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Food Niche of Solitary and Social Bees (Hymenoptera: Apoidea) in a Neotropical Savanna

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Abstract

In this study, we investigated the group of floral resources that support bee populations in a savanna area and how bee species use these food resources, with an emphasis on the breadth and overlap of trophic niches. The interactions between 75 bee species and 62 plant species were recorded on a Brazilian savanna area. The bee species explored a diverse set of plant species, but concentrated the collection of resources in a few species. The trophic niche breadth of the eusocial bees ranged from 0.77 to 2.59, while in non-eusocial bees the variation was from 0.35 to 1.99. The distribution of the samples over a long period favored a robust characterization of the food niche of the bee populations. *Byrsonima sericea*, *Serjania faveolata*, and *Stigmaphyllon paralias* were the plant species with the highest number of links with bees. In general, the trophic niche overlap was low, with 75% of pairs of bee species having a niche overlap (NO) less than 0.33. Only four pairs showed high overlap (NO>0.70) and all cases were related to the exploitation of floral resources provided by *B. sericea*, a key resource for the maintenance of the local bee fauna, an oil and pollen provider.

Introduction

Bee populations are at risk in several parts of the world. The removal of native vegetation to expand agricultural areas has been one of the factors with a significant contribution to the fragmentation and reduction of natural and semi-natural habitats. Deforestation reduces the diversity of plants used as food resources, nesting substrates, and sources of materials necessary for bee nesting (Freitas et al., 2009; Kevan, 2018). Knowledge about food plants used by bees is important to support habitat restoration programs and the conservation of bee populations, as well as to subsidize beekeeping (Maia-Silva et al., 2020). In addition, it is necessary to produce a scientific knowledge basis capable of subsidizing friendly agricultural practices to pollinators. Therefore, efforts must be made to identify the resources necessary for the persistence of bee populations in these habitats.

Vizentin-Bugoni et al. (2018) pointed out that there is a notable gap in plant-pollinator network studies in Central Neotropical Savanna and that studies should be conducted in these areas of geographical gaps so that the spatial variation in plant-pollinator networks is better understood. The available database on the food plants exploited by bees is best known in the most southern part of the Brazilian savanna (= Cerrado) (19° to 24° S) (Pedro & Camargo, 1991; Carvalho & Bego, 1997; Andena et al., 2005; 2012; Biesmeijer & Slaa, 2006), however in the northern and middle portions of the Cerrado domain studies are scarce (Martins, 1995; Pacheco-Filho et al., 2015; Souza et al., 2018).

In this study, we investigated bee-plant interactions, focusing on which plants are most important for maintaining bee populations in an area in the middle portion of the Brazilian Cerrado domain, which has undergone rapid agricultural expansion in the past two decades. This is an area of high



interest for biodiversity conservation because it is located in the buffer zone of the Chapada Diamantina National Park (CDNP). The aim of this study was to investigate the resources utilization by bee populations, i.e., measuring their realized niches, which are delimited by interspecific interactions (Chesson, 2000; Biesmeijer & Slaa, 2006). We seek to use niche analysis tools to assess the interactions between bee species and between them and the associated flora. Our hypothesis is that bee species with similar requirements use a similar set of resources. For example, oil-collecting bees depend on a specific floral resource (Neff & Simpson, 2017), which is produced by a small subset of the melitophilous flora. Eusocial bees have similar requirements, as they continually depend on pollen and nectar sources to maintain their perennial colonies (Roubik, 1989). Our prediction is that regardless of the richness of flowering plant species, some plant species will be primarily exploited by bees, determining that bee species with similar requirements have higher rates of overlap with each other, than with species with different requirements.

Material and Methods

Study area

In this region there is a mosaic of phytophysiognomies, such as campo rupestre (rupestrian fields, sandstone outcrop vegetation), cerrado (Brazilian savanna), caatinga (seasonally dry forest), sub-montane to montane semi-deciduous seasonal forests, sub-montane to montane evergreen riparian forests, wetlands and capitinga (Harley, 1995; Funch et al., 2009), sometimes separated by only a few kilometers. The climate is tropical humid, characterized by a marked seasonality. The rainiest period usually occurs from December to April while August to November is the driest period (Jesus et al., 1983). The mean annual rainfall in the area varies from 600 to 1000 mm, with a mean temperature of 22° C (CEI, 1994).

Three sites, 900 to 1,500 m apart, located in the buffer zone of the Chapada Diamantina National Park (CDNP; 12° 20' - 12° 25' S; 41° 35' - 41° 15' W), municipality of Palmeiras, Bahia State, Brazil, were sampled. The local vegetation is a cerrado type with phytophysiognomy of herbaceous–shrubby field, with small, scattered trees. The species *Byrsonima sericea* DC and *Byrsonima cydoniifolia* A. Juss. (Malpighiaceae) were very abundant plant species in the three locations (Aguiar et al., 2017a).

Sampling

We collected bees that visited plants to gather floral resources in 2013 (October, November, and December), 2014 (January, February, March, September, and November) 2015 (February, March, April, August, October) and 2016 (January, March, May and July). In each of the 17 collection expeditions, bee-plant interactions were recorded over two consecutive days, from 8:00 to 16:00, over three transects (1,500 x 6m each). Each bee collected on a flower was considered a sampling unit. The bees were captured with entomological

nets, without choice, for 5 to 10 minutes in each flowering plant, according to Sakagami et al. (1967). Fertile material from the plants visited by the bees was collected and herborized.

