Oil-collecting bee–flower interaction network: do bee size and anther type influence the use of pollen sources?

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Abstract – Pollination is an ecosystem service sustained by a differentiated use of resources among sympatric species. The bee size can influence the similarity in the use of resources, and poricidal anthers limit the access to pollen. Therefore, we evaluated the influence of body size and the anther type of pollen sources in Centridini–flower interaction network. We expected that the low niche overlap, promoted by these morphological parameters, would result in the formation of subgroups and lead to greater network resilience. We studied 15 bee species ($n=73$ females) and identified their pollen sources. The bee size and anther type influenced the formation of subgroups in the community, and the larger bees used a higher proportion of flowers with poricidal anthers. Only the anther type influenced the robustness of the network. We conclude that the parameters analyzed influence both the use of resources by oil-collecting bees and their food niche breadth.

pollen analysis / robustness / ecosystem services / solitary bees / trophic niche

1. INTRODUCTION

Organisms interact with each other in search of resources and the ecosystem services, such as pollination, depend on the maintenance of these interactions. The maintenance of pollination services is associated with the differentiated use of resources among sympatric species due to morphological and behavioral differences (Begon et al. 2006). In bee–plant systems, the body size influences the foraging distance of bees (Greenleaf et al. 2007) and the similarity in the use of resources, which seems to be greater between species with similar body size

(Cortopassi-Laurino et al. 2003; Nogueira-Ferreira and Augusto 2007). In plants, the presence of poricidal anthers limits the access of bees to pollen, because the release of the grains results from the energy produced by the vibration of anthers at the proper frequency (Buchmann 1978). Bees are able to vibrate at different frequencies according to their body size (Buchmann 1978; Harder and Barclay 1994). Larger bees present a lower buzzing frequency during pollen collection in poricidal anthers than smaller species, which is likely to lead to lower energy consumption (Burkart et al. 2011).

The recognition of the influence of these characteristics in the community structure can be performed using analyses of pollen and interaction network. The first tool allows identifying food sources used by bees (Jones and Jones 2001). The second tool is used for the construction of a visual model of the community structure and the

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identification of network properties, such as robustness and niche overlap (Jordano et al. 2003; Memmott et al. 2004; Lewinsohn et al. 2006; Dormann and Gruber 2012). The robustness represents the tolerance of the networks to species extinctions (Memmott et al. 2004) and can be affected by generalization of the species or number of links (Memmott et al. 2004; Staniczenko et al. 2010), connectance of the network (Dunne et al. 2002), and habitat loss (Evans et al. 2013).

The niche overlap represents the resource sharing among different species in a community (Begon et al. 2006). In bee–plant systems, characteristics such as the tongue length (Goulson and Darvill 2004), level of specialization of bees and flower abundance (Aguiar et al. 2013), and temporal aspects of resource availability (Carvalho et al. 2013; Santos et al. 2013) can influence the niche overlap among the species.

Centridini bees are important pollinators of cultivated species (Freitas and Paxton 1998; Vilhena et al. 2012; Yamamoto et al. 2012; Oliveira et al. 2013). The bees of this group are specialized in collecting floral oils, especially from Malpighiaceae species, which can be used as bait plants (Alves-dos-Santos et al. 2007; Ribeiro et al. 2008; Vilhena et al. 2012; Oliveira et al. 2013). Centridini bees present variation in the body size among the species, i.e., bees of medium–large body length (≥ 1.2 cm) and small bees (≤ 1.2 cm) (sensu Frankie et al. 1983), and can vibrate at different frequencies according to their body size (Buchmann 1978).

Thus, the chief goal of this study was to evaluate if the parameters, body size of the Centridini species and the anther type presented by their pollen sources, influence in the structure of this bee–plant community. We expect that these parameters influence the use of pollen sources to reduce the niche overlap. The lower niche overlap would result in the formation of subgroups and, therefore, lead to a greater resilience of the network to the removal of species and to the maintenance of the pollination services. The presence of subgroups in the community may hinder the cascade effect of extinction in plant–pollinator networks (Bosch et al. 2009).

