Sociobiology

An international journal on social insects

RESEARCH ARTICLE - BEES

The Similar Usage of a Common Key Resource Does Not Determine Similar Responses by Species in A Community of Oil-collecting Bees

CML Aguiar[1], S Lua[2], M Silva[3], PEC Peixoto[1], HM Alvarez[4], GMM Santos[1]

1 - Departamento de Ciências Biológicas, Universidade Estadual de Feira de Santana, Bahia, Brazil

2 - PPG Zoologia–UEFS, Universidade Estadual de Feira de Santana, Bahia, Brazil

3 - Faculdade de Tecnologia e Ciências, Salvador, Bahia, Brazil

4 - Departamento de Ciências Exatas, Universidade Estadual de Feira de Santana, Bahia, Brazil

Corresponding author
Cândida M. L. Aguiar
Departamento de Ciências Biológicas
Universidade Estadual de Feira de Santana
Av. Transnordestina, s/n, Novo Horizonte
44036-900, Feira de Santana-BA, Brasil
E-Mail: candida.aguiar @gmail.com

Abstract

Variations in abundance and species richness among communities are often determined by interactions between biotic and abiotic factors. However, for communities composed of species that share a common specialization (such as similar foraging adaptations) it may be a key ecological factor involved in the common specialization that affects community variations. To evaluate this possibility, we characterized the guild of oil-collecting bees of a Neotropical savanna in Brazil and tested whether differences in *Byrsonima* abundance and availability of floral oil explain differences in species richness and abundance of oil-collecting bees of different tribes. Both the number of species and total abundance of Centridini species increased with the abundance of *Byrsonima*. One plausible explanation for the stronger adjustment between the abundance of Centridini and *Byrsonima* is that the abundance of these plants affects not only the availability of floral oil, but also of pollen. These findings indicate that the existence of a common specialization among different species does not homogenize their response to variations in a common explored resource.

Introduction

The comprehension of the factors that affect variations in abundance and species richness in natural systems is one of the most explored questions in ecology (Morin, 1999; Agrawal et al., 2007). In many situations, such variations seem to be determined by an interaction between both biotic (such as competition or predation) and abiotic (such as temperature and rainy fluctuations) factors (Morin & Lawler, 1995; Ritchie, 2000; Dyer & Letourneau, 2003). However, there are groups of species that present similar specialized traits related to foraging behavior, predator avoidance strategies or even adaptations to specific conditions. In these cases, it may be that the existence of a similar adaptation makes the species bearing it more dependent on the variation of one or a few key ecological factors. Consequently, variations in such factors should trigger similar responses in the species that share similar adaptations.

One species group that may respond to variations in a key ecological factor is oil-collecting bees that explore the resources produced by oil-flower species of different families. These plant-pollinator systems are highly specialized, with interactions based one resource of high energetic value (oil). Few plant families provide oil on specialized flower structures (elaiophores), which are accessible only to flower visitors that are able to "scratch" epithelial elaiophores with specialized structures (combs) on their legs, or use specialized setae on their legs to obtain oil from trichomatic elaiophores (Neff & Simpson, 1981; Vogel & Machado, 1991). As consequence of these adaptations, oil-collecting bees and oil-producing

plants have interactions of high intimacy: floral oil is essential to feed the larvae and build nests (Vinson & Frankie, 2000; Aguiar & Garófalo, 2004; Michener, 2007), while the pollination services provided by these bees are needed for the plant reproduction (Vogel & Machado, 1991; Sigrist & Sazima, 2004; Costa et al., 2006; Sazan et al., 2014).

Despite the high dependence between oil-collecting bees and oil-producing flowers, the effects of the abundance of floral resources on the communities of oil-collecting bees had been poorly studied. The few existing studies report that both the abundance and richness of Centridini species (a tribe composed of oil-collecting bee species) may be determined by the abundance Malpighiaceae species, mainly *Byrsonima sericea* DC. This relationship between bee abundance or richness and Malpighiaceae species seems to hold both in local and regional scales (Ramalho & Silva, 2002; Rosa & Ramalho, 2011). However, it is important to note that other bee tribes, such as Tetrapediini and Tapinotaspidini possess similar specializations and dependency to explore oil-flowers as Centridini bees. Consequently, if the foraging specialization observed in these bees is responsible for the strong relationship between Centridini and Malpighiaceae species, this pattern should also be detected in the other two bee tribes. In addition, since oil is the main food source for oil-collecting bees, it is possible that the abundance and richness of these insects are more dependent on oil availability than plant abundance.

To evaluate the hypothesis that the specialization in foraging behavior is responsible for the tight relationship between the abundance and richness of oil-collecting bees and oil producing flowers, we made focal samplings of the flower visitors of two *Byrsonima* species. We tested whether differences in the amount of floral oil available and in the local abundance of two *Byrsonima* species explain differences in the richness and abundance of oil-collecting bees of different tribes at local scale.

Material and Methods

Study area

We carried out the study in the surroundings of the Chapada Diamantina National Park (12°25' S; 41°29' W), Palmeiras municipality, state of Bahia, northeastern Brazil. The local climate is hot, with humid summer, and four to five dry months. Rains occur from December to April (Jesus et al., 1983; Nimer, 1989) and the annual rainfall varies from 600 to 1,000 mm (CEI, 1994). The region of Chapada Diamantina has diverse vegetation, including campos rupestres (sandstone outcrop vegetation), campos gerais (grasslands), cerrados (savannas), caatingas (deciduous thorny woodlands), and montane forests, which form a vegetation mosaic (Conceição et al., 2005). We collected samples in a cerrado area, with a predominance of herbaceous plants and shrubs, and sparse trees with up to 5 m.