Data analysis

To evaluate the trophic niche breadth, we used the Shannon diversity index (H') (Shannon, 1948). Additionally, we used the Pielou equitability index (J') as an indicator of how plant diversity was used by each bee species (Ludwig & Reynolds, 1988). The level of niche overlap (NO_{ih}) between each pair of bee species was assessed using the Schoener index (1968), $NO_{ih} = 1 - 1/2 \sum_k |p_{ik} - p_{hk}|$, where: i and h are the bee species compared, p_{ik} and p_{hk} are the proportions of individuals, respectively of the bee species i and h collected in the plant species k . The p_{ik} value was obtained by dividing the number of individuals of species i collected in plant k by the total number of individuals of species i collected in all plants. The Schoener index is symmetrical and varies from 0 to 1. Only bee species represented by eight or more individuals were included in the analysis. The overlap between each bee species-pair (NO_{ih}) was analyzed in 105 possible combinations of pairs formed by 15 bee species. Following Aguiar (2003) and Aguiar et al. (2017b), the overlap of the trophic niche was considered low when the NO_{ih} value was less than or equal to 0.30, it was moderate when the value was greater than 0.30 and equal to or less than 0.70, and high if the NO_{ih} values were greater than 0.70.

The data of the bee species (i) in each plant species (j) were used to build a P_{ij} incidence matrix and calculate the connectance, which is the relationship between the actual number of interactions found and the theoretical number of possible interactions. To draw our network, we order the matrix in decrease frequencies of interactions between plants and bees and then we used the function `plotweb` from `bipartite` package (Dormann et al., 2009) in R program (R Core Team, 2020).

Results

The interactions between 75 bee species of bees and 62 plant species were recorded on this cerrado site (Fig 1, Table 1, Supplementary material 1). *Byrsonima sericea*, *Serjania faveolata* Radlk., *Stigmaphyllon paralias* A. Juss and *Pityrocarpa moniliformis* (Benth.) Luckow & R.W. Jobson were the plants with greatest number of links with bee species. Additionally, these plants received together almost half of the total visits (Table 1). The guild of oil-collecting bees, here composed of the species included in the Centridini, Tetrapiidiini and Tapinotaspidiini tribes, showed high diversity and many interactions with *B. sericea* and *S. paralias* (Malpighiaceae) (Supplementary material 1). The bee-plant network showed connectance = 4.67%, with 242 interactions found out of 4,650 theoretically possible interactions. Considering only the guild of oil-collecting bees (26 species) and oil-plants (8 species), 75 interactions were recorded out of 208 theoretically possible and connectance was 16.8%.

