



## Pollen sources used by *Frieseomelitta* Ihering 1912 (Hymenoptera: Apidae: Meliponini) bees along the course of the Rio Negro, Amazonas, Brazil

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### ABSTRACT

Insect pollination has influenced the evolution and diversification of angiosperms. Consequently, knowing plants used as food sources by bees, the most important pollinator group, is the first step toward understanding how their ecological relationships works. Pollen source information is also highly relevant for bee management and associated fruit and seed production. Accordingly, to improve understanding of the trophic ecology of these bees and their relationships with native Amazonian plants the current study identified, quantified and compared pollen stored in nests of *Frieseomelitta* stingless bees along the Rio Negro, Amazonas, Brazil. A total of 31 pollen pots were sampled and found to contain 65 pollen types distributed across 52 genera and 29 botanical families (predominantly Arecaceae, Araliaceae, Fabaceae and Urticaceae). *Euterpe* was the commonest pollen type, being present in 32.2 % of the analyzed samples. Although the studied bees were generalists, pollen analysis suggested that different *Frieseomelitta* species may have distinct food preferences. The pollen profile of the studied bees was influenced more by nest location than by species phylogenetic proximity. The current study also provides a list of important plants for native bee management, which could improve beekeeping when grown near managed meliponarine colonies.

**Keywords:** Amazon, feeding behavior, meliponicultura, stingless bees, trophic resources

### Introduction

Insect pollination influenced the evolution and diversification of Angiosperms (Lima 2000; Soltis *et al.* 2019), especially in the tropics where the dependence of plants on biotic pollinators appears to be higher than in more temperate environments (Maués *et al.* 2012; Rech *et al.* 2016). Within the tropics, where pollinators are central to biodiversity maintenance, bees appear as especially important, being identified as key floral visitors in many plant families (Ollerton 2017). For bees, pollination is driven by their dependence on plant-produced trophic resources

since, from the larval phase until senescence, nectar and pollen provide bees with their sole sources of glucose and protein, respectively (Corbet *et al.* 1991; Nogueira-Neto 1997; Absy *et al.* 2018).

Therefore, understanding the network of interactions between bees and plants is essential, as knowledge of the diet of each bee species provides the first step towards understanding the multiple levels of plant-insect interdependence, and the dynamics of these relationships (Absy *et al.* 2018). In addition, such studies can generate data that informs guidelines for defining conservation strategies for both plants and pollinators, as well as assisting in the evaluation of pollination as an ecosystem service (Kearns *et*

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al. 1998; Kremen *et al.* 2004; Wolowski *et al.* 2018). In the Neotropics stingless bees of the Tribe Meliponini (Family Apidae) are especially important in this regard (Imperatriz-Fonseca & Nunes-Silva 2010).

One of the ways of accessing species involvement in the bee/plant interaction network is through direct observation (Freitas *et al.* 2014). However, due to the number of species involved, this method becomes very complex in tropical forest environments (Absy *et al.* 2018). Instead, palynology offers an indirect tool for the identification of the pollen collected by bees, one which allows access to the preferred food sources of various bee species, as well as others used as alternative and occasional resources (Rech & Absy 2011a; b). This method can be very effective because it provides access to the full spectrum of resources used by the bees, such as tall flowering trees, small flowering herbs and/or individual plants far-removed from study colonies, and which cannot be accessed easily by direct observation (Imperatriz-Fonseca *et al.* 1989). Therefore, once the dynamics and resources of meliponines are known, it becomes possible to test their effectiveness as pollinators, and so manage them to increase fruit production and so reduce extinction risk for endangered plant species, among other benefits.

*Frieseomelitta* is an ecologically important stingless bee genus in Amazonia, where its members are commonly called *breu*, *moça branca* or *marmelada* (Nogueira-Neto 1997). The genus is poorly known, with scattered papers on biogeography, phylogeny and autoecology of member species (Teixeira 2003). Moreover, it comprises a relatively large, diversified group, with a wide geographical distribution, ranging from the Mexican southwest to the Brazilian southeast (Marques-Souza *et al.* 1995; Silveira *et al.* 2002). Thus, many species still lack key baseline information. Species belonging to this genus are generally small (about 6 mm) and usually build their nests in rotting holes in tree trunks. The literature indicates that these bees are generalist foragers, visiting many plant species, but concentrating sequentially on a few species (Marques-Souza *et al.* 1995; Teixeira 2003).