To evaluate these possible effects, we identified the pollen sources used by Centridini bees and

their food niche breadth. We verified whether there were subgroups in the community, considering the anther type of flowers and body size of bees. We also calculated the robustness of the community to the systematic removal of bee species in descending order of body size and according to the anther type.

2. MATERIAL AND METHODS

2.1. Study area

The study was conducted at the Experimental Station of Água Limpa (19° 05' 48" S/48° 21' 05" W), belonging to the Federal University of Uberlândia, located in Uberlândia, Minas Gerais State, Brazil. The station comprises 1,040,000 m² of woody savanna and 1,947,200 m² of pastures, crops, and orchards (Neto 2008). The climate is characterized by two distinct seasons, one hot and wet (from October to March) and other cold and dry (from April to September) (Rosa et al. 1991).

2.2. Sampling of Centridini bees

The Centridini bees were collected during their visits to flower of West Indian cherry or *acerola* (*Malpighia emarginata* DC) crop. Among the cultivated species in the study area, there were approximately 11,000 m² of West Indian cherry trees. This species is self-incompatible and dependent upon pollination made mainly by Centridini bee species (Freitas et al. 1999; Vilhena et al. 2012; Oliveira et al. 2013). In a long-term study about West Indian cherry pollination, Vilhena et al. (2012) collected 23 species of Centridini bees collecting mainly oil as floral resource.

Most of species of Centridini bees are active during the wet season, the flowering period of *M. emarginata* and other Malpighiaceae species (Gaglinone 2003; Vilhena et al. 2012). To identify the pollen sources used by them and calculate the niche breadth, we collected females with pollen loads on their scopa while they were visiting West Indian cherry flowers. The females were collected in October/November and January/February (one sample/month) from 2004 to 2011, totaling 24 sampling days and 120 h of observation. The bees were sampled between 9:00 A.M. and 14:00 P.M. One researcher carried out the collections walking along the inter-rows. Each shrub that presented inflorescences

was observed for about 5 min. Because individuals of this tribe visit West Indian cherry trees preferably to collect oil (Vilhena and Augusto 2007), and there is a variation in the frequency of visits of these pollinators over the years (Vilhena et al. 2012), we needed to realize a long-term study (2004–2011) to obtain samples of pollen loads from most species of floral visitors. We considered the pollen load of each female as a sample.

Females were collected using entomological nets. They were placed individually in plastic bottles and taken to the laboratory, where they were frozen. Only the pollen grains present in their scopas were removed, to prevent contamination by grains present in the bee's abdomen. The samples were stored in 2 mL 70 % ethanol and then acetolized (Erdtman 1960). For each individual, we prepared three slides that were deposited in the collection of the Laboratory of Ecology and Behavior of Bees, Federal University of Uberlândia, Brazil.

We analyzed 73 samples from 15 bee species, and the number of sample per species ranged from two to eight. Due to the difference in the number of samples among the bee species, we verified the quality of pollen sampling effort constructing extrapolation curves using EstimateS (Colwell 2013). The extrapolation analysis is able to estimate the asymptotic number of species ("target richness"), including species not documented by the reference sample (Colwell 2013). Based on the fact that the estimation is adequate, it is expected that the higher percentage of pollen types observed best is the sampling.

The niche breadth was calculated using the Shannon-Wiener index (H'), as proposed by Camillo and Garófalo (1989). We also verified whether the number of samples influences the niche breadth and the percentage of the expected number of pollen types collected, using Spearman correlation tests (Zar 2010).

Pollen grains were identified from morphological characteristics by comparing literature (Salgado-Labouriau 1973; Roubik and Moreno 1991), a database of pollen images (Bastos et al. 2008), and by comparison with reference material of the study area. This study used the taxonomic classification proposed by Angiosperm Phylogeny Group II (Souza and Lorenzi 2005). The pollen grains that presented similar morphology were grouped into pollen types according to which were previously proposed in the literature (Vilhena et al. 2012; Rabelo et al. 2012).

After the identification of the plants used as pollen sources by Centridini bees, we performed quantitative analysis dividing the coverslip into four quadrants. There were counted approximately 100 pollen grains in each quadrant, and among those with fewer than 100 grains, we counted all grains, totaling 1,200 grains per sample (Vilhena et al. 2012). For this analysis, we used 200× increase of magnification. Pollen types with proportion lower than 3 % in each sample were discarded, as they were considered contaminants or only sources of oil or nectar.