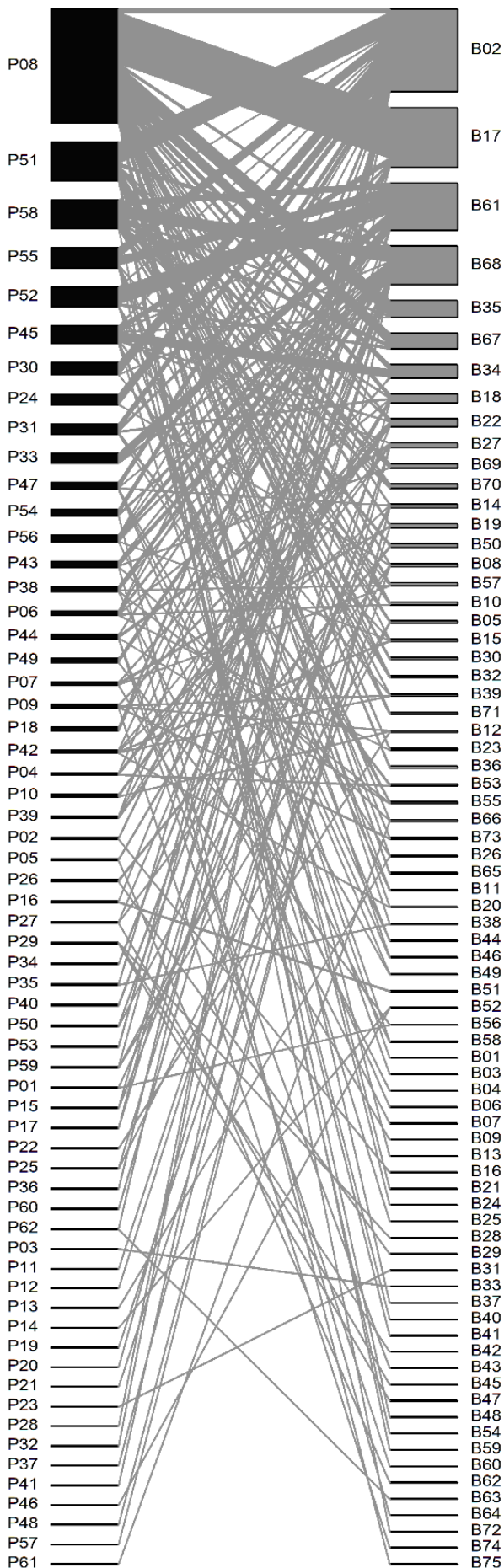


Fig 1 Plant-bee network in a cerrado area. **Plant species:** P01 - *Anemopaegma* sp. 1, P02 - *Banisteriopsis harleyi*, P03 - *Borreria verticillata*, P04 - *Bowdichia virgilioides*, P05 - *Byrsonima correifolia*, P06 - *Byrsonima cydoniifolia*, P07 - *Byrsonima dealbata*, P08 - *Byrsonima sericea*, P09 - *Centrosema coriaceum*, P10 - *Chamaecrista mucronata*, P11 - *Cordia rufescens*, P12 - *Croton* sp. 1, P13 - *Cuphea sessiliflora*, P14 - *Dalechampia brasiliensis*, P15 - *Diplopterys pubipetala*, P16 - *Eremanthus capitatus*, P17 - *Erythroxylum loefgrenii*, P18 - *Eugenia* cf. *punicifolia*, P19 - *Eugenia excelsa*, P20 - *Eugenia pistaciifolia*, P21 - *Evolvulus* sp. 1, P22 - *Fridericia cinerea*, P23 - *Gymnea* sp.1, P24 - *Herissantia crispa*, P25 - *Ipomoea incarnata*, P26 - *Ipomoea* sp. 1, P27 - *Jacquemontia* sp. 1, P28 - *Lasiolaena lychnophorioides*, P29 - *Lepidaploa chalybaea*, P30 - *Lippia* sp. 1, P31 - *Lippia* sp. 2, P32 - *Malpighiaceae* sp. 1, P33 - *Manihot* sp. 1, P34 - *Microstachys corniculata*, P35 - *Mikania elliptica*, P36 - *Mimosa somnians*, P37 - *Mimosa* sp.1, P38 - *Moquiniastrum blanchetianum*, P39 - *Myrtaceae* sp. 1, P40 - *Myrtaceae* sp. 2, P41 - *Passiflora edmundoi*, P42 - *Passiflora edulis*, P43 - *Periandra mediterranea*, P44 - *Piriqueta sidifolia*, P45 - *Pityrocarpa moniliformis*, P46 - *Rhaphiodon echinus*, P47 - *Senegalia langsdorffii*, P48 - *Senna acuruensis*, P49 - *Senna macranthera*, P50 - *Senna macranthera*, P51 - *Serjania faveolata*, P52 - *Serjania lethalis*, P53 - *Serjania* sp. 1, P54 - *Serjania* sp. 2, P55 - *Serjania* sp. 3, P56 - *Simarouba amara*, P57 - *Stachytarpheta crassifolia*, P58 - *Stigmaphyllon paralias*, P59 - *Stylosanthes scabra*, P60 - *Turnera* sp. 1, P61 - *Urochloa decumbens*, P62 - *Waltheria* cf. *indica*. **Bee species:** B01 - *Acanthopus excellens*, B02 - *Apis mellifera*, B03 - *Augochlora (Augochlora)* sp. 5, B04 - *Augochlora (Oxystoglossella)* sp. 2, B05 - *Augochlora (Oxystoglossella)* sp. 3, B06 - *Augochloropsis* sp. 3, B07 - *Augochloropsis* sp. 4, B08 - *Augochloropsis* sp. 5, B09 - *Augochloropsis* sp. 6, B10 - *Augochloropsis* sp. 7, B11 - *Augochloropsis* sp. 8, B12 - *Bombus morio*, B13 - *Centris varia*, B14 - *Centris moerens*, B15 - *Centris tetrazona*, B16 - *Centris lutea*, B17 - *Centris aenea*, B18 - *Centris caxienses*, B19 - *Centris* cf. *spilopoda*, B20 - *Centris decolorata*, B21 - *Centris nitens*, B22 - *Centris perforator*, B23 - *Centris* sp. 1, B24 - *Centris* sp. 3, B25 - *Centris* sp. 6, B26 - *Centris tarsata*, B27 - *Ceratina (Crewella)* sp.1, B28 - *Ceratina (Crewella)* sp.2, B29 - *Ceratina (Crewella)* sp.3, B30 - *Colletes* sp.1, B31 - *Diadasia* sp.1, B32 - *Dialictus opacus*, B33 - *Dicranthidium* sp. 1, B34 - *Epicharis analis*, B35 - *Epicharis bicolor*, B36 - *Epicharis cockerelli*, B37 - *Epicharis flava*, B38 - *Euglossa cordata*, B39 - *Eulaema nigrita*, B40 - *Exomalopsis (Exomalopsis)* sp. 2, B41 - *Exomalopsis (Phanomalopsis)* sp. 1, B42 - *Florilegus* sp. 1, B43 - *Frieseomelitta francoi*, B44 - *Geotrigona mombuca*, B45 - *Leiopodus abnormis*, B46 - *Lophopedia nigrispinis*, B47 - *Megachile (Pseudocentron)* sp. 3, B48 - *Megachile* sp. 8, B49 - *Melipona quadrifasciata*, B50 - *Melitoma* sp. 1, B51 - *Melitomella grisescens*, B52 - *Mesoplia friesei*, B53 - *Mesoplia rufipes*, B54 - *Monoeca* affs. *moure*, B55 - *Nannotrigona testaceicornis*, B56 - *Oxaea flavescens*, B57 - *Paratrigona incerta*, B58 - *Partamona combinata*, B59 - *Pseudaugochlora pandora*, B60 - *Pseudaugochlora* sp. 1, B61 - *Scaptotrigona* aff. *postica*, B62 - *Tapinotaspoidea* sp.1, B63 - *Temnosoma* cf. *metallicum*, B64 - *Tetragonisca* sp. 1, B65 - *Tetrapedia amplitarsis*, B66 - *Tetrapedia diversipes*, B67 - *Trigona hyalinata*, B68 - *Trigona spinipes*, B69 - *Tropidopedia nigrocarinata*, B70 - *Urbanapsis diamantina*, B71 - *Xanthopoda* sp., B72 - *Xylocopa subcyanea*, B73 - *Xylocopa cearensis*, B74 - *Xylocopa* sp. 2, B75 - *Xylocopa frontalis*.

Fifteen bee species were included in the niche analyzes. The eusocial species *Trigona spinipes* (Fabricius) and *Apis mellifera* L. exploited the largest plant spectrum (Fig 1; Supplementary material 1) and showed high equitability in the distribution of visits to the plants, with broader trophic niches ($H' > 2.00$) (Table 2). *Epicharis bicolor* Smith, *Centris aenea*

Lepeletier and *Melitoma* sp.1 presented the narrowest trophic niches, and the first two showed a foraging concentration in *B. sericea*, causing low equitability of visits to the spectrum of exploited plants, which decreased the value of the H' index downwards (Table 2; Supplementary material 1).

Table 1. Plant species exploited by bee species in a cerrado area in the Chapada Diamantina, Bahia, Brazil. N1: Number of bee species visiting each plant species. N2: Number of individual bees collected from each plant species.