The current study is part of a series conducted in the Rio Negro-Amazonas region aiming to gain key baseline in a variety of aspects of meliponin ecology. Previous results of this initiative were presented by Rech & Absy (2011a; b) who worked with several genera of stingless bees from the region, including: *Aparatrigona*; *Cephalotrigona*; *Nogueirapis*; *Oxytrigona*; *Partamona*; *Plebeia*; *Ptilotrigona*; *Scaptotrigona*; *Scaura*; *Schwarzula*; *Tetragonisca* and *Trigona*. In these studies, the authors identified important meliponine diet plants and noted temporary specialization events (collection concentrated on specific pollen sources). The results of these previous studies also indicated that collection site was more important than phylogeny in the amplitude and identity of trophic resources used as food by the stingless bees along the Rio Negro.

The current study continues the investigation of pollen resources used by Meliponini species from the Rio Negro region so as to further improve understanding of the trophic ecology of these bees and their relationships with Amazon region native plants. Based on the previous findings, we expect that *Frieseomelitta* pollen diversity will be more strongly influenced by the sampling site than by the species phylogenetic relationship. Also, given the non-aggressive behavior exhibited by *Frieseomelitta* (Marques-Souza *et al.* 2002), we expect they will have a generalist pollen profile similar to the other non-aggressive bees already studied in Amazon, and have foraging behavior characterized by a series of brief resource-specialization events (*sensu* Rech & Absy 2011a; b).

## Materials and methods

The studied pollen material was collected along a stretch of approximately 1,600 km, between the municipalities of Manaus and São Gabriel da Cachoeira, western Brazilian Amazonia (Fig. 1). The collection area was covered by seasonally-flooded igapó vegetation, with some points under the influence of never-flooded Terra-Firme rainforest. According to Wittmann *et al.* (2006), the seasonally-flooded Amazon forest environment has many species tolerant to flooding, in a system considered the world's most species-rich rainforest.

Collections of material used for this study were made in the natural habitat of the bees by Dr. João Maria Franco de Camargo (*in memoriam*) and team (M. Mazucato and SRM Pedro) in five communities (Fig. 1) along the Rio Negro main river and its tributaries, during a collection expedition carried out from 15/ July/ 1999 to 15/ August/ 1999. Analyzed pollen samples were collected from nests of *Frieseomelitta* Ihering bees. Nests found in nature were opened and pollen pots already closed by bees removed and stored in labeled plastic bags and then placed in boxes to avoid pollen pot breakage.

Collection occurred at each nest found. Each pot of closed pollen was considered a separate sample and, for this reason, the number of samples per species varied according to the number of pots found per nest. In total, 31 samples from four bee species (*Frieseomelitta flavicornis* Fabricius, 1798; *Frieseomelitta* sp. Ihering, 1912; *Frieseomelitta portoi* Friese, 1900; *Frieseomelitta trichocerata* Moure, 1990), encountered across a total of five different locations (Tab. 1), were analyzed. For analysis samples were withdrawn from pots using sterile plastic straws, placed in Petri dishes, weighed (to the nearest 0.5 g), then placed in falcon tubes with 3 ml of glacial acetic acid. After 24 hours, the material was acetolysed, following the protocol described by Erdtman (1960). Slide assembly was performed with glycerinated gelatin and sealed with parafinn (Salgado-Labouriau 1973). Three slides were prepared per sample.



