.1	221
		Xylocopini		*Xylocopa* (*Neoxylocopa*) *suspecta* Moure & Camargo	MBC-339
Colletidae	Hylaeinae			*Hylaeus* cf. *nasutus* (Vachal)	220
				Hylaeus cf. *transversus* (Vachal)	135
				Hylaeus sp.1	146
				Hylaeus sp.2	148
		Augochlora sp.1		*Augochlora* sp.1	MBC-367
				Augochlora sp.2	305
				Augochlora sp.3	132
				Augochlora sp.4	137
				Augochlora sp.5	155
				Augochloropsis cf. *aurifluens* (Vachal)	MBC-216
				Augochloropsis cf. *hebescens* (Smith)	MBC-225
				Augochloropsis cf. *patens* (Vachal)	MBC-223
				Augochloropsis sp.1	MBC-364
				Augochloropsis sp.2	MBC-365
				Augochloropsis sp.3	MBC-366
				Pseudaugochlora graminea (Fabricius)	MBC-369
				Thectoclora sp.	149
				Temnosoma sp.	MBC-368
		Halictini		*Dialictus* sp.	MBC-322
Megachilidae	Megachilinae	Anthidiini		*Anthodioctes megachiloides* Holmberg	MBC-316
				Larocanthidium sp.	MBC-318
		Lithurgini		*Lithurgus huberi* Ducke	MBC-320
		Megachilini		*Megachile* (*Moureapis*) sp.	MBC-317

Bees visited flowers of 25 plant species belonging to 14 families (Supplementary Material). The most representative families were Sapindaceae, with 4 species of visited plants, followed by Fabaceae and Bignoniaceae, with 3 species each.

The network of interactions consisted of 70 species of bees and 25 species of plants and presented a nested pattern, NODF = 10.97 ($P = 0.03$) (Figure 2). *Merremia macrocalyx* was the plant with the highest betweenness centrality index, followed by *Coccoloba mollis* and *Banisteriopsis argyrophylla* (Table 2). Bees that had the highest centrality were *Apis mellifera*, *Paratrigona lineata* and *Paratetrapedia lugubris*, respectively (Table 2).