Family	Plant species	Code	N1	N2
Asteraceae	<i>Eremanthus capitatus</i> (Spreng.) MacLeish	P16	2	3
Asteraceae	<i>Lasiolaena lychnophorioides</i> Roque et al.	P28	1	1
Asteraceae	<i>Lepidaploa chalybaea</i> (Mart. ex DC.) H.Rob.	P29	3	3
Asteraceae	<i>Mikania elliptica</i> DC.	P35	2	3
Asteraceae	<i>Moquiniastrum blanchetianum</i> (DC.) G. Sancho	P38	5	11
Bignoniaceae	<i>Anemopaegma</i> sp. 1	P01	2	2
Bignoniaceae	<i>Fridericia cinerea</i> (Bureau ex K.Schum.) L.G.Lohmann	P22	1	2
Boraginaceae	<i>Cordia rufescens</i> A.DC.	P11	1	1
Convolvulaceae	<i>Evolvulus</i> sp. 1	P21	1	1
Convolvulaceae	<i>Ipomoea incarnata</i> (Vahl) Choisy	P25	2	2
Convolvulaceae	<i>Ipomoea</i> sp. 1	P26	2	4
Convolvulaceae	<i>Jacquemontia</i> sp1. Choisy	P27	3	3
Erythroxylaceae	<i>Erythroxylum loefgrenii</i> Diogo	P17	2	2
Euphorbiaceae	<i>Croton</i> sp. 1	P12	1	1
Euphorbiaceae	<i>Dalechampia brasiliensis</i> Lam.	P14	1	1
Euphorbiaceae	<i>Manihot</i> sp. 1	P33	2	20
Euphorbiaceae	<i>Microstachys corniculata</i> (Vahl) Griseb.	P34	1	3
Fabaceae	<i>Bowdichia virgilioides</i> Kunth	P04	4	5
Fabaceae	<i>Centrosema coriaceum</i> Benth.	P09	5	7
Fabaceae	<i>Chamaecrista mucronata</i> (Spreng.) H.S.Irwin & Barneby	P10	2	5
Fabaceae	<i>Mimosa somnians</i> Humb. & Bonpl. ex Willd.	P36	1	2
Fabaceae	<i>Mimosa</i> sp.1	P37	1	1
Fabaceae	<i>Periandra mediterranea</i> (Vell.) Taub.	P43	5	12
Fabaceae	<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W.Jobson	P45	12	36
Fabaceae	<i>Senegalia langsdorffii</i> (Benth.) Seigler & Ebinger	P47	6	15
Fabaceae	<i>Senna acuruensis</i> (Benth.) H.S.Irwin & Barneby	P48	1	1
Fabaceae	<i>Senna macranthera</i> (DC. ex Collad.) H.S.Irwin & Barneby	P49	2	9
Fabaceae	<i>Senna macranthera</i> var. <i>micans</i> (Nees) H.S.Irwin & Barneby	P50	2	3
Fabaceae	<i>Stylosanthes scabra</i> Vogel	P59	3	3
Lamiaceae	<i>Gymneia</i> sp. 1	P23	1	1
Lamiaceae	<i>Rhaphiodon echinus</i> Schauer	P46	1	1
Lythraceae	<i>Cuphea sessiliflora</i> A.St.-Hil.	P13	1	1
Malpighiaceae	<i>Banisteriopsis harleyi</i> B.Gates	P02	2	4

Table 1. Plant species exploited by bee species in a cerrado area in the Chapada Diamantina, Bahia, Brazil. N1: Number of bee species visiting each plant species. N2: Number of individual bees collected from each plant species. (Continuation)

Family	Plant species	Code	N1	N2
Malpighiaceae	<i>Byrsonima correifolia</i> A.Juss.	P05	2	4
Malpighiaceae	<i>Byrsonima cydonifolia</i> A.Juss.	P06	6	9
Malpighiaceae	<i>Byrsonima dealbata</i> Griseb.	P07	4	7
Malpighiaceae	<i>Byrsonima sericea</i> DC.	P08	20	232
Malpighiaceae	<i>Diplopterys pubipetala</i> (A.Juss.) W.R.Anderson & C.C.Davis	P15	2	2
Malpighiaceae	Malpighiaceae sp. 1	P32	1	1
Malpighiaceae	<i>Stigmaphyllon paralias</i> A.Juss.	P58	13	58
Malvaceae	<i>Herissantia crispa</i> (L.) Brizicky	P24	2	21
Malvaceae	<i>Waltheria</i> cf. <i>indica</i> L.	P62	2	2
Myrtaceae	<i>Eugenia</i> cf. <i>punicifolia</i> (Kunth) DC.	P18	2	7
Myrtaceae	<i>Eugenia excelsa</i> O.Berg	P19	1	1
Myrtaceae	<i>Eugenia pistaciifolia</i> DC.	P20	1	1
Myrtaceae	Myrtaceae sp. 1	P39	4	5
Myrtaceae	Myrtaceae sp. 2	P40	1	3
Passifloraceae	<i>Passiflora edmundoi</i> Sacco	P41	1	1
Passifloraceae	<i>Passiflora edulis</i> Sims	P42	6	7
Poaceae	<i>Urochloa decumbens</i> (Stapf) R.D.Webster	P61	1	1
Rubiaceae	<i>Borreria verticillata</i> (L.) G.Mey	P03	1	1
Sapindaceae	<i>Serjania faveolata</i> Radlk.	P51	18	78
Sapindaceae	<i>Serjania lethalis</i> A.St.-Hil.	P52	6	39
Sapindaceae	<i>Serjania</i> sp. 1	P53	1	3
Sapindaceae	<i>Serjania</i> sp. 2	P54	3	14
Sapindaceae	<i>Serjania</i> sp. 3	P55	9	41
Simaroubaceae	<i>Simarouba amara</i> Aubl.	P56	6	14
Turneraceae	<i>Piriqueta sidifolia</i> (Cambess.) Urb.	P44	5	9
Turneraceae	<i>Turnera</i> sp. 1	P60	1	2
Verbenaceae	<i>Lippia</i> sp. 1	P30	3	25
Verbenaceae	<i>Lippia</i> sp. 2	P31	5	21
Verbenaceae	<i>Stachytarpheta crassifolia</i> Schrad.	P57	1	1