Sampling

We carried out field work during the flowering period of *Byrsonima sericea* and *Byrsonima cydoniifolia* A. Juss (Malpighiaceae), the most common oil-producing plants in this area. The total abundance of *Byrsonima* was variable among the sampled sites (23 to 233 individuals per transect), but in general there were more than 55 individuals per transect. Details on the morphology and floral biology of these plant species can be found in Teixeira and Machado (2000), and Sazan et al. (2014). The flowers of *B. sericea* are attractive to bees for about a day and a half (Teixeira & Machado, 2000), and the flowers of *B. cydoniifollia* for approximately two days (Sazan et al., 2014). In this region, *B. sericea* flowering season lasts from December to March, while *B. cydoniifolia* blooms in December and January (personal observation).

We selected four sites, with distances varying from 1.1 to 3.8 km from one another. In each site, we established three transects, 1,000 m in length. In each month, we randomly selected four transects (one per site) for sampling on consecutive days. Each whole transect was sampled from 0900 h to 1600 h, by two collectors. The collection of bees on *B. sericea* and *B. cydoniifolia* flowers lasted eight months, from January to March 2011, from October to December 2012, and from January to February 2013, a total of 175 h of sampling effort. The specimens were deposited in the Johann Becker Entomological Collection (Zoology Museum of the State University of Feira de Santana, MZFS) and in the Entomological Collection of the University of Brasília.

Quantification of the number of flowers

To estimate the number of flowers produced by *B. sericea* and *B. cydoniifolia*, we randomly picked ten individuals of each species, during the peak flowering period. For each plant individual, we randomly placed on the canopy a "square box" measuring 25 x 25 cm x the height of the "square box" (range 1.40 m – 1.70 m), which varied according to plant height. Then, we counted all inflorescences that fitted inside the "square box". After counting, we removed ten inflorescences of each individual plant to count the total number of open flowers. We also measured the radius and height of the tree canopy of each plant and used these measures to estimate the volume of flowers per canopy on each plant individual (10 individuals per each *Byrsonima* species). Hence, based on the volume of the "square box" and the volume of the canopy flowers, we estimated the amount of inflorescences per *Byrsonima* individual (number of inflorescences per canopy on blossom= number of inflorescences x (volume of the canopy on blossom/ volume of the "square box"). To estimate the total number of flowers produced per individual of *B. sericea* and *B.cydoniifolia*, we multiplied the total number of flowers per inflorescence by the average number of flowers per inflorescence. Finally, we counted all individuals of *B. sericea* and *B. cydoniifolia* observed in each transect, to estimate the abundance of *Byrsonima*.

*Oil quantification in **Byrsonima** flowers*

To estimate the amount of oil produced by *B. sericea* and *B. cydoniifolia* in each transect, we multiplied the average amount of oil produced by one flower by the estimated number of flowers per plant. We used the value obtained as an estimate of the amount of oil produced by an individual plant. Then, to estimate the total amount of oil available in each of the 12 transects, we multiplied the amount of oil produced by an individual plant by the number of individual *B. sericea* and *B. cydoniifolia* with elaiophores recorded in each transect.

To quantify oil production per flower, we collected ten inflorescences from ten individuals of *B. sericea* and *B. cydoniifolia* separately, with pre-anthesis flowers that had opened on the same day. We dried the flowers in an oven for 72 h at 60 ºC, and then removed the petals and reproductive structures of each flower, leaving only the floral receptacle and the elaiophores. Then, for each of the two *Byrsonima* species, we separated the dried material into eight samples of 1 g each. We extracted floral oil using the Soxhlet system, with hexane solvent. We placed each sample (n = 8) on a

cellulose disk (filter paper) and maintained it in the extractor system for 24 h. We subjected the resulting mixture (solvent plus floral oil) to a low pressure system in a rotaevaporator, to remove the excess of solvent and recover the oil. We weighted the oil obtained per sample in a high precision analytical balance. The oil content (OC) per sample was calculated as a percentage, using the equation:

Where:

Bu = biomass of flowers used (g);

V% = humidity extracted of the flowers (%)

To calculate the amount of oil produced per flower, we divided the amount of oil extracted from 1 g of flowers by the total number of flowers used for the extraction.

Data analysis

To estimate the species richness of bees collected on *Byrsonima* flowers, we used the Chao-2 and Jackknife-1estimators. These estimators are based on the incidence of unicates and duplicates and on the number of singletons, respectively, using 150 randomizations (Colwell, 2013). To

Table 1. Oil-collecting bees visiting *Byrsonima sericea* (BS) and *Byrsonima cydoniifolia* (BC) (Malpighiaceae) flowers in a cerrado area in Chapada Diamantina, northeastern Brazil.