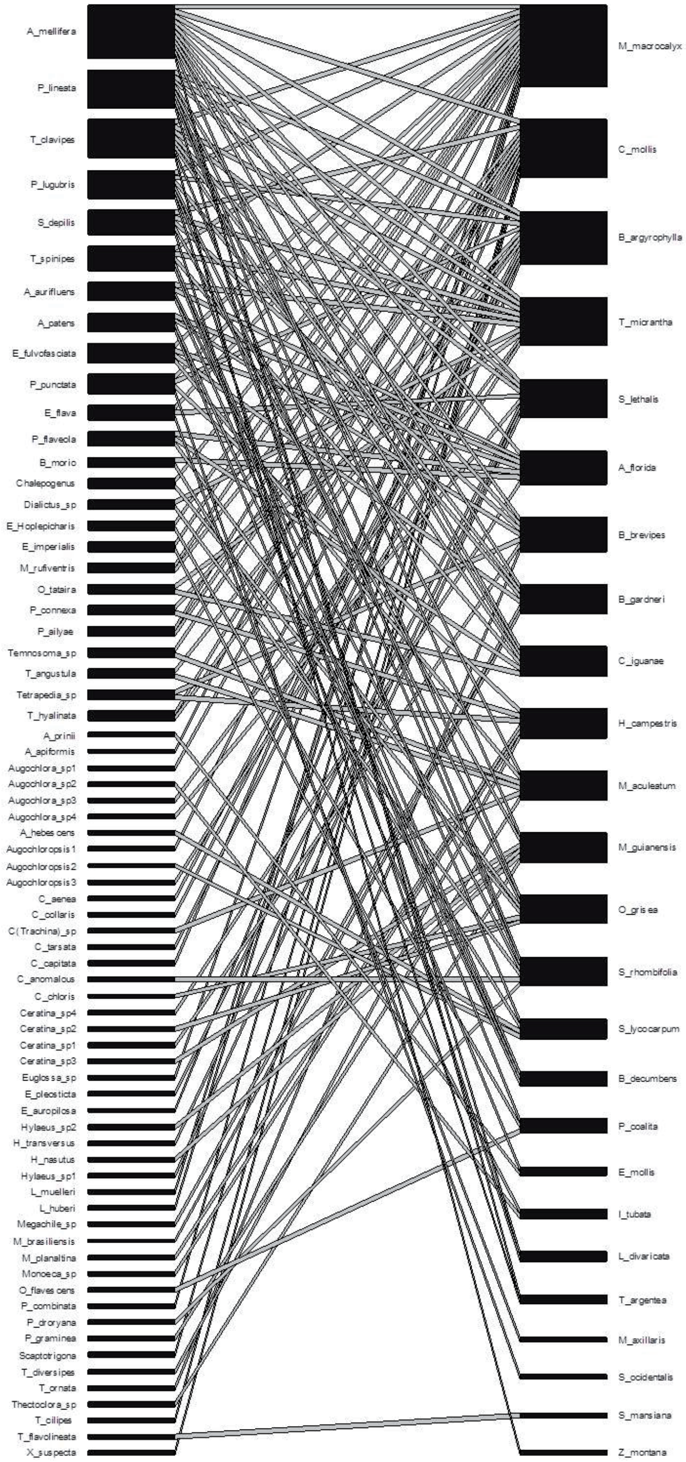

Fig 2. Bipartite graph of bee-plant interaction's network sampled in the Semideciduous Forest of "Fazenda São José", Uberlândia-MG, in 2010 and 2011. Bees are represented on the left side of the graph and plants on the right side.

Table 2. Values of the Betwenness Centrality Index for species of the network of bee-plant interaction sampled in the Semidecidous Forest of "Fazenda São José", Uberlândia-MG, in 2010 and 2011.

Bee species	Index	Plant	Index
Apis mellifera	0.305	*Merremia macrocalyx*	0.319
Paratrigona lineata	0.108	*Coccoloba mollis*	0.152
Tetragona clavipes	0.105	*Banisteriopsis argyrophylla*	0.174
Paratetrapedia cf. *lugubris*	0.097	*Trema micrantha*	0.107
Scaptotrigona aff. *depilis*	0.040	*Serjania lethalis*	0.100
Trigona spinipes	0.053	*Arrabidaea florida*	0.084
Augochloropsis cf. *aurifluens*	0.016	*Bauhinia brevipes*	0.101
Augochloropsis cf. *patens*	0.049	*Bidens gardneri*	0.058
Exomalopsis fulvofasciata	0.039	*Celtis iguanae*	0.035
Paratetrapedia punctata	0.079	*Heteropterys* cf. *campestris*	0.068
Epicharis flava	0.028	*Machaerium aculeatum*	0.056
Paratetrapedia cf. *flaveola*	0.010	*Matayba guianensis*	0.083
Bombus morio	0.010	*Oxalis grisea*	0.052
Chalepogenus sp.	0.008	*Sida rhombifolia*	0.052
Dialictus sp.	0.002	*Solanum lycocarpum*	0.045
E. (*Hoplepicharis*) affinis	0.012	*Brachiaria decumbens*	0.009
Euglossa imperialis	0.041	*Prestonia coalita*	0.022
Melipona rufiventris	0.013	*Elephantopus* cf. *mollis*	0.021
Oxytrigona cf. *tataira*	0.0003	*Ipomoea tubata*	0.021
Paratetrapedia connexa	0.015	*Luehea divaricata*	0.003
Partamona ailyae	0.013	*Terminalia argentea*	0.001
Temnosoma sp.	0.009	*Memora axillaris*	0.000
Tetragonisca angustula	0.006	*Senna ocidentalis*	0.000
Tetrapedia sp.	0.018	*Serjania mansiana*	0.000
Trigona hyalinata	0.011	*Zeyheria montana*	0.000

Note: Bee species that were not presented in the table obtained index equal to zero.

Bees presented the highest richness in May and September, both with 19 species (Figure 3). The greatest richness of flowering plants visited by bees occurred in April, with nine species (Figure 3).