The trophic niche overlap between each bee species pair ranged from 0.01 to 0.87, being higher between *E. bicolor* and *C. aenea*, and between *Trigona hyalinata* (Lepelletier) and *E. bicolor* (Table 2). The vast majority of species pairs analyzed (~75%) showed low overlap of the trophic niche (NO<0.33), and approximately half of them had a very low level of overlap (NO<0.1). Only four pairs showed high overlap (NO>0.7): *E. bicolor*/*C. aenea*; *T. hyalinata*/*E. bicolor*; *Urbanapsis diamantina* Aguiar and Melo/*T. hyalinata*; *T. hyalinata*/*C. aenea*. The high level of overlap found in these pairs was mainly influenced by the exploitation of resources from *B. sericea* (P08), floral oil and/or pollen (Supplementary material 1). *A. mellifera*

showed a low overlap of the trophic niche with the other bee species (Table 2), due mainly to scattered foraging in 23 plant species. However, this exotic species heavily exploited *S. faveolata*, a food plant visited by many native bee species (Supplementary material 1).

Discussion

Bees exploited a diverse flora, however a small set of plant species, either due to their abundance or by providing specific resources, can be considered as key species for the maintenance of bee populations in this community.

Table 2. Trophic niche overlap among bee species in a cerrado area in Chapada Diamantina, Bahia, Brazil. H': Niche breadth. J': Equitability index. Spl: Number of plant species visited by each bee species. Nab: number of individuals of each bee species. **B02** - *Apis mellifera*, **B14** - *Centris moerens*, **B17** - *Centris aenea*, **B18** - *Centris caxienseis*, **B19** - *Centris* cf. *spilopoda*, **B22** - *Centris perforator*, **B27** - *Ceratina (Crewella)* sp.1, **B34** - *Epicharis analis*, **B35** - *Epicharis bicolor*, **B50** - *Melitoma* sp.1, **B61** - *Scaptotrigona* aff. *postica*, **B67** - *Trigona hyalinata*, **B68** - *Trigona spinipes*, **B69** - *Tropidopedia nigrocarinata*, **B70** - *Urbanapsis diamantina*

	B02	B14	B17	B18	B19	B22	B27	B34	B35	B50	B61	B67	B68	B69	B70
B14	0.11														
B17	0.11	0.26													
B18	0.14	0.25	0.43												
B19	0.05	0.25	0.50	0.39											
B22	0.18	0.24	0.28	0.18	0.18										
B27	0.02	0.00	0.08	0.06	0.00	0.20									
B34	0.06	0.25	0.44	0.37	0.44	0.29	0.10								
B35	0.07	0.25	0.87	0.45	0.50	0.21	0.03	0.40							
B50	0.01	0.00	0.00	0.11	0.00	0.00	0.00	0.00	0.06						
B61	0.14	0.00	0.02	0.10	0.00	0.01	0.03	0.01	0.07	0.10					
B67	0.06	0.25	0.72	0.50	0.50	0.18	0.00	0.37	0.78	0.19	0.20				
B68	0.21	0.09	0.07	0.21	0.05	0.12	0.01	0.05	0.11	0.28	0.21	0.24			
B69	0.30	0.22	0.22	0.33	0.22	0.29	0.00	0.22	0.28	0.11	0.13	0.33	0.32		
B70	0.16	0.25	0.56	0.50	0.50	0.29	0.00	0.37	0.61	0.33	0.10	0.74	0.40	0.44	
H'	2.45	1.91	0.69	1.72	0.97	1.99	1.75	0.89	0.35	0.66	1.89	0.77	2.59	1.15	0.94
J'	0.78	0.98	0.31	0.88	0.89	0.96	0.90	0.81	0.32	0.95	0.79	0.70	0.85	0.83	0.85
Spl	23	7	9	7	3	8	7	3	3	2	11	3	21	4	3
Nab	168	8	121	18	8	17	10	27	34	8	96	32	78	9	9

B. sericea and *S. paralias* are plants that produce floral oil. In addition, *B. sericea* pollen is collected by several distinct bee groups (Teixeira & Machado, 2000), which increases its attractiveness for both oil-bees and non-oil-bees. Another aspect that increases the possibilities of *B. sericea* interactions with bees is the great local abundance of this plant species (Aguiar et al., 2017a). The *Serjania* genus comprises nectar-producing species (Matos & Santos, 2017), and *P. moniliformis* is a nectar (Santos et al., 2018) and pollen source for bees (Maia-Silva et al., 2012).

The visits of oil-bees to oil-plant flowers are not optional as these bees demand floral oil to complete their reproductive cycle (Alves-dos-Santos et al., 2007; Neff & Simpson, 2017). Oil-bees have, at least in part, the same requirements, all of which demand floral oil, which explains the high overlap of trophic niche. It is expected that species with similar ecological requirements will show some redundancy in the use of resources and high overlap in their niches. In fact, the connectance in the oil-bees guild and oil-plants is approximately four times greater than the connectance found in the entire community. In the small world formed by the oil-bees and oil-plants, species share evolutionary histories and mutually specialized structures (Bezerra et al., 2009), forming modules in which interactions have higher intimacy than in the network as a whole. Hembry et al. (2018) demonstrated that the level of interaction intimacy affects the structure of communities.