Oil-collecting bee species	Number of individuals on BS flowers	Number of individuals on BC flowers	Total of individuals
Centridini	**259**	**115**	**374**
Centris (*Centris*) *aenea* Lepeletier	108	60	168
Centris (*Centris*) *nitens* Lepeletier	2	4	6
Centris (*Centris*) *spilopoda* Moure	24	9	33
Centris (*Centris*) sp.1	1	1	2
Centris (Hemisiella) tarsata Smith	10	2	12
Centris (Ptilotopus) moerens (Perty)	8	0	8
Centris (Ptilotopus) sponsa Smith	3	0	3
Centris (Trachina) longimana Fabricius	1	0	1
Epicharis (*Epicharis*) *bicolor* Smith	32	10	42
Epicharis (Epicharis) sp.1	4	0	4
Epicharis (Epicharitides) cockerelli Friese	0	2	2
Epicharis (Epicharoides) xanthogastra Moure & Seabra	2	0	2
Epicharis (Epicharoides) sp.1	35	17	52
Epicharis (Triepicharis) analis Lepeletier	29	10	39
Tapinotaspidini	**137**	**17**	**154**
Lophopedia sp.1	15	0	15
Monoeca mourei Aguiar	1	0	1
Paratetrapedia punctata Aguiar & Melo	1	1	2
Tropidopedia nigrocarinata Aguiar & Melo	42	4	46
Xanthopedia **sp.1**	21	5	26
Urbanapsis diamantina Aguiar & Melo	57	7	64
Tetrapediini	**80**	**21**	**101**
Tetrapedia amplitarsis Friese	72	21	93
Tetrapedia diversipes Klug	8	0	8
Total	**476**	**153**	**629**

assess whether the sampling effort was suitable, we built a rarefaction curve based on the species observed (Mao Tau). These analyses were made in the program EstimateS 8.20.

We used generalized linear mixed-effects models to assess whether the number of bee species and individuals of different tribes varied with oil availability and plant abundance. We built models containing bee richness or abundance as the response variables, and tribe, oil abundance, and plant abundance as fixed factors. However, as oil availability and plant abundance were correlated (r = 0.53, p < 0.001), we built different models containing only oil availability or plant abundance as explanatory variables. To assess which model better explained the variations in abundance and richness of bees, we used the Akaike information criterion corrected for small samples (AICc - Burnham and Anderson 2002). The AICc represents a heuristic approach used to select the most parsimonious model that best approximates the true process under investigation among a set of candidate models. Consequently, for each response variable, the model with the smaller AICc value will represent the best one. In all models, we fitted each sampled area nested per field trip as a random factor. Whenever necessary, we performed planned contrasts to test for differences in response variables among Centridini, Tapinotaspidini, and Tetrapediini tribes. We made all analyses using the packages lme4 (Bates et al., 2014), bbmle (Bolker & R Development Core Team, 2012), and multcomp (Hothorn et al., 2008) in R software (R Development Core Team, 2014).

Results

The guild of oil-collecting bees sampled on flowers of *B. sericea* and *B. cydoniifolia* was composed of 22 species (Table 1). The species rarefaction curve showed signs of

stabilization, with the sampled species richness corresponding to 89% and 97% of the estimates provided by Jackknife-1 and Chao-2, respectively. The Centridini tribe showed higher richness (14 species; 64%) and abundance (n=374; 59% of all oil-collecting bees sampled) than the other tribes. *Centris aenea* (Lepeletier) and *Tetrapedia amplitarsis* Friese were the most abundant species (Table 1).

The total number of open flowers per crown in blossom (n=10 plants) varied from 5,411 to 204,863 flowers in *B. sericea,* and from 2,426 to 226,324 flowers in *B. cydoniifolia* (Table 2). The oil content extracted from flowers (1 g samples) was higher in *B. sericea* (0.074%) than in *B. cydoniifolia*

Table 2. Number of flowers and amount of oil in ten individuals of *Byrsonima cydoniifolia* and *B. sericea* (Malpighiaceae) in a cerrado area in the Chapada Diamantina, northeastern Brazil.

| Individuals | *B. cydoniifolia* | | *B. sericea* | |
	No. flowers/plant	Amount of oil/canopy (g)	No. flowers/plant	Amount of oil/canopy (g)
1	3,803.77	0.82	341,004.00	181.88
2	13,972.95	3.01	51,606.53	27.52
3	25,162.70	5.42	220,912.31	117.83
4	226,324.37	48.77	145,068.00	77.37
5	47,481.72	10.23	5,411.45	2.89
6	20,216.98	4.36	162,225.76	86.52
7	112,486.56	24.2	204,863.65	109.27
8	79,943.49	17.23	98,626.34	52.60
9	13,975.71	3.01	60,345.88	32.19
10	2,426.59	0.52	123,855.67	66.06

Table 3. Abundance of the two species of *Byrsonima* (BS: *B. sericea*, BC: *B. cydoniifolia*), the amount of floral oil estimated at each transect, abundance (A) and richness (R) of each tribe of oil-collecting bees per transect, sampling effort (hours) to capture bees in each transect in a cerrado area in the Chapada Diamantina, northeastern Brazil.

| Site/Transect | | Total oil estimated (g) | Number of individuals *Byrsonima* | | Centridini | | Tapinotaspidini | | Tetrapediini | | Sampling effort (h) |
			BS	BC	A	R	A	R	A	R	
I	T1	7,773.4	102	7	29	4	15	3	14	2	21
I	T2	1,602.4	20	8	1	1	10	3	31	1	7
I	T3	3,005.8	7	210	56	8	0	0	0	0	14
II	T4	3,025.6	19	135	40	5	6	2	0	0	21
II	T5	4,021.4	20	213	17	7	2	2	0	0	14
II	T6	1,320.4	10	48	10	5	1	1	0	0	7
III	T7	9,575.8	127	0	26	3	8	2	1	1	14
III	T8	4,321.4	57	2	1	1	45	4	23	1	7
III	T9	14,627.6	194	0	43	10	15	4	13	2	21
IV	T10	16,397.2	217	3	146	10	22	4	1	1	28
IV	T11	4,297.8	57	0	5	3	30	5	13	2	14
IV	T12	1,734.2	23	0	2	1	0	0	5	2	7