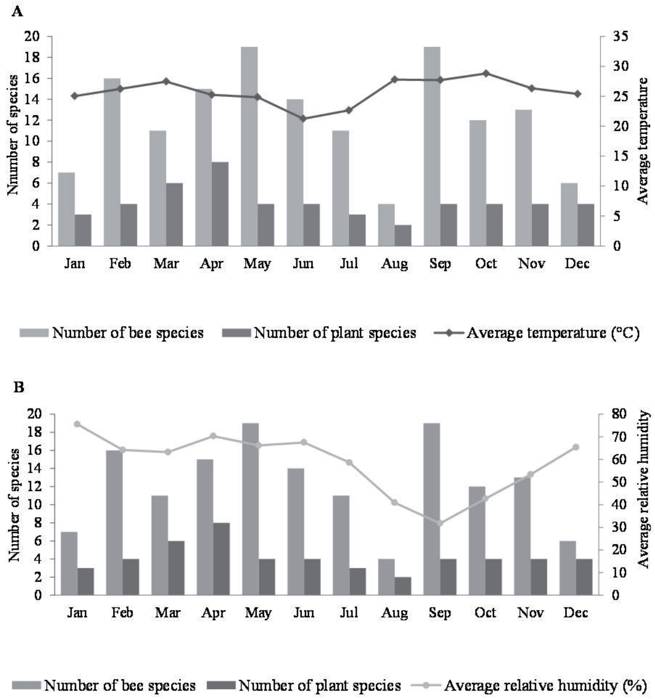

Fig 3. Richness of bees and plants and averages of abiotic data collected throughout the year of study at "Fazenda São José", Uberlândia-MG. (A) Average temperature. (B) Average relative humidity.

Discussion

The network was essential for the identification of key-species in the studied area. The nestedness pattern found in this study corroborates other researches in other types of vegetation.

One of the most important factors associated with the richness of bees is environmental heterogeneity. The more varied the floristic composition of the site, the greater the possibility of available niches providing a larger number of species living in the same area (Andena et al., 2009). Regarding bee fauna in any particular location, the greater the diversity of plants, the greater the variety of bees, since they are their potential pollinators (Michener, 2000). Thus, a high diversity of plants contributes to a high diversity of pollinators, which are one of the key components responsible for the maintenance of plant diversity (Michener, 2000).

For the maintenance of potential pollinators in an area, the preservation of nesting sites for bees, such as rotten tree trunks and bounds in the case of solitary bees are essential. Trees with hollows and abandoned ant and termite nests should be preserved to be used for social bee nesting sites (Cortopassi-Laurino et al., 2009). Thus, the conservation of the studied area subject of this research is extremely relevant. Its significance lies in the fact that it is a fragment located near an urban area that maintains important and diverse plant species, offering a possible refuge, and providing food resources for many bee species.

Regarding the bee richness, it was expected that the rarefaction curve was not stabilized, since samplings including all the species present in an area is not common in insect inventories due to the high diversity of this group (Gotelli & Colwell, 2001; Brosi et al., 2007). The extreme incidence of the Apidae family seems to be a characteristic pattern in the Brazilian Cerrado biome, since similar results have been found in other surveys of different types of vegetation in the Cerrado biome (Carvalho & Bego, 1996; Antonini & Martins, 2003; Anacleto & Marchini, 2005; Andena et al., 2012).

Apidae is one of the most diverse families widely distributed in Brazil and worldwide. It occurs in different biomes and under different environmental characteristics (Michener, 2000), which may explain the major representativeness of this family in this study and in others.

The Halictidae family, the second most representative in this study, has a worldwide distribution. However, it is more diverse in temperate regions, despite possessing some unique Neotropical genera (Michener, 1979). In ecosystems with disturbances, there is a trend towards increased species of Halictidae (Roubik, 1989), which may indicate that the studied semideciduous forest is a disturbed area.

The Andrenidae and Colletidae families had low occurrence in this study, and are poorly represented in the Neotropical region (Silveira & Campos, 1995), which may have contributed to the results. Colletidae is an Australian family, although some genera occur in South America (Silveira et al., 2002).

Silveira & Campos (1995) found that bees of the Cerrado biome compared to the fauna from other Brazilian biomes are characterized by the high representativeness of the tribes that collect oil (Centridini, Tapinotaspidini and Tetrapediini). For example, the species *Centris tarsata, Epicharis flava, Paratetrapedia flaveola, Tetrapedia diversipes,* and bee species of the subtribe Meliponina, have high representativeness, as we verified in this study.