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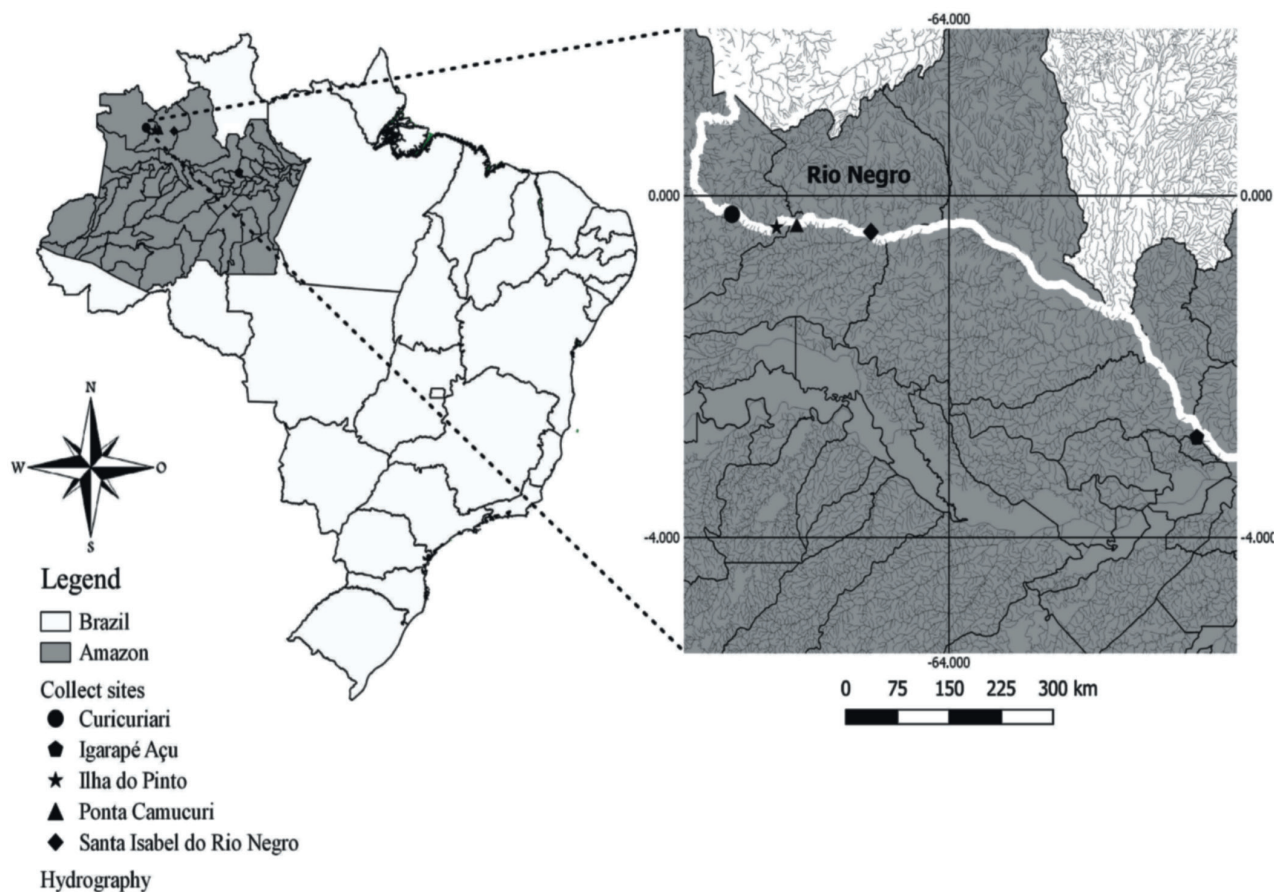
Pollen type identification was performed by comparison with the reference collection for the current study areas maintained at the Laboratório de Palinologia of the Instituto Nacional de Pesquisas da Amazonia (INPA), as well as consultation with specialized literature (Roubik & Moreno 1991; Carreira *et al.* 1996; Lorente *et al.* 2017). For pollen grain taxonomic characterization, the concept of “pollen type” proposed by Joosten & Klerk (2002) and Klerk & Joosten (2007) was adopted. Measurements and photomicrographs were obtained with a Zeiss PrimoStar microscope combined with the AxionCam ICc image capture program.

For each sample, 600 pollen grains were counted for richness/abundance quantification and statistical analysis. To ensure that 600 pollen counts was enough to reach the saturation of the curve required for our analyses, we produced species accumulation curves using rarefaction for each sample (run using R software - R Development Core Team 2019). Following Ramalho *et al.* (1985), a minimum representation of 10 % in the sample was used to define when a plant species was considered attractive to the bee species in question.

To visualize the operational limits underwhich the bee-plant interactions were operating, information relating to

**Table 1.** Species of *Frieseomelitta* bees, location of studied nests, Coordinate and number of collected pollen pots at five sites along the Rio Negro, between the cities of Manaus and São Gabriel da Cachoeira, Amazonas, Brazil.