(0.024%) (t = 13.5; df = 13; p<0.001). The average amount of oil produced per flower was 0.0005 g in *B. sericea* and 0.0002 in *B. cydoniifolia*. The amount of oil produced per plant varied from 2.89 to 181.88 g (μ = 75.41 ± 34.98 sd, n=10) in *B. sericea,* and from 0.52 to 48.77 g (μ = 11.75 ± 210.53 sd, n = 10) in *B. cydoniifolia.*

The abundance of the two *Byrsonima* species varied largely among the 12 transects (from 23 to 233 individuals/transect), which resulted in differences in floral oil availability among transects. The estimates of floral oil produced per transect varied from 1,320.4 to 16,397.2 g (Table 3). Despite the high abundance of *Byrsonima* in transects T3 and T5, they had relatively low oil availability (T3: 3,005.8 g and T5: 4,021.4 g). This low oil availability resulted from the predominance of *B. cydoniifolia* in these transects.

Richness (1-10 species) and abundance (1-146 individuals) of Centridini varied largely among transects. Centridini was more abundant in the transects T10, T9, and T3, which are three out of the four transects with the highest number of *Byrsonima* plants (194-220 individuals) (Table 3).

The abundance of oil-bees was more strongly related to the abundance of *Byrsonima* than to floral oil availability (Table 4). The most parsimonious model indicated that the relationship between total oil-bee abundance and *Byrsonima* abundance differed among tribes (χ^2 = 334.18, df = 5, p < 0.001). In fact, the removal of the interaction term between tribe and plant abundance from the model indicated that this interaction was important to explain variations in total bee abundance (χ^2 = 248.41, df = 2, p < 0.001). The total abundance of Centridini increased with *Byrsonima* abundance (Fig 1A),
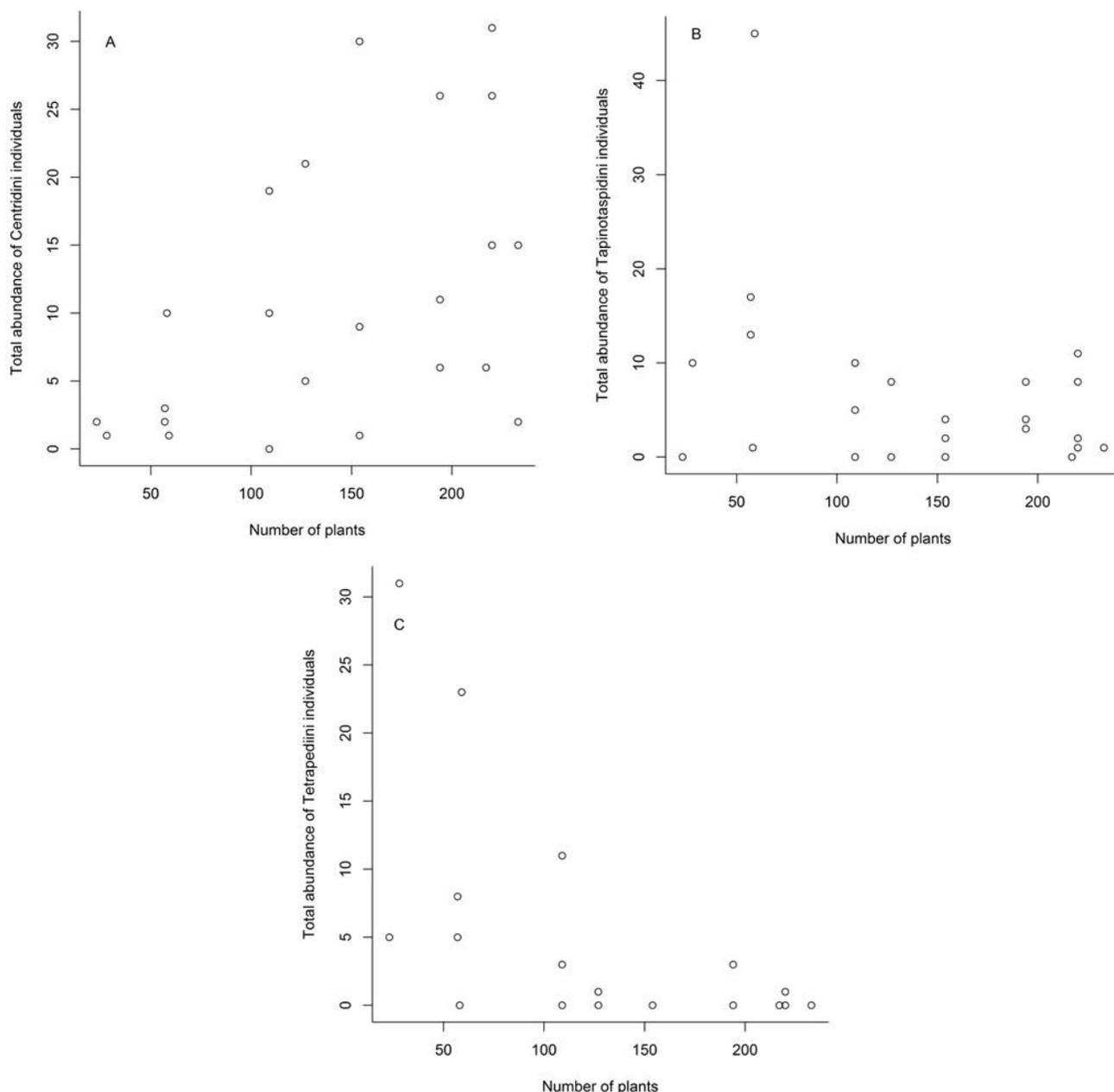
Fig 1. Total number of individuals of Centridini (A), Tapinotaspidini (B) and Tetrapediini (C) in relation to the number of *Byrsonima* plants in a *cerrado* area in Chapada Diamantina, northeastern Brazil. Each dot represents one sampled transect per month (there are superimposed dots).