The high centrality of *Apis mellifera* shows that this species is essential for the maintenance of the interactions network studied. *Apis mellifera* was the species that had the broadest niche, as it interacted with the largest number of plant species in the present study. Similar results were found in an area of Cerrado biome in the state of São Paulo (Andena et al., 2012) and in a review of inventories carried out in several regions of Brazil (Kleinert & Giannini, 2012). This fact may be related to its long daily and annual periods of foraging, high population density and sophisticated communication system (Roubik, 1989), allowing for a large number of plant species to be visited by these bees, resulting in a broader niche (Andena et al., 2012). *A. mellifera* is an exotic species scattered throughout various biomes, well adapted to different climatic conditions and presents generalist behaviour (Kleinert & Giannini, 2012). It is among the most important pollinators of natural environments and crops (Potts et al., 2010).

Amidst the most generalist bees sampled in this study, there were several species of Meliponina, such as *Paratrigona lineata*, *Tetragona clavipes*, *Scaptotrigona depilis* and *Trigona spinipes*. Other surveys carried out in the Cerrado biome have also reported large amplitude niches for some of these species

(Antonini & Martins, 2003; Nogueira-Ferreira & Augusto, 2007). The niche size may be related to their eusocial group behavior, perenniality of their colonies and generalized foraging and recruitment habits (Roubik, 1989). In general, social species are more generalists and, therefore, have broader niches than solitary bees (Biesmeijer et al., 2005).

The nestedness of the network observed in this study means that plants with few interactions are associated with generalist animals. However, specialist animals are associated with plants with many interactions, and generalists of one group interact with generalists of the other group, forming a dense core of interactions (Lewinsohn et al., 2006). Nested networks of bee-plant interactions were also found in studies in the Caatinga in the state of Bahia (Pigozzo & Viana, 2010) and in another area of cerrado *sensu stricto* in the State of São Paulo (Andena et al., 2012).

Nested networks are thoroughly cohesive, present a dense mass of interactions that extend throughout the community. They also have heterogeneity in their distribution of connections and possess possible alternative routes in response to environmental perturbations (Bascompte et al. 2003; Bascompte & Jordano, 2007). Thus, nested networks are asymmetric, with generalist species interacting with specialists, providing pathways for rare species to withstand environmental adversities and alternative routes for system responses to perturbations, such as deletion of a mutualist (Jordano, 1987). These characteristics exert fundamental influence on the network stability (Bascompte et al., 2006; Santos et al., 2010) and maintenance of biodiversity (Bascompte et al., 2006). Thus, the network of bee-plant interactions found in this study has important properties for the maintenance of the community of bees and plants.

In pollination systems, the most generalist species are usually key species in the network (Martín González et al., 2010). These species are vital to the network structure, functioning and resilience, playing a pivotal role in community cohesion (Martín González et al., 2010; Kleinert & Giannini, 2012). Not all nodes (species) are equally important for the dynamics and stability of the system (Jordán, 2009; Martín González et al., 2010). The importance of a node can be quantified by centrality indices (Freeman, 1979). In the present study, the plants that had the highest centrality indices compared to other species were *Merremia macrocalyx*, *Coccoloba mollis* and *Banisteriopsis argyrophylla*, which were also the plant species visited by more bee species. These plants are essential to the structure and stability of the network (Martín González et al., 2010), in other words, they are indispensable to the maintenance of the community, and suppression of these species can quickly affect other species (Jordán, 2006).

M. macrocalyx presents the highest centrality index and can be considered a key species in the obtained network of interactions. It is extremely relevant for conservation in the studied fragment since it contributes to the maintenance of the existing bee community. As a climbing plant, *M. macrocalyx* is a substantial element in the structure of the forest, helping maintain optimal microclimate conditions for germination and contributes to increased resistance to wind on the edges of the fragment (Engel et al., 1998). The considerable number of bee species foraging on *M. macrocalyx* observed in this study may be associated with the supply of available resources offered by its flowers, as corroborated by Neves et al. (2006). They reported that pollen remains available from the time of anthesis, early in the morning, and decreases after 15h. Nectar secretion is intensive in the morning with a decreasing tendency during the day.

Coccoloba mollis, the second most important species in our study, has inflorescences in terminal panicles, with many small and fragrant flowers with nectaries (Lorenzi, 1992). According to Lorenzi (1992), the flowers of this species are considered apicultural, which explains the high number of bee species collected visiting its flowers. The greatest richness of bees occurred in May and September coinciding with the flowering periods of *M. macrocalyx and C. mollis*, respectively, which attracted a large proportion of species sampled in these months.