2.3. Body size of bees and use of pollen sources according to anther type

The body size of bees was determined from measurements of mean of intertegular span (mean in millimeters±SD) (Cane 1987) measured with the aid of a caliper. For each species, we measured four individuals (total=60 females).

We used the Non-metric Multidimensional Scale (NMDS) analysis to explore how Centridini bee species could be grouped in a multidimensional space based on the dissimilarity in the use of pollen sources according to anther type (Quinn and Keough 2002). For this analysis, the pollen sources were separated into three categories [Malpighiaceae, non-Malpighiaceae/non-poricidal (NMNP), and poricidal]. The Malpighiaceae and NMNP categories comprised species with non-poricidal anthers but were separated due the close relationship between oil-collecting bees and oil-plants. The category poricidal was composed of species that present flowers with poricidal anthers. The analysis was performed in R, using the Vegan package. The anther type and the flower's resources of each plant were determined according to literature (see Anderson 1979; Buchmann 1983; Oliveira et al. 1987; Oliveira and Gibbs 1994; Kill et al. 2000; Carvalho and Oliveira 2003; Fracasso and Sazima 2004; Pereira and Barbosa 2004; Andena et al. 2005; Ragusa-Netto 2005; Souza and Lorenzi 2005; Del Lama and Peruquetti 2006; Filho et al. 2007; Pool 2009).

To verify the influence of body size on the ordination of the species in the multidimensional space, we used a Spearman correlation between the intertegular span of all bee species and the scores generated in NMDS for the first axes (which represents all the pollen sources

used by the bees and the major variance of data) (Zar 2010).

2.4. Robustness and niche overlap

The network between oil-collecting bees and their pollen sources was constructed based on an adjacency matrix, in which bee species were arranged in rows and pollen types in columns. The matrix cells were filled with the number of pollen grains counted for each bee species.

To verify the effect of body size of the bees and anther type of flowers (Malpighiaceae, NMNP, and poricidal), the robustness of the structure was calculated based on systematic and random removals. The exclusion criterion was the removal of bee species based on their body size (first the largest, then the smallest one) and anther type (first Malpighiaceae, then poricidal and NMNP).

The value of robustness varies between 0 and 1. Values of robustness near 0 indicate a fragile system in which the extinction of a small number of species can lead to a great number of co-extinctions, due to the loss of all interactions. On the other hand, robustness near 1 represents a resilient system, in which the removal of a large number of species results in a small number of co-extinctions (see Dormann and Gruber 2012). This parameter was calculated using the Bipartite-R package for `second.extinct` and `robustness` functions. To investigate whether the robustness observed was significantly different from the random values, we compared the observed values with the mean value obtained from null models ($n=1,000$) using the one-sample t test (Zar 2010). The null models were constructed using the `nullmodel` function and the method 1, from the Bipartite-R package (Dormann and Gruber 2012).

We used the function `networklevel` from the Bipartite-R package to calculate the niche overlap (mean $\pm$ SEM), separately for bee species and pollen types. The niche overlap represents the mean pattern of similarity in interactions among bees or pollen types, based on Horn's index. Values of this parameter near 0 indicate low sharing of resources, and 1 indicates perfect niche overlap (see Dormann and Gruber 2012).

Considering that the greater density of *M. emarginata* compared to the native species may cause a bias in the analyses of robustness and niche overlap, we repeated these analyses excluding this bait plant.

3. RESULTS

Among the bee species sampled, 11 belong to *Centris* Fabricius, 1804 genus, and four to *Epicharis* Klug, 1807 genus, while the pollen sources belong to nine botanical families and 26 pollen types (Table I and Figure 1). Based on the anther type, 80.77 % ($n=21$) of pollen types used by bees presented non-poricidal anthers [Malpighiaceae=19.23 % ($n=5$) and NMNP=61.54 % ($n=16$)], and 19.23 % ($n=5$) of them presented poricidal anthers. Only *Epicharis* (*Epicharoides*) *albofasciata* Smith, 1874 did not use any poricidal sources (Table I).