whereas the effect was the opposite for Tetrapediini species (Fig 1B). The total abundance of Tapinotaspidini species was unrelated to plant abundance (Fig 1C, Table 5).

The number of oil-collecting bee species was also more strongly related to *Byrsonima* abundance than to oil availability (Table 4). The most parsimonious model indicated that the relationship between oil-collecting bee richness and *Byrsonima* abundance differed among tribes ($\chi^2 = 74.42$, df =

5, p < 0.001). The removal of the interaction term between tribe and plant abundance from the model indicated that this interaction was important to explain variations in oil-collecting bee richness ($\chi^2 = 19.04$, df = 2, p < 0.001). The number of Centridini species increased with *Byrsonima* abundance (Fig 2A), whereas the number of Tetrapediini and Tapinotaspidini species was unrelated to *Byrsonima* abundance (Fig 2B and 2C, Table 5).

Table 4. Summary of the models describing variation in total bee abundance and richness in relation to the tribe (Centridini, Tapinotaspidini, and Tetrapediini), plant abundance, and oil availability, in two species of *Byrsonima* (Malpighiaceae) in a cerrado area in Chapada Diamantina, northeastern Brazil. AICc represents the value of the Akaike Information Criterion corrected for small samples; Δi is the difference between the most parsimonious model i, *wi* is the Akaike weight of model i. *Wi* is the probability that the model is the best one among all candidate models.

| Response	Model	AICc	Df	Δ_i	w_i
	tribe + plant abundance + tribe*plant abundance	470.8	8	0.0	1
	tribe + oil availability + tribe*oil availability	615.4	8	144.6	<0.001
	tribe + oil availability	711.7	6	240.9	<0.001
Abundance	Tribe	712.9	5	242.0	<0.001
	tribe + plant abundance	714.2	6	243.4	<0.001
	oil availability	791.9	4	321.1	<0.001
	plant abundance	794.1	4	323.3	<0.001
	tribe + plant abundance + tribe*plant abundance	241.7	8	0.0	0.988
	tribe + oil availability	251.3	6	9.6	0.008
	tribe + oil availability + tribe*oil availability	255.0	8	13.3	0.001
Richness	Tribe	255.1	5	13.4	0.001
	tribe + plant abundance	255.8	6	14.0	<0.001
	oil availability	300.3	4	58.5	<0.001
	plant abundance	304.8	4	63.0	<0.001

Table 5. Planned contrasts for slope differences between tribes. Each slope was calculated from the relationship between bee abundance or bee richness (response variables) and plant abundance (explanatory variable). Estimated values indicate the difference in slope values between the first and the second tribe mentioned in each contrast.

Response	Contrast	Estimate	SE	Z	p
	Centridini vs. Tapinotaspidini	18.47	0.19	-9.60	<0.001
Abundance	Centridini vs. Tetrapediini	36.07	0.35	-10.38	<0.001
	Tapinotaspidini vs. Tetrapediini	17.60	0.33	-5.38	<0.001
	Centridini vs. Tapinotaspidini	0.783	0.28	-2.78	0.027
Richness	Centridini vs. Tetrapediini	15.89	0.42	-3.80	<0.001
	Tapinotaspidini vs. Tetrapediini	0.81	0.43	-1.85	0.241

Discussion

The guild of oil-collecting bees of the studied savanna was diverse, with many rare and a few dominant species. The richness of oil-collecting bees of the studied savanna in Chapada Diamantina was in part a result from concentrating the sampling effort on *Byrsonima* species, with which oil-bees have a close relationship (Ramalho & Silva, 2002; Rosa & Ramalho, 2011). In others studies on bee communities in the same region (Martins, 1994; Silva-Pereira & Santos, 2006), sampling effort was equally distributed among all melittophilous flora. The savannas in Chapada Diamantina seem to harbor much richer bee faunas than sandstone outcrop vegetation, which are contiguous to the savannas in many sites of this region.