The network of bee-plant interactions presented is nested. This aspect can be positive in case of disturbances since nested networks offer alternative routes for the maintenance of rare species. *M. macrocalyx* can be considered a key species in the studied area since it attracted a large number of bee species and presented the highest centrality in the network of interactions. This plant species is essential to the cohesion of the network as a whole, and greatly relevant to the conservation of the Cerrado biome.

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References

Almeida-Neto M., Guimarães P., Guimarães P. R. Jr., Loyola R. D. & Ulrich W. A. (2008). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos, 117: 1227-1239. doi: 10.1111/j.0030-1299.2008.16644.x.

Alves, K. A. & Rosa. (2008). Espacialização de dados climáticos do Cerrado mineiro. Hor. Cient., 8: 1-28.

Anacleto, D. A. & Marchini, L. C. (2005). Análise faunística de abelhas (Hymenoptera, Apoidea) coletadas no cerrado do Estado de São Paulo. Acta Scientarum-Biological Sciences, 27: 277-284. doi: 10.4025/actascibiolsci.v27i3.1315.

Andena, S. R., Nascimento, F. S., Bispo, P. C., Mechi, M. R., Mateus, S. & Bego, L. R. (2009). Bee communities (Hymenoptera: Anthophila) of the “Cerrado” ecosystem in São Paulo State, Brazil. Genetics and Molecular Research, 8: 766-774.

Andena, S. R., Santos, E. F. & Noll, F. B. (2012). Taxonomic diversity, niche width and similarity in the use of plant resources by bees (Hymenoptera: Anthophila) in a cerrado area. Journal of Natural History, 46: 1663–1687. doi: 10.1080/00222933.2012.681317.

Antonini, Y. & Martins, R. P. (2003). The Flowering-Visiting Bees at the Ecological Station of the Universidade Federal de Minas Gerais, Belo Horizonte, MG, Brazil. Neotropical Entomology, 32: 565-575. http://dx.doi.org/10.1590/S1519-566X2003000400006.

Bascompte, J. (2009). Disentangling the Web of Life. Science, 325, 416-419. doi: 10.1126/science.1170749.

Bascompte, J. & Jordano, P. (2007). Plant-Animal Mutualistic Networks: The Architecture of Biodiversity. Annual Review of Ecology Evolution and Systematics, 38: 567-93. doi: 10.1146/annurev.ecolsys. 38.091206.095818.

Bascompte, J., Jordano, P., Melián, C. J. & Olesen, J. M. (2003). The nested assembly of plant-animal mutualistic networks. Proceedings of the National Academy of Sciences U.S.A, 100: 9383-9387. doi: 10.1073pnas.1633576100.

Bascompte, J., Jordano, P. & Olesen, J. M. (2006). Asymmetric Coevolutionary Networks Facilitate Biodiversity Maintenance. Science, 312: 431-433. doi: 10.1126/science.1123412.

Batagelj, V. & Mrvar, A. (1998). Pajek - Program for Large Network Analysis. Connections, 21: 47-57.

Biesmeijer, J. C., Slaa, E. J., Castro, M. S., Viana, B. F., Kleinert, A. M. P. & Imperatriz-Fonseca, V. L. (2005). Connectance of Brazilian social bee – food plant networks is influenced by habitat, but not by latitude, altitude or network size. Biota Neotropica, 5: 1-9. http://dx.doi.org/10.1590/S1676-06032005000100010.

Borgatti, S. P. & Everett, M. G. (2006). A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Social Networks, 28: 466-484. doi: 10.1111/j.2008.0030-1299.16644.x.

Brosi, B. J., Daily, G. & Ehrlich, P. (2007). Bee community shifts with landscape context in a tropical countryside. Ecological Applications, 17: 418-430. http://dx.doi.org/10.1890/06-0029.

Carvalho, A. M. C. & Bego, L. R. (1996). Studies on Apoidea fauna of cerrado vegetation at the Panga Ecological Reserve, Uberlândia, MG, Brazil. Revista Brasileira de Entomologia, 40: 147-156.

Colwell, R. K. (2006). EstimateS: Statistical estimation of species richness and shared species from samples. Version 8. Available on: <purl.oclc.org/estimates>.