The analyses showed that for all bee species, a few pollen types comprised most of the pollen grains used by the females. According to the pollen abundance, the Malpighiaceae family was the main pollen source used by almost all bee species, except for *Centris* (*Centris*) *nitens* Lepeletier, 1841, which used similarly the Malpighiaceae species (44.91 %) and the *Solanum* spp. (54.50 %).

The use of *M. emarginata* varied among the bee species. *Centris* (*Centris*) *varia* (Erichson, 1849) was the only species for which this pollen type was more representative than the native species of Malpighiaceae (Figure 2). Other pollen sources besides Malpighiaceae, with or without poricidal anthers, were also notably important (>30 %) for *Centris* (*Trachina*) *longimana* Fabricius, 1804, *Centris* (*Centris*) *flavifrons* (Fabricius, 1775), *Centris* (*Aphemisia*) *mocsaryi* Friese, 1899, and *Epicharis* (*Hoplepicharis*) *affinis* Smith, 1874 (Table I).

The pollen types used by the largest number of bee species were *Heteropterys* type ($n=14$ species), *Solanum lycocarpum* ($n=13$ species), *Byrsonima* type ($n=12$ species), and *M. emarginata* ($n=12$ species) (Table I). The number of pollen types used by the bee species ranged from three [*E. albofasciata* and *C. mocsaryi*] to nine [*C. varia* and *C. flavifrons*] (Table II). The niche breadth presented by bees ranged from $H'=0.55$ (*E. albofasciata*) to $H'=1.95$ (*C. flavifrons*) (Table II).

The extrapolation analyses showed that the sampling effort ranged from 57.66 to 100.00 % of the pollen types expected (Table II). The

Table 1. Relative abundance (%) of pollen sources used by Centridini bees in woody savanna area. Other families are represented by Anacardiaceae (A) (one type), Bignoniaceae (B) (two types), Leguminosae (L) (five types), Melastomataceae (M) (one type), Myrtaceae (My) (one type), Rubiaceae (R) (two types), Vochysiaceae (V) (five types), and not determined (ND) (one type).

Bee species	Pollen sources		Solanaceae ^b						Other families
	Malpighiaceae						Solanaceae ^b		
	<i>B. malifolia</i>	<i>Byrsonima</i> type	<i>H. byrsonimifolia</i>	<i>Heteropterys</i> type	<i>M. emarginata</i>	<i>Solanum cf paniculatum</i>	<i>S. lycocarpum</i>	<i>Solanum</i> spl	
<i>Centris aenea</i>	–	22.88	3.22	25.06	35.35	–	3.14	–	10.35 (L, V)
<i>Centris analis</i>	3.16	20.29	–	70.96	–	–	2.49	–	3.10 (L)
<i>Centris denudans</i>	–	6.61	–	40.97	38.68	–	13.74	–	–
<i>Centris flavifrons</i>	0.87	16.15	–	26.31	17.30	4.82	5.85	–	28.7 (A, L ^a)
<i>Centris longimana</i>	–	9.05	–	27.20	28.38	–	33.21	–	2.17 (B, L, V)
<i>Centris mocsaryi</i>	–	–	–	69.92	–	–	28.67	–	1.40 (B)
<i>Centris nitens</i>	18.89	18.22	–	–	7.80	–	50.45	4.05	0.59 (R)
<i>Centris poecila</i>	–	11.20	–	69.78	–	–	–	1.51	17.51 (My)
<i>Centris scopipes</i>	–	14.51	–	54.55	12.78	–	15.89	–	2.28 (B, L, V)
<i>Centris spilopoda</i>	0.55	43.83	–	11.76	41.70	–	1.75	–	0.41 (B, L)
<i>Centris varia</i>	12.30	1.13	–	10.01	58.71	–	3.06	–	14.79 (L, M ^b , V ^a)
<i>Epicharis affinis</i>	8.03	–	–	36.94	12.70	–	39.21	–	3.11 (R)
<i>Epicharis albofasciata</i>	–	–	–	77.93	21.56	–	–	–	0.52 (V)
<i>Epicharis bicolor</i>	11.67	44.52	–	31.64	3.15	–	6.46	–	2.57 (V, ND)
<i>Epicharis flava</i>	–	42.97	3.92	19.59	14.42	–	16.65	–	2.45 (L ^{a,b})