Centridini, in particular the genus *Centris*, was the group with highest richness in the studied guild, similarly as recorded in other Brazilian savannas (Martins, 1994; Silveira & Campos, 1995; Andena et al., 2005; 2012) and other Neotropical biomes (Araújo et al., 2006; Santos et al., 2013; Silva et al., 2015). Mello et al. (2013), who used a network approach to assess the interactions between oil-flowers and oil-bees at the biome level, highlighted the importance of
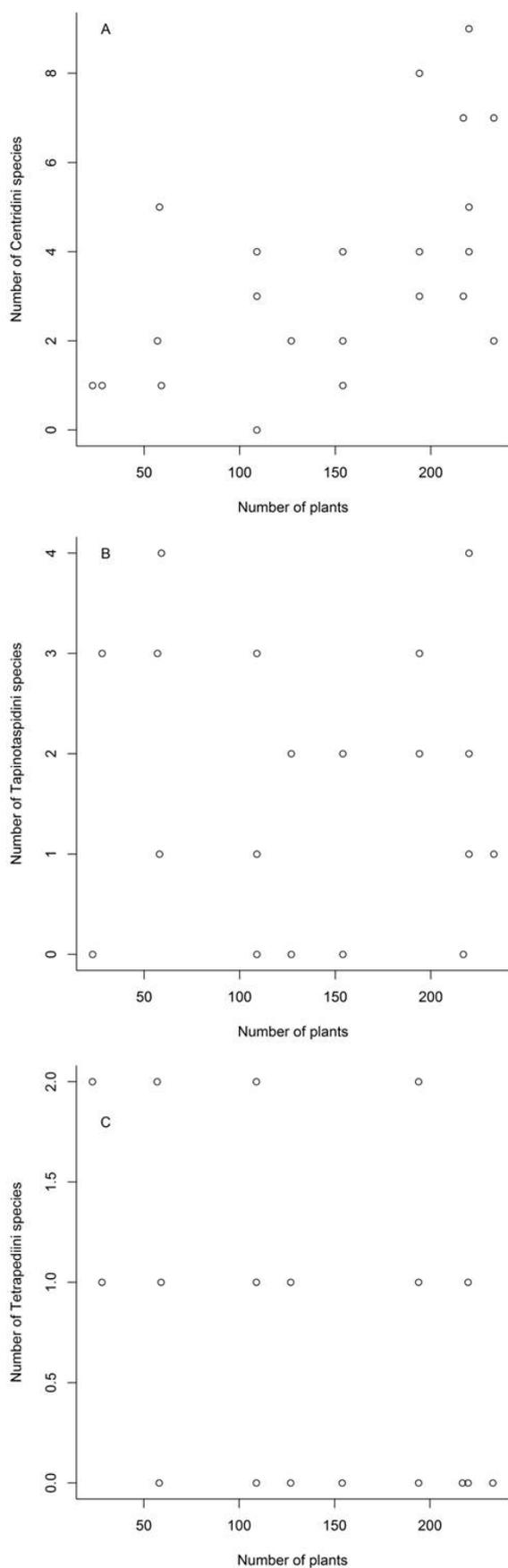
Fig 2. Number of bee species belonging to Centridini (a), Tapinotaspidini (b) and Tetrapediini (c) in relation to the number of *Byrsonima* plants in a cerrado area in Chapada Diamantina, northeastern Brazil.

Centris and *Epicharis* to the guild of oil-collecting bees. The authors reported that these two taxa occupy highly central roles in each network, because they showed a very large number of interactions (hubs) or connected different modules in the networks (connectors).

Although presenting similar foraging needs, distinct taxonomic groups that compose the local guild of oil-bees responded differently to the abundance of *Byrsonima*. The abundance of Centridini increased with the abundance of *Byrsonima*, whereas the abundance of Tetrapediini (*Tetrapedia* spp) decreased and the abundance of Tapinotaspidini showed no correlation. A similar trend was observed in species richness: the number of Centridini species increased with the abundance of *Byrsonima*, whereas the number of Tetrapediini and Tapinotaspidini species showed no correlation. These findings indicate that *Centris* and *Epicharis* species are more dependent on the resources provided by *Byrsonima* than *Tetrapedia* and Tapinotaspidini species. Perhaps species of *Tetrapedia* and Tapinotaspidini use other plants more intensively as food sources, as suggested by studies on the diet of the larvae of *Tetrapedia diversipes* Klug (Menezes et al., 2012; Neves et al., 2014) and *Tetrapedia curvitarsis* Friese (Campos, unpubl. data). In addition, females of *Centris* and *Epicharis* species are often larger than females of *Tetrapedia* and Tapinotaspidini species. Because oil-collecting bees typically "hug" the flower while foraging, it may be that the greater body size of Centridini species prevent flower exploitation by other species. The abundance of *Centris* and *Epicharis* species associated with this possible exclusion behavior may result in exploitation dominance of *Byrsonima* by Centridini.

The total abundance of oil-collecting bees was more strongly related to the abundance of *Byrsonima* than to the amount of oil offered by these flowers. One possible explanation for the best adjustment between abundance of Centridini and *Byrsonima* plants (in detriment of oil availability) is that the abundance of these plants affects not only floral oil, but also pollen availability. Pollen represents one of the main aspects of habitat quality for bee populations. Many Centridini species use *Byrsonima* as a pollen source (Aguiar & Gaglianone, 2003; Dórea et al., 2010; Rabelo et al., 2012), and, therefore, we expect that fluctuations in *Byrsonima* abundance directly influence bee reproduction.

The local availability of resources to supply food and material to build nests (e.g., floral oil used to coat brood cells and nest plugs) should strongly influence the movement of females in the landscape. This movement in search of resources is expected to affect the local abundance of these bees in parts of the habitat. We can assume that Centridini females that decide to nest in areas with a higher abundance of *Byrsonima*, and, therefore, with high availability of oil and pollen, face lower costs to produce offspring. Hence, this decision would contribute to an increase in fitness. As a result, we would expect an increase in the local abundance of these

bees in habitats with high availability of resources.