Nest	Species	Location	Coordinate	Pollen pots
1	<i>Frieseomelitta flavicornis</i> Fabricius, 1798	Santa Isabel do Rio Negro	0° 25' 04" S, 65° 01' 07" W	4
2	<i>Frieseomelitta flavicornis</i> Fabricius, 1798	Curicuriari	0° 13' 09" S, 66° 56' 26" W	6
3	<i>Frieseomelitta</i> sp. Ihering, 1912	Ponta Cumucurí, right bank	0° 20' 02" S, 65° 59' 20" W	6
4	<i>Frieseomelitta portoi</i> Friese, 1900	Santa Isabel do Rio Negro	0° 25' 04" S, 65° 01' 07" W	6
5	<i>Frieseomelitta portoi</i> Friese, 1900	Igarapé Açú, São Francisco	02° 49' 58" S, 60° 46' 51" W	1
6	<i>Frieseomelitta trichocerata</i> Moure, 1990	Santa Isabel do Rio Negro	0° 25' 04" S, 65° 01' 07" W	6
7	<i>Frieseomelitta trichocerata</i> Moure, 1990	Ponta Camucuri, right bank	0° 20' 02" S, 65° 59' 20" W	1
8	<i>Frieseomelitta trichocerata</i> Moure, 1990	Ilha do Pinto, left bank	0° 22' 17" S, 66° 15' 06" W	1
Total				31



**Figure 1.** Map showing sample sites along the Rio Negro channel, Amazonas, Brazil.

floral biology (flowering strategy, compatibility system, flower morphology, nectar production) was obtained via bibliographical research for species operationally defined as attractive. When investigating temporary specialization events (collection concentrated on a specific pollen source), a minimum cut-off of 90 % representation of a single pollen type in a sample was used (following Rech & Absy 2011a; b).

We used collected pollen type abundances to perform a pair-wise cluster analysis. Similarity between each pair of samples was determined using the Bray-Curtis Index, with this index chosen due to its robustness and because it ignores the multiple zeros that are not necessarily true absences in the data matrix (Michin 1987). As defined by Bray & Curtis (1957), the index of dissimilarity is:

$$BC_{ij} = \frac{2C_{ij}}{S_i + S_j}$$

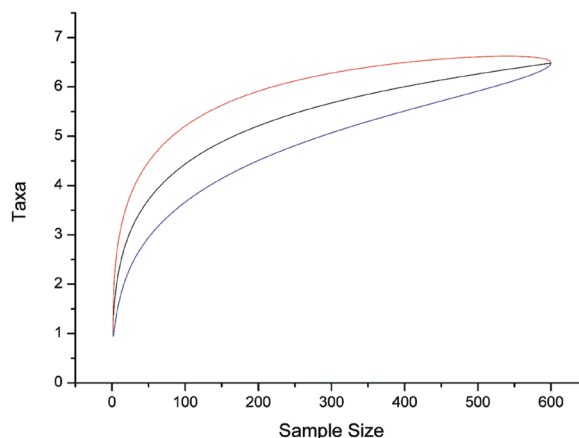
Where  $C_{ij}$  is the sum of the lowest values for only those species in common between both sites, and  $S_i$  and  $S_j$  are the total number of specimens counted at both sites. The Index value varies from 0 to 1, being 1 when both communities have identical compositions. We used a dominance index to evaluate the frequency distribution of pollen types in each sample. For this we used the Simpson Diversity Index  $((n_i/N)^2)$ , where  $n_i$  is the amount of pollen types in the sample  $i$  and  $N$  is the total pollen grains counted in the sample. Dominance varies from zero to one, being 0 when all pollen types have identical frequencies, and 1 when all pollen-grains come from a single species. Analyzes were performed using PAST software (Hammer *et al.* 2001).

Sample specimens of the studied bee species were deposited in the “Camargo” – RPSP collection in the Departamento de Biologia, Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo. Pollen slides were placed in the Palynological Library of the Laboratório de Palinologia of the Instituto Nacional de Pesquisas da Amazônia-INPA. Bee specimens were identified by João M. F. Camargo, using the classification of Camargo & Pedro (2008). Plant nomenclature followed Tropicos.org (GARDEN-MOBOT MB 2016) and the classification proposed by APG III (2009) and IV (2016).