^a Botanical families for which two types were identified

^b Plants that present poricidal anthers

Figure 1. Interaction network between oil-collecting bees and their pollen sources. The bee species are located in the left column, and the colors represent the genus (Black: *Centris*; gray: *Epicharis*). The pollen sources are shown in the right column, and the different colors represent the anther type of pollen sources (Malpighiaceae: light gray; non-Malpighiaceae/non-poroidal: black; and poroidal: white). The thickness of the lines and the length of the rectangle are proportional to the number of pollen grains sampled. The flower resources are between parentheses, P pollen, O oil, and N nectar, and were determined according to literature.

number of samples did not influence either the niche breadth ($r_s=0.34$; $n=15$; $P>0.05$) or the

percentage of the expected number of pollen types sampled ($r_s=0.27$; $n=15$; $P>0.05$).

Figure 2. Relative abundance of pollen grains of *Malpighia emarginata* and other Malpighiaceae species for each Centridini bee species.

The smallest species was *Centris* (*Heterocentris*) *analis* (Fabricius, 1804), whose intertegular span was 3.14 ± 0.08 mm and the largest species was *Centris* (*Ptilotopus*) *denudans* Lepeletier, 1841 with 8.86 ± 0.11 mm (Table II).

The Non-metric Multidimensional Scale analysis showed that the bee species studied were assembled into three groups, according to proportion of

Malpighiaceae, NMNP, or poricidal sources used by each species (stress=0.01) (Figure 3). The first group, composed of *C. flavifrons* and *Centris* (*Centris*) *poecila* Lepeletier, 1841, was associated with the NMNP pollen sources. The second group, consisted of *Centris* (*Centris*) *aenea* Lepeletier, 1841, *C. analis*, *C. denudans*, *Centris* (*Ptilotopus*) *scopipes* Friese, 1899, *Centris*

Table II. Body size of the Centridini bees based on the mean intertegular span (IS) of four specimens of each species, number of pollen load samples obtained (Samples), number of pollen types sampled (Richness), niche breadth (H'), and the number of the richness estimated by the extrapolation analysis.

Bee species (Codes)	Parameters				
	IS $\pm$ SD	Samples	Richness	(H')	Extrapolation $\pm$ SD (%)
<i>Centris analis</i> (CAN)	3.14 $\pm$ 0.08	5	5	0.88	5.56 $\pm$ 1.11 (89.93 %)
<i>Centris spilopoda</i> (CSP)	4.70 $\pm$ 0.15	6	7	1.10	8.29 $\pm$ 1.87 (84.44 %)
<i>Centris varia</i> (CV)	4.84 $\pm$ 0.48	8	9	1.40	9.47 $\pm$ 1.05 (95.04 %)
<i>Epicharis albofasciata</i> (EAL)	4.96 $\pm$ 0.10	7	3	0.55	3.00 $\pm$ 0.00 (100.00 %)
<i>Centris nitens</i> (CN)	4.98 $\pm$ 0.03	3	6	1.33	6.97 $\pm$ 1.50 (86.08 %)
<i>Centris poecila</i> (CP)	5.21 $\pm$ 0.10	2	4	0.86	6.15 $\pm$ 2.91 (65.04 %)
<i>Centris aenea</i> (CA)	5.35 $\pm$ 0.10	6	7	1.56	9.53 $\pm$ 3.08 (73.45 %)
<i>Epicharis bicolor</i> (EB)	5.36 $\pm$ 0.07	4	7	1.37	9.05 $\pm$ 2.40 (77.35 %)
<i>Epicharis affinis</i> (EA)	5.94 $\pm$ 0.35	2	5	1.31	8.65 $\pm$ 4.11 (57.80 %)
<i>Epicharis flava</i> (EF)	7.13 $\pm$ 0.04	6	8	1.50	10.64 $\pm$ 2.85 (75.19 %)
<i>Centris flavifrons</i> (CF)	7.32 $\pm$ 0.21	6	9	1.95	15.61 $\pm$ 5.18 (57.66 %)
<i>Centris mocsaryi</i> (CM)	7.53 $\pm$ 0.05	3	3	0.67	3.32 $\pm$ 0.87 (90.36 %)
<i>Centris longimana</i> (CL)	7.75 $\pm$ 0.11	7	7	1.40	8.38 $\pm$ 1.94 (83.53 %)
<i>Centris scopipes</i> (CSC)	8.78 $\pm$ 0.17	6	7	1.28	8.15 $\pm$ 1.69 (85.89 %)
<i>Centris denudans</i> (CD)	8.86 $\pm$ 0.11	2	4	1.19	4.50 $\pm$ 1.00 (88.89 %)