The species richness and abundance of Centridini increased with the abundance of *Byrsonima*, which corroborates Rosa and Ramalho (2011). Since we developed our study in a different vegetation type than previous studies, it is probable that the positive relationship between the abundance of Centridini and *Byrsonima* does not depend on phytophysiognomy. However, we showed that plant abundance *per se* was more important to determine the abundance and richness of Centridini than the amount of oil available. This finding suggests that other resources, together with oil, are important for the development and maintenance of these bees. However, such relationship does not seem to be the result of the foraging specialization observed in oil-collecting bees, since the abundance and richness of species of Tetrapediini and Tapinotaspidini were unrelated to the abundance of *Byrsonima*. Consequently, it seems that even for species that share a common dependency and similar adaptations to exploit a specific resource (e.g. floral oil), other traits may be equally important in affecting community dynamics.

Acknowledgments

References

Agrawal, A.A., Ackerly, D.D., Adler, F., Arnold, A.E., Cáceres et al. (2007). Filling key gaps in population and community ecology. Frontiers in Ecology and the Environment, 5: 145–152. doi:10.1890/1540-9295(2007)5[145:FKGIPA]2.0.CO;2

Aguiar, C.M.L. & Gaglianone, M.C. (2003). Nesting biology of *Centris* (*Centris*) *aenea* Lep. (Hymenoptera, Apidae, Centridini). Revista Brasileira de Zoologia, 20: 601-606. doi: 10.1590/S0101-81752003000400006

Aguiar, C.M.L. & Garófalo, C.A. (2004). Nesting biology of *Centris* (*Hemisiella*) *tarsata* Smith (Hymenoptera, Apidae, Centridini). Revista Brasileira de Zoologia, 21: 477-486. doi: 10.1590/S0101-81752004000300009

Andena, S.R., Bego, L.R. & Mechi, M.R. (2005). A comunidade de abelhas (Hymenoptera, Apoidea) de uma área de cerrado (Corumbataí, SP) e suas visitas às flores. Revista Brasileira de Zoociências, 7: 55-91.

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: DOI:10 .1080/00222933.2012.681317

Araújo, V.A., Antonini, Y. & Araújo, A.P.A. (2006). Diversity of bees and their floral resources at altitudinal areas in the Southern Espinhaço Range, Minas Gerais, Brazil. Neotropical Entomology, 35: 30-40. doi: 10.1590/S1519-566X2006000100005

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2014). lme4: Linear mixed-effects models using Eigen and S4. R package version 1.1-5 [online] http://CRAN.R-project.org/package=lme4 (accessed date: 3 February, 2013)

Bolker, B. & R Development Core Team (2012). Bbmle: Tools for general maximum likelihood estimation. R package version 1.0.5.2. [online] http://CRAN.R-project.org/package=bbmle (accessed date: 15 January, 2013).

Burnham, K.P. & Anderson, D.R. (2002). Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach. 2th ed. New York: Springer.

Centro de Estatística e Informações [CEI], (1994) Informações básicas dos municípios baianos: Região Chapada Diamantina. Salvador: Secretaria de Planejamento.

Colwell, R.K. (2013). EstimateS: Statistical estimation of species richness and shared species from samples. Version 8.2. [Online] purl.oclc.org/estimates (accessed date: 15 January, 2013)

Conceição, A.A., Rapini, A., Pirani, J.R., Giulietti, A.M., Harley, R.M. et al. (2005). Campos Rupestres. In F.A. Juncá, L. Funch & W. Rocha (Eds.), Biodiversidade e Conservação da Chapada Diamantina, (pp. 151-166). Brasília: Ministério do Meio Ambiente.

Costa, C.B.N., Costa, J.A.S. & Ramalho, M. (2006). Biologia reprodutiva de espécies simpátridas de Malpighiaceae em dunas costeiras da Bahia, Brasil. Revista Brasileira de Botânica, 29: 103-114. doi: 10.1590/S0100-84042006000100010

Dórea, M.C., Aguiar, C.M.L., Figueroa, L.E.R., Lima, L.C.L. & Santos, F.A.R. (2010). Pollen residues in nests of *Centris tarsata* Smith (Hymenoptera, Apidae, Centridini) in a tropical semiarid area in NE Brazil. Apidologie, 41: 557–567. doi: 10.1051/apido/2010005

Dyer, L.A. & Letourneau, D. (2003). Top-down and bottom-up diversity cascades in detrital vs. living food webs. Ecology Letters, 6: 60-68. doi: 10.1046/j.1461-0248.2003.00398.x

Hothorn, T., Bretz, F. & Westfall, P. (2008). Simultaneous inference in general parametric Models. Biometrical Journal, 50: 346-363. doi: 10.1002/bimj.200810425

Jesus, E.F.R., Falk, F.H. & Marques, T.M. (1983).

Caracterização geográfica e aspectos geológicos da Chapada Diamantina, Bahia. Salvador: Centro Editorial e Didático da Universidade Federal da Bahia.

Martins, C.F. (1994). Comunidade de abelhas (Hymenoptera: Apoidea) da caatinga e do Cerrado com elementos de campos rupestres do estado da Bahia, Brasil. Revista Nordestina de Biologia, 9: 225-257.