The most abundant oil-bee species in this assemblage was *C. aenea*, who exploited floral resources of a diversity of non-phylogenetically related plant species, that is, a tendency to a generalist foraging behavior, previously pointed out in other habitats (Aguiar & Gaglianone, 2003; Mello et al., 2013). However, its niche breadth, measured by the H' index, showed one of the lowest values among these bee species, because of the high concentration of nesting females on the oil-plant *B. sericea*. The strong mutualistic interaction between *C. aenea* and *B. sericea* has been reported in many habitats (Mello et al., 2013), as well as the behavior of this oil-bee to nest in aggregations near this food plant (Aguiar & Gaglianone, 2003). *B. sericea* played a central role in the trophic niche of *C. aenea* and other oil-bees, since the exploitation of the floral resources of this plant explains all the cases in which there was a high overlap of trophic niche (NO>0.70), even when one of the species involved was not an oil-bee, such as *T. hyalinata* (Meliponini), whose visits to *B. sericea* were probably for pollen foraging.

Among the eusocial species, *T. spinipes* showed the broader trophic niche, as expected based on its supergeneralist foraging behavior (Biesmeijer & Slaa, 2006; Giannini et al., 2015; Pacheco-Filho et al., 2015). Its trophic niche breadth in this habitat was influenced both by the richness of plant species visited and by the distribution of the foragers in many floral resources. This scattered foraging in several plant

species contributed to the low level of niche overlap of this species with the other bee species, including *A. mellifera* and the congeneric species *T. hyalinata*. Biesmeijer and Slaa (2006) highlighted that these two congeneric species, despite having aggressive group forager behavior (Nieh et al., 2003, 2005; Slaa et al., 2003), in general present different diets and probably do not interact regularly during foraging.

Surprisingly, *T. spinipes* and *A. mellifera*, species that have a strong association with each other in the use of floral resources (e.g. Biesmeijer & Slaa, 2006) and are supergeneralists species in bee-plant networks (Giannini et al., 2015), also showed low overlap level in our study, which was influenced by the allocation of many honeybee foragers in three plant species that received few visits of *T. spinipes*. These two supergeneralist species have been considered fundamental to the maintenance of the bee-plant networks, although they have different effects on network structure, with *A. mellifera* having a strong effect on nestedness, whereas *T. spinipes* has a main effect on the niche overlap of the bees (Giannini et al., 2015). The low overlap of the trophic niche of *A. mellifera* with the other bee species was also caused by scattering of foragers in many plant species. However, some of these plant species, such as *S. faveolata*, were important in the diet of other bees.

The distribution of the samples over a long period (almost 4 years), as well as the large sampling effort, favored a more robust characterization of the food niche of the bee populations, as it allows recording of bee-plant interactions in different periods of flowering of the melitophilous plants, as well as the registration of different generations of bee species. On the other hand, it probably contributed to the very low values of niche overlap found, which may be related to the differences between flowering periods of the melitophilous plants and between periods of nesting activity of different species of solitary bees. Additionally, the low levels of niche overlap found may be, at least in part, influenced by the sampling method, collection of bees during foraging, as previously discussed by Ranta and Lundberg (1981). These authors compared the overlapping levels of the food niche between *Bombus* species using three sampling methods, and found that the mean niche overlap values were significantly lower when calculated using direct observations of flower visits data than when using analyses of pollen contents in pollen loads and in nectar loads. According to the authors, these differences in overlapping levels would be largely explained by differences in the contribution of different food plants in number of pollen grains for the pollen loads, since only a few plant species were dominant, as they are represented by many pollen grains in the pollen loads, resulting in an increase in the niche overlap values. Finally, we emphasize that the method of collecting bees on flowers is more viable for the analysis of the food niche in tropical bee assemblages, even although only a few species can be evaluated according to their abundance.

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Supplementary Material 1. Species of bees and plants visited in a cerrado area in the Chapada Diamantina, Bahia, Brazil. Nab: number of individuals of each bee species. Within the brackets the number of individuals of each bee species collected in each plant species is presented. The plant species codes according to Table 1.