Figure 3. The ordination of the Centridini bee species in a multidimensional space according to the Non-metric Multidimensional Scale analysis based on anther type of pollen sources (NMNP non-Malpighiaceae/non-poroidal). The species codes are presented in Table II.

(*Centris*) *spilopoda* Moure, 1969, *C. varia*, *E. albofasciata*, *Epicharis* (*Epicharis*) *bicolor* Smith, 1854, and *Epicharis* (*Epicharana*) *flava* Friese, 1900, whose main sources of pollen were Malpighiaceae. The third group, whose representatives were *C. longimana*, *C. mocsaryi*, *C. nitens*,

and *E. affinis*, used great amount of sources with poricidal anthers compared to others Centridini species.

Additionally, there was a significant correlation between the intertegular span of all bee species and the scores generated in NMDS for the first axis ($r_s=0.589$; $P<0.05$; $n=15$). This result showed that the body size is an important factor in determining the groups. The largest bees used a higher proportion of flowers with poricidal anthers compared to the smallest ones (Figures 3 and 4).

The robustness analyses showed that the systematic removal of the plant species according their anther type (Malpighiaceae, poricidal, and NMNP) reduced 19.91 % of the structure resilience, given that in this case the network presented a smaller robustness index (0.676) than random removal (0.844). However, the removal of bee species from the largest to the smallest had no effect on the resilience of the structure, since the robustness' index (0.680) was similar to that observed from random removal (0.652). All robustness values were significantly different from the observed for null models ($P<0.001$; Table III).

Figure 4. Influence of body size in the ordination of the Centridini bee species in the multidimensional space evaluated by the Spearman test.

According to the niche overlap analysis, the bee species shared more pollen types (0.60) than the plants shared bee species (0.11).

Although *M. emarginata* presents greater density compared to the plant native species, the removal of this species from the system did not cause significant changes in the observed values of robustness (Table III) and niche overlap among bees (0.62) and plants (0.09).

4. DISCUSSION

Although there was an identification of a large number of pollen types used as pollen sources by Centridini bees in our study only a few pollen types were quantitatively important for each bee species, as also observed for other species of *Centris* (Quiróz-García et al. 2001; Quiroz-García and Arreguin-Sánchez 2006; Dórea et al. 2010, 2013; Rabelo et al. 2012, 2014; Santos et al. 2013).

The sources of resources used by the greatest number of bee species studied herein are the families Malpighiaceae and Solanaceae, which offer pollen/oil and pollen, respectively, as floral rewards (Anderson 1979; Buchmann 1983). The oil-collecting bees gathered resources in both native (*Banisteriopsis*, *Byrsonima*, and *Heteropterys*) and exotic species (*M. emarginata*), probably because of the similarity in floral morphology among Malpighiaceae species, regardless of the petal's colors, which may be yellow, pink, or white (Anderson 1979).

The West Indian Cherry is an introduced species in Brazil (Cardoso et al. 2003) and a well-adapted cultivar used as source of both pollen and oil by ground-nesting and cavity-nesting oil-bee species (Vilhena and Augusto 2007; Oliveira and Schilindwein 2009; Santos et al. 2013).

Species of *Solanum* were also reported as important pollen sources for other Centridini bees, such as *Centris* (*Hemisiella*) *trigonoides* Lepelletier, 1841 (Quiróz-García et al. 2001; Dórea et al. 2013), *C. analis* (Quiróz-García et al. 2001; Rabelo et al. 2012; Santos et al. 2013), and *Centris* (*Hemisiella*) *tarsata* Smith, 1874 (Dórea et al. 2010; Gonçalves et al. 2012; Rabelo et al. 2014). This genus is an important pollen source for oil-collecting bees due their capacity to remove pollen using vibration (Buchmann 1983). Other pollen sources with poricidal anthers as *Senna* and *Cambessedesia* species were also registered as important pollen sources for Centridini species (Fracasso and Sazima 2004; Dórea et al. 2010; Gonçalves et al. 2012).