Cortopassi-Laurino, M., Araujo, D. A. & Imperatriz-Fonseca, V. L. (2009). Árvores neotropicais, recursos importantes para a nidificação de abelhas sem ferrão (Apidae: Meliponini). Mensagem Doce 100, http://www.apacame.org.br/mensagemdoce /100/ artigo4.htm

Dormann, C. F., Gruber, B. & Fründ, J. (2008) Introducing the bipartite Package: Analysing Ecological Networks. R News, 8: 8-11.

Engel, V. L., Fonseca, R. C. B. & Oliveira, R. E. (1998). Ecologia de lianas e o manejo de fragmentos florestais. Série Técnica IPEF, 12: 43-64.

Freeman, L. C. (1979). Centrality in Social Networks Conceptual Clarification. Social Networks, 1: 215-239. doi: 10.1016/0378-8733(78)90021-7.

Freitas, B. M., Imperatriz-Fonseca, V. L., Medina, L. M., Kleinert, A. M. P., Galetto, L., Nates-Parra, G. & Quezada-Euán, J. J. G. (2009). Diversity, threats and conservation of native bees in the Neotropics. Apidologie, 40: 332-346. doi: 10.1051/apido/2009012.

Gotelli, N. & Colwell, R. K. (2001). Quantifying biodiversity: Procedures and pitfalls in the measurement and comparison of species richness. Ecology Letters, 4: 379-391. doi: 10.1046/j.1461-0248.2001.00230.x.

Guimarães, P. R. & Guimarães, P. (2006). Improving the analyses of nestedness for large sets of matrices. Environmental Modeling Software, 21: 1512-1513. doi: 10.1016/j. envsoft.2006.04.002.

Guimarães Jr, P. R., Sazima, C., Reis, S. F. & Sazima, I. (2006). The nested structure of marine cleaning symbiosis: is it like flowers and bees? Biology Letters, 3: 51-54. doi: 10.1098/rsbl.2006.0562.

Jordán, F. (2009). Keystone species and food webs. Philosophical Transactions of the Royal Society B, 364: 1733–1741. doi:10.1098/rstb.2008.0335.

Jordán, F., Liu, W. & Davis, A. J. (2006). Topological keystone species: measures of positional importance in food webs. Oikos, 112: 535-546. doi: 10.1111/j.0030-1299.2006.13724.x.

Jordano, P. (1987). Patterns of mutualistic interactions on pollination and seed dispersal: connectance, dependence asymmetries, and coevolution. American Naturalist, 12: 657-677.

Kleinert, A. M. P. & Giannini, T. C. (2012). Generalist Bee Species on Brazilian Bee-Plant Interaction Networks. Psyche, 2012: 1-7. doi: 10.1155/2012/291519.

Krebs, C. J. (1999). Ecological Methodology. California: Benjamin Cummings.

Lewinsohn, T. M., Inácio Prado, P., Jordano, P., Bascompte, J. & Olesen, J. M. (2006). Structure in plant–animal interaction assemblages. Oikos, 113: 174-184. doi: 10.1111/j.0030-1299.2006.14583.x.

Lorenzi, H. (1992). Árvores brasileiras: manual de identificação e cultivo de plantas arbóreas nativas do Brasil. Nova Odessa: Plantarum.

Martín González, A. M., Dalsgaard, B. & Olesen, J. M. (2010). Centrality measures and the importance of generalist species in pollination networks. Ecological Complexity, 7: 36–43. doi:10.1016/j.ecocom.2009.03.008.

Michener, C. D. (1979). Biogeography of the Bees. Annals of the Missouri. Botanical Garden, 66: 277-347.

Michener, C. D. (2000). The bees of the world. Baltimore, Maryland: Johns Hopkins Univ Press.

Neves, E. L., Taki, H., Silva, F. O., Viana, B. F. & Kevan, P. G. (2006). Flower characteristics and visitors of *Merremia macrocalyx* (Convolvulaceae) in the Chapada Diamantina, Bahia, Brazil. Lundiana, 7: 97-102.

Nogueira-Ferreira, F. H. & Augusto, S. C. (2007). Amplitude de nicho e similaridade no uso de recursos florais por abelhas eussociais em uma área de cerrado. Bioscience Journal, 23: 45-51.

Palmer, M. W. (1990). The Estimation of Species Richness by Extrapolation. Ecology, 71: 1195-1198. doi: 10.2307/1937387.