Bee species	Bee Code	Nab	Plant species
ANDRENIDAE			
Oxaeini			
<i>Oxaea flavescens</i> Klug, 1807	B56	2	P1(1), P49(1)
APIDAE			
Apini			
<i>Apis mellifera</i> Linnaeus, 1758	B02	168	P6(1), P8(8), P17(1), P18(6), P24(20), P28(1), P30(23), P31(11), P32(1), P35(2), P36(2), P39(2), P45(2), P47(10), P51(42), P52(1), P53(3), P54(10), P55(18), P56(1), P58(1), P59(1), P62(1)
Bombini			
<i>Bombus morio</i> (Swederus, 1787)	B12	4	P9(1), P10(1), P22(2)
Centridini			
<i>Centris aenea</i> Lepeletier, 1841	B17	121	P4(1), P6(1), P8(102), P15(1), P18(1), P31(4), P42(1), P45(9), P56(1)
<i>Centris caxienses</i> Ducke, 1907	B18	18	P5(3), P6(2), P8(7), P20(1), P31(2), P39(1), P58(2)
<i>Centris decolorata</i> Lepeletier, 1841	B20	2	P8(1), P42(1)
<i>Centris nitens</i> Lepeletier, 1841	B21	1	P8(1)
<i>Centris varia</i> (Erichson, 1849)	B13	1	P8(1)
<i>Centris tarsata</i> Smith, 1874	B26	3	P8(1), P13(1), P31(1)
<i>Centris moerens</i> (Perty, 1833)	B14	8	P1(1), P8(2), P42(1), P47(1), P48(1), P50(1), P57(1)
<i>Centris lutea</i> Friese, 1899	B16	1	P2(1)
<i>Centris perforator</i> (Smith, 1874)	B22	17	P4(2), P8(3), P9(2), P10(4), P15(1), P42(1), P45(2), P51(2)
<i>Centris cf. spilopoda</i> Moure, 1969	B19	8	P7(3), P8(4), P19(1)
<i>Centris tetrazona</i> Moure & Seabra, 1962	B15	5	P8(1), P42(2), P45(1), P56(1)
<i>Centris</i> sp. 1	B23	4	P6(1), P8(3)
<i>Centris</i> sp. 3	B24	1	P8(1)
<i>Centris</i> sp. 6	B25	1	P45(1)
<i>Epicharis analis</i> Lepeletier, 1841	B34	27	P7(2), P8(10), P45(15)
<i>Epicharis bicolor</i> Smith, 1854	B35	34	P8(31), P45(1), P58(2)
<i>Epicharis cockerelli</i> Friese, 1900	B36	4	P8(4)
<i>Epicharis flava</i> Friese, 1900	B37	1	P8(1)
Emphorini			
<i>Diadasia</i> sp. 1	B31	1	P23(1)
<i>Melitoma</i> sp. 1	B50	8	P26(3), P58(5)
<i>Melitomella grisescens</i> (Ducke, 1907)	B51	2	P16(2)
Ericrocidini			
<i>Acanthopus excellens</i> Schrottky, 1902	B01	1	P55 (1)
<i>Mesoplia friesei</i> (Ducke, 1902)	B52	2	P14(1), P46(1)
<i>Mesoplia rufipes</i> (Perty, 1833)	B53	4	P4(1), P31(3)
Eucerini			
<i>Florilegus</i> sp. 1	B42	1	P29(1)
Euglossini			
<i>Euglossa cordata</i> (Linnaeus, 1758)	B38	2	P8(1), P35(1)
<i>Eulaema nigrata</i> Lepeletier, 1841	B39	5	P9(1), P30(1), P42(1), P51(2)
Exomalopsini			
<i>Exomalopsis (Phanomalopsis)</i> sp. 1	B41	1	P55(1)
<i>Exomalopsis (Exomalopsis)</i> sp. 2	B40	1	P55(1)

Bee species	Bee Code	Nab	Plant species
Meliponini			
<i>Frieseomelitta francoi</i> (Moure, 1946)	B43	1	P44(1)
<i>Geotrigona mombuca</i> (Smith, 1863)	B44	2	P45(1), P55(1)
<i>Melipona quadrifasciata</i> Lepeletier, 1836	B49	2	P45(1), P47(1)
<i>Nannotrigona testaceicornis</i> (Lepeletier, 1836)	B55	4	P38(1), P44(1), P52(1), P55(1)
<i>Paratrigona incerta</i> Camargo & Moure, 1994	B57	7	P7(1), P8(4), P38(1), P55(1)
<i>Partamona combinata</i> Pedro & Camargo, 2003	B58	2	P47(1), P55(1)
<i>Scaptotrigona</i> aff. <i>postica</i> (Latreille, 1807)	B61	96	P16(1), P17(1), P33(17), P38(7), P43(2), P44(2), P45(1), P52(32), P55(16), P56(7), P58(10)
<i>Tetragonisca</i> sp. 1	B64	1	P43(1)
<i>Trigona hyalinata</i> (Lepeletier, 1836)	B67	32	P8(23), P52(3), P58(6)
<i>Trigona spinipes</i> (Fabricius, 1793)	B68	78	P2(3), P6(3), P8(4), P25(1), P27(1), P30(1), P33(3), P34(3), P38(1), P39(1), P40(3), P41(1), P43(7), P47(1), P49(8), P50(2), P51(5), P54(3), P56(3), P58(22), P60(2)
Protepeolini			
<i>Leiopodus abnormis</i> (Jørgensen, 1912)	B45	1	P27(1)
Tapinotaspidini			
<i>Lophopedia nigrispinis</i> (Vachal, 1909)	B46	2	P45(1), P51(1)
<i>Monoeca</i> affs. <i>moure</i> Aguiar, 2012	B54	1	P58(1)
<i>Tapinotaspoides</i> sp. 1	B62	1	P5(1)
<i>Tropidopedia nigrocarinata</i> Aguiar & Melo, 2007	B69	9	P8(2), P43(1), P51(5), P58(1)
<i>Urbanapsis diamantina</i> Aguiar & Melo, 2007	B70	9	P8(5), P51(1), P58(3)
<i>Xanthopedia</i> sp.	B71	5	P8(4), P51(1)
Tetrapediini			
<i>Tetrapedia amplitarsis</i> Friese, 1899	B65	3	P8(3)
<i>Tetrapedia diversipes</i> Klug, 1810	B66	4	P43(1), P51(2), P61(1)
Xylocopini			
<i>Ceratina</i> (<i>Crewella</i>) sp.1	B27	10	P4(1), P11(1), P12(1), P37(1), P39(1), P44(4), P45(1)
<i>Ceratina</i> (<i>Crewella</i>) sp.2	B28	1	P29(1)
<i>Ceratina</i> (<i>Crewella</i>) sp.3	B29	1	P26(1)
<i>Xylocopa cearensis</i> Ducke, 1910	B73	4	P9(2), P51(2)
<i>Xylocopa frontalis</i> (Olivier, 1789)	B75	1	P54(1)
<i>Xylocopa subcyanea</i> Pérez, 1901	B72	1	P51(1)
<i>Xylocopa</i> sp. 2	B74	1	P9(1)
COLLETIDAE			
<i>Colletes</i> sp.1	B30	5	P51(5)
HALICTIDAE			
Augochlorini			
<i>Augochlora</i> (<i>Oxystoglossella</i>) sp. 2	B04	1	P56(1)
<i>Augochlora</i> (<i>Oxystoglossella</i>) sp. 3	B05	5	P25(1), P51(2), P58(1), P59(1)
<i>Augochlora</i> (<i>Augochlora</i>) sp. 5	B03	1	P52(1)
<i>Augochloropsis</i> sp. 3	B06	1	P47(1)
<i>Augochloropsis</i> sp. 4	B07	1	P38(1)
<i>Augochloropsis</i> sp. 5	B08	7	P8(3), P21(1), P24(1), P27(1), P59(1)
<i>Augochloropsis</i> sp. 6	B09	1	P7(1)
<i>Augochloropsis</i> sp. 7	B10	6	P6(1), P8(1), P51(3), P58(1)
<i>Augochloropsis</i> sp. 8	B11	2	P51(1), P52(1)
<i>Pseudaugochlora pandora</i> (Smith, 1853)	B59	1	P51(1)
<i>Pseudaugochlora</i> sp. 1	B60	1	P44(1)