The formation of three groups composed of different numbers of bee species ordered by body size and another type was observed. The groups formed suggest that Centridini bees present three strategies for the use of provision sources: (1) collection of pollen mainly in Malpighiaceae species (relative abundance of pollen >80 %; Table I); (2) collection of pollen from Malpighiaceae and plants with poricidal anthers; or (3) collection of pollen from Malpighiaceae and the exploitation of pollen from other non-poricidal flowers. The first strategy is probably the most basal in this group of bees. This

Table III. Robustness (R) of interaction networks according to systematic removal of bee species in descending order of body size and plants based on the anther type and random removal. The results were compared with null models using one-sample t tests ($df=999$).

	With <i>M. emarginata</i>		Without <i>M. emarginata</i>	
	R	t	R	t
Systematic removal of bees (body size)	0.680	7,551.690*	0.671	7,395.557*
Radom removal of bees	0.652	8,253.667*	0.633	8,303.912*
Systematic removal of plants (anther type)	0.676	4,379.139*	0.663	4,364.779*
Radom removal of plants	0.844	1,694.099*	0.870	1,207.006*

* $P<0.001$

idea can be supported by the fact that *Centris* and *Epicharis* are as old as the Malpighiaceae family whose diversification was fundamental for the oil-foraging behavior development, as discussed by Neff and Simpson (1981) and Renner and Schaefer (2010). Therefore, this fist strategy was the most frequently observed among the species of Centridini sampled. Pollen of Malpighiaceae composed more than 80 % of the pollen grains observed for ten bee species. *Epicharis albofasciata*, e.g., probably used exclusively Malpighiaceae as pollen sources (99.48 %). This species is considered a univoltine species with its activity restricted to the hot and wet season (Gaglinone 2003, 2005). Information about its food niche is scarce, but there are records of this bee species visiting only *Byrsonima intermedia* A. Juss. (Gaglinone 2003; Andena et al. 2012).

Although all Centridini bees are able to shake pollen out of poricidal anthers regardless of their body size, larger bees used more sources with poricidal anthers. In this context, the use of the poricidal anther could be favored by the economy of energy in the exploitation of poricidal sources and be considered as a mechanism to reduce the competition for exploitation among the species of the same guild (Burkart et al. 2011).

Only the anther type caused some effect on the resilience of the network. This result may be associated with the lower niche overlap among plants species, i.e., almost 50 % of the pollen types were visited by only one bee species. On the other hand, the absence of the effect of bee body size on the resilience of the network could be a result of functional redundancy among the bee species. All of them present similar structures that allow them to collect oil (Neff and Simpson 1981; Alves-dos-Santos et al. 2007) and are able to vibrate the body (Thorpe 2000), despite the differentiation in the proportion of the use of this behavior to collect pollen. Therefore, as regards the anther type, the niche overlap was more related to the plant characteristic.

In conclusion, our results supported the hypotheses proposed considering that this study showed that the parameters analyzed influenced both the use of resources by oil-collecting bees

and their food niche breadth. We verified that body size of bees and anther type seems to influence the formation of subgroups in the community of Centridini bees and their pollen sources, the bee species shared more pollen types as sources of resources than the plants shared bee species as flower's visitors and that the anther type influenced the network robustness.

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Réseau d'interactions fleurs-abeilles récolteuses d'huile: la taille de l'abeille et le type d'anthère ont-ils une influence sur l'utilisation des sources de pollen?

analyse pollinique / robustesse / service écosystémique / abeille solitaire / niche trophique

Ein Bienen-Blüten-Interaktions-Netzwerk für ölsammelnde Bienen: Haben die Grösse der Bienen und der Antheren-Typ einen Einfluss auf die Pollenquelle?

Pollenanalyse / Robustheit / Ökosystemservice / solitäre Bienen / trophische Nische

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