Mello, M.A.R., Bezerra, E.L.S. & Machado, I.C. (2013). Functional roles of Centridini oil bees and Malpighiaceae oil flowers in biome-wide pollination networks. Biotropica, 45: 45-53. doi: 10.1111/j.1744-7429.2012.00899.x

Menezes, G.B., Gonçalves-Esteves, V., Bastos E.M.A. F., Augusto, S.C. & Gaglianone, M.C. (2012). Nesting and use of pollen resources by *Tetrapedia diversipes* Klug (Apidae) in Atlantic Forest areas (Rio de Janeiro, Brazil) in different stages of regeneration. Revista Brasileira de Entomologia, 56: 86–94. doi: 10.1590/S0085-56262012000100014

Michener, C.D. (2007). The bees of the world. Baltimore: The Johns Hopkins University Press.

Morin, P.J. (1999). Community Ecology. Massachusetts: Blackwell.

Morin, P.J. & Lawler, S.P. (1995). Food web architecture and population dynamics: theory and empirical evidence. Annual Review of Ecology and Systematics, 26**:** 505-529. doi: 10.1146/annurev.es.26.110195.002445

Neff, J.L. & Simpson, B.B. (1981). Oil-collecting structures in the Anthophoridae: Morphology, function and use in systematics. Journal of the Kansas Entomological Society, 54: 95-123.

Neves, C.M.L., Carvalho, C.A.L., Machado, C.S., Aguiar, C.M.L. & Sousa, F.S.M. (2014). Pollen consumed by the solitary bee *Tetrapedia diversipes* (Apidae: Tetrapediini) in a tropical agroecosystem. Grana, 53: 302-308. doi: 10.1080/00173134.2014.931455

Nimer, E. (1989). Climatologia do Brasil. Rio de Janeiro: IBGE.

R Core Team (2014). R: A language and environment for statistical   computing. R Foundation for Statistical Computing, Vienna, Austria. [online] http://www.R-project.org/ (accessed date: 14 January, 2013).

Rabelo, L.S., Vilhena, A.M.G.F., Bastos, E.M.A.F. & Augusto, S.C. (2012). Larval food sources of *Centris (Heterocentris) analis* (Fabricius, 1804) (Hymenoptera, Apidae). an oil-collecting bee. Journal of Natural History, 46: 11-29-1140. doi: 10.1080/00222933.2011.651798

Ramalho, M. & Silva, M. (2002). Flora oleífera e sua guilda de abelhas em uma comunidade de restinga tropical. Sitientibus, Série Ciências, 2: 34-43.

Ritchie, M.E. (2000). Nitrogen limitation and trophic vs. abiotic influences on insect herbivores in a temperate grassland. Ecology, 81: 1601-1612. doi: 10.1890/0012-9658(2000)081[1601:NLATVA]2.0.CO;2

Rosa, J.F. & Ramalho, M. (2011). The spatial dynamics of diversity in Centridini bees: the abundance of oil-producing flowers as a measure of habitat quality. Apidologie, 42: 669-678. doi: 10.1007/s13592-011-0075z

Santos, G.M.M., Carvalho, C.A.L., Aguiar, C.M.L., Macêdo, L.S.S.R & Mello, M.A.R. (2013). Overlap in trophic and temporal niches in the flower-visiting bee guild (Hymenoptera, Apoidea) of a tropical dry forest. Apidologie, 44: 64-74. doi: 10.1007/s13592-012-0155-8

Sazan, M.S., Bezerra, A.D., & Freitas, B.M. (2014). Oil collecting bees and *Byrsonima cydoniifolia* A. Juss. (Malpighiaceae) interactions: the prevalence of long-distance cross pollination driving reproductive success. Anais da Academia Brasileira de Ciências, 86: 347-357. doi: 10.1590/0001-3765201420130049

Sigrist, M.R. & Sazima, M. (2004). Pollination and reproductive biology of twelve species of Neotropical Malpighiaceae: stigma morphology and its implication for breeding system. Annals of Botany, 94: 33–41. doi: 10.1093/aob/mch108

Silva, M., Ramalho, M., Aguiar, C.M.L. & Silva, M.D. (2015). Apifauna (Hymenoptera, Apoidea) em uma área de restinga arbórea-mata atlântica na costa atlântica do Nordeste do Brasil. Magistra, 27: 110-121.

Silva-Pereira, V. & Santos, G.M.M. (2006) Diversity in bee (Hymenoptera: Apoidea) and social wasp (Hymenoptera: Vespidae, Polistinae) community in "Campos Rupestres", Bahia, Brazil. Neotropical Entomology, 35: 165-174. doi: 10.1590/S1519-566X2006000200003

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

Teixeira, L.M. & Machado, I.C. (2000). Sistemas de polinização e reprodução de *Byrsonima sericea* DC (Malpighiaceae). Acta Botânica Brasílica, 14: 347-357

Vinson, S.B. & Frankie, G.W. (2011). Nest selection, Ususrpation, and a Function for the Nest Entrance Plug of *Centris bicornuta* (Hymenoptera: Apidae). Annals of the Entomological Society of America, 93: 254-260.

Vogel, S. & Machado, I.C.S. (1991). Pollination of four sympatric species of *Angelonia* (Scrophulariaceae) by oil collecting bees in NE Brazil. Plant Systematics and Evolution, 178: 153-178. doi: 10.1007/BF00937962