Bee species	Bee Code	Nab	Plant species
<i>Temnosoma</i> cf. <i>metallicum</i> Smith, 1853	B63	1	P62(1)
Halictini			
<i>Dialictus opacus</i> (Moore, 1940)	B32	5	P8(1), P51(1), P58(3)
MEGACHILIDAE			
Anthidiini			
<i>Dicranthidium</i> sp. 1	B33	1	P3(1)
Megachilini			
<i>Megachile</i> (<i>Pseudocentron</i>) sp. 3	B47	1	P29(1)
<i>Megachile</i> sp. 8	B48	1	P51(1)

Plant Species	Code	Plant Species	Code
<i>Anemopaegma</i> sp. 1 Mart. ex Meisn.	P01	Malpighiaceae sp.1	P32
<i>Banisteriopsis harleyi</i> B. Gates	P02	<i>Manihot</i> sp.1	P33
<i>Borreria verticillata</i> (L.) G. Mey	P03	<i>Microstachys corniculata</i> (Vahl) Griseb.	P34
<i>Bowdichia virgilioides</i> Kunth	P04	<i>Mikania elliptica</i> DC.	P35
<i>Byrsonima correifolia</i> A.Juss.	P05	<i>Mimosa somnians</i> Humb. & Bonpl. ex Willd.	P36
<i>Byrsonima cydoniifolia</i> A.Juss.	P06	<i>Mimosa</i> sp.1	P37
<i>Byrsonima dealbata</i> Griseb.	P07	<i>Moquiniastrum blanchetianum</i> (DC.) G. Sancho	P38
<i>Byrsonima sericea</i> DC.	P08	Myrtaceae sp.1	P39
<i>Centrosema coriaceum</i> Benth.	P09	Myrtaceae sp.2	P40
<i>Chamaecrista mucronata</i> (Spreng.) H.S.Irwin & Barneby	P10	<i>Passiflora edmundoi</i> Sacco	P41
<i>Cordia rufescens</i> A.DC.	P11	<i>Passiflora edulis</i> Sims	P42
<i>Croton</i> sp.1	P12	<i>Periandra mediterranea</i> (Vell.) Taub.	P43
<i>Cuphea sessiliflora</i> A.St.-Hil.	P13	<i>Piriqueta sidifolia</i> (Cambess.) Urb.	P44
<i>Dalechampia brasiliensis</i> Lam.	P14	<i>Pityrocarpa moniliformis</i> (Benth.) Luckow & R.W.Jobson	P45
<i>Diplopterys pubipetala</i> (A.Juss.) W.R.Anderson & C.C.Davis	P15	<i>Rhaphiodon echinus</i> Schauer	P46
<i>Eremanthus capitatus</i> (Spreng.) MacLeish	P16	<i>Senegalia langsdorffii</i> (Benth.) Seigler & Ebinger	P47
<i>Erythroxylum loefgrenii</i> Diogo	P17	<i>Senna acuruensis</i> (Benth.) H.S.Irwin & Barneby	P48
<i>Eugenia</i> cf. <i>punicifolia</i> (Kunth) DC.	P18	<i>Senna macranthera</i> (DC. ex Collad.) H.S.Irwin & Barneby	P49
<i>Eugenia excelsa</i> O.Berg	P19	<i>Senna macranthera</i> var. <i>micans</i> (Nees) H.S.Irwin & Barneby	P50
<i>Eugenia pistaciifolia</i> DC.	P20	<i>Serjania faveolata</i> Radlk.	P51
<i>Evolvulus</i> sp.1	P21	<i>Serjania lethalis</i> A.St.-Hil.	P52
<i>Fridericia cinerea</i> (Bureau ex K.Schum.) L.G.Lohmann	P22	<i>Serjania</i> sp. 1	P53
<i>Gymneia</i> sp. 1 (Benth.) Harley & J.F.B.Pastore	P23	<i>Serjania</i> sp. 2	P54
<i>Herissantia crispa</i> (L.) Brizicky	P24	<i>Serjania</i> sp. 3	P55
<i>Ipomoea incarnata</i> (Vahl) Choisy	P25	<i>Simarouba amara</i> Aubl.	P56
<i>Ipomoea</i> sp.1	P26	<i>Stachytarpheta crassifolia</i> Schrad.	P57
<i>Jacquemontia</i> sp1. Choisy	P27	<i>Stigmaphyllon paralias</i> A.Juss.	P58
<i>Lasiolaena lychnophorioides</i> Roque et al.	P28	<i>Stylosanthes scabra</i> Vogel	P59
<i>Lepidaploa chalybaea</i> (Mart. ex DC.) H.Rob.	P29	<i>Turnera</i> sp. 1	P60
<i>Lippia</i> sp.1	P30	<i>Urochloa decumbens</i> (Stapf) R.D.Webster	P61
<i>Lippia</i> sp.2	P31	<i>Waltheria</i> cf. <i>indica</i> L.	P62