Pigozzo, C. M. & Viana, B. F. (2010). Estrutura da rede de interações entre flores e abelhas em ambiente de caatinga. Oecologia Australis, 14: 100-114.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O. & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. Trends in Ecology and Evolution, 25: 345-353. doi: 10.1016/j.tree.2010.01.007.

Prado Júnior, J. A. Lopes, S. F., Vale, V. S., Oliveira, A. P., Gusson, A. E., Neto, O. C. D. & Schiavini, I. (2011) Estrutura e caracterização sucessional da comunidade arbórea de um remanescente de floresta estacional semidecidual, Uberlândia, MG. Caminhos da Geografia, 12: 81-93.

Roubik, D. W. (1989). Ecology and natural history of tropical bees. New York, Cambridge: University Press.

Santos, G. M. M., Aguiar, C. M. L. & Mello, M. A. R. (2010). Flower-visiting guild associated with the Caatinga flora: trophic interaction networks formed by social bees and social wasps with plants. Apidologie, 41: 466-475. doi: : 10.1051/apido/2009081.

Santos, K., Kinoshita, L. S. & Rezende, A. A. (2009). Species composition of climbers in seasonal semideciduous forest fragments of Southeastern Brazil. Biota Neotropica, 9: 175-188. http://dx.doi.org/10.1590/S1676-06032009000400018.

Silva, J. F., Fariñas, M. R., Felfili, J. M. & Klink, C. A. (2006). Spatial heterogeneity, land use and conservation in the cerrado region of Brazil. Journal of Biogeography, 33: 536-548. doi: 10.1111/j.1365-2699.2005.01422.x.

Silveira, F. A. & Campos, M. J. O. (1995). A melissofauna de Corumbataí (SP) e Paraopeba (MG) e uma análise biogeográfica das abelhas do cerrado brasileiro (Hymenoptera: Apoidea). Revista Brasileira de Entomologia, 39: 371-401.

Silveira, F. A., Melo, G. A. R. & Almeida, E. A. B. (2002). Abelhas brasileiras: sistemática e identificação. Belo Horizonte: Ministério do Meio Ambiente, Probio – PNUD, Fundação Araucária.

Siqueira, E. N. L., Bartelli, B. F., Nascimento, A. R. T. & Nogueira-Ferreira, F. H. (2012). Diversity and nesting substrates of stingless bees (Hymenoptera, Meliponina) in a forest remnant. Psyche, 2012: 1-9. doi: 10.1155/2012/370895.

Supplementary Material. Plant species visited by bees in the Semideciduous Forest of "Fazenda São José", Uberlândia-MG, in 2010 and 2011.

Family	Species	Voucher Number
Apocynaceae	*Prestonia coalita* (Vell.) Woodson	60686
Asteraceae	*Bidens gardneri* Baker	60836
	Elephantopus mollis Kunth	60835
Bignoniaceae	*Arrabidaea florida* DC.	PL18
	Memora axillaris K. Schum.	60688
	Zeyheria montana Mart.	PL38
Cannabaceae	*Celtis iguanae* (Jacq.) Sarg.	58978
	Trema micrantha (L.) Blume	58977
Combretaceae	*Terminalia argentea* Mart.	PL45
Convolvulaceae	*Ipomoea tubata* Nees	PL26
	Merremia macrocalyx (Ruiz & Pav.) O'Donell	60685
Fabaceae	*Bauhinia brevipes* Vogel	PL41
	Machaerium aculeatum Raddi	60690
	Senna occidentalis (L.) Link	PL27
Malvaceae	*Luehea divaricata* Mart.	PL42
	Sida rhombifolia L.	PL23
Malpighiaceae	*Banisteriopsis argyrophylla* (A. Juss.) B. Gates	60166
	Heteropterys campestris A. Juss.	60164
Oxalidaceae	*Oxalis grisea* A. St.-Hil. & Naudin	PL12
Poaceae	*Brachiaria decumbens* Stapf	PL15
Polygonaceae	*Coccoloba mollis* Casar.	58980
Sapindaceae	*Matayba guianensis* Aubl.	PL6
	Serjania lethalis A. St.-Hil.	58972
	Serjania mansiana Mart.	60687
Solanaceae	*Solanum lycocarpum* A. St.-Hil.	PL8