## Results

We analysed a total of 31 pollen pots and identified 65 pollen types assigned to 29 botanical families. Of these, 24 were identified to species, 37 to genus category and three to botanical family (Tab. 2). On average, per pot pollen samples contained seven pollen types (range three to 12 types per sample). For most samples, mean species accumulation curve showed saturation below 600 pollen grains, so indicating sampling completeness (Fig. 2). The species *Frieseomelitta flavicornis* (nest two) and *Frieseomelitta*

*portoi* (nest five) had the broadest pollen spectra (21 and 18 pollen types, respectively). The most restricted pollen spectrum was recorded for *Frieseomelitta trichocerata* (nest seven) with just three types (Tab. 3).



**Figure 2.** Mean accumulation curve (rarefaction) calculated for each counted sample of pollen found inside the nests of *Frieseomelitta* spp. along Rio Negro riverside, Amazonas, Brazil. Upper and lower lines correspond to the standard errors.

The commonest pollen type was *Euterpe*, present in 32.2 % of analysed samples. Species considered attractive to the bees were (frequency >10 %): *F. flavicornis* (*Cecropia* type, *Euterpe precatória*, *Iriartella* type, *Schefflera* type, *Swartzia* type); *Frieseomelitta* sp. (*Croton cajucara*, *Cynometra* type, *Scleria* type); *F. portoi* (*Cecropia* type, *Pourouma* type, *Schizolobium amazonicum*, *Desmodium* type, *Iriartella setigera*, *Mabea* type, *Ryania speciosa*); *F. trichocerata* (*Araliaceae* type, *Euterpe* type, *Schefflera* type, *Bactris brongniartii*, *Bactris gasipaes*, *Cynometra marginata*, *Cynometra* type). Eight temporary specialization events were recorded (frequency > 90 %); four in the ten *F. flavicornis* pots, three in the six *Frieseomelitta* sp. pots, and one in the eight *F. trichocerata* pots. The plant species linked to the temporary specialization events were: *Cecropia* type, *Croton cajucara* and *Euterpe* type (Tab. 3).

For *F. flavicornis*, the pollen type with the highest relative frequency was *Cecropia* type, which was dominant at the two locations at which the bee was sampled, followed by *Swartzia* type at Curicuriari and *Schefflera* type at Santa Isabel. For *F. portoi* nests, the pollen spectrum was distinct at the two sampling localities (Igarapé Açu and Santa Isabel). At Igarapé Açu, the most commonly-collected pollen types were *Cecropia* type, followed by *Schizolobium amazonicum* (both with 34 % frequency) and *Pourouma* type (~12 %). At Santa Isabel, the most frequent pollen types were *Ryania speciosa* (~38 %), *Iriartella setigera* (~33 %) and *Mabea nitida* (~13 %) (Tab. 2).

For *Frieseomelitta* sp., a taxon recorded only at Ponta do Camucuri, a broad pollen spectrum was recorded, with 16 species of plants collected in the analyzed samples,

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**Table 2.** Pollen types found in the nests of *Frieseomelitta* stingless bees along the Negro river between Manaus and São Gabriel da Cachoeira, Amazonas, Brazil. *F. flavicornis* (1-Curicuriari; 2-Santa Isabel), *Frieseomelitta* sp. (3-Ponta do Camucuri), *F. portoi* (4-Igarapé Açu; 5-Santa Isabel) e *F. trichocerata* (6-Ilha do Pinto; 7- Santa Isabel; 8- Ponta do Camucuri), and their relative frequency (%) in the total samples of each bee analyzed along the Rio Negro, between the cities of Manaus and São Gabriel da Cachoeira, Amazonas, Brazil.

Nº	Botanical family	Pollen type	1	2	3	4	5	6	7	8
1	Achariaceae	Lindackeria type	0.17	-	-	-	-	-	-	-
2	Araliaceae	Araliaceae type	-	-	-	-	-	-	15.61	-
3		Schefflera type	-	20.63	-	-	-	-	34.36	-
4	Arecaceae	Astrocaryum type	-	-	-	0.50	-	-	-	-
5		Bactris brongniartii	-	-	-	-	-	-	-	20.0
6		Bactris gasipaes	-	-	-	-	-	-	-	79.0
7		Cocos nucifera	-	-	-	-	-	-	0.53	-
8		Euterpe precatoria	-	5.46	-	-	-	-	-	-
9		Euterpe type	0.11	3.46	0.05	-	0.03	0.50	48.19	-
10		Iriartella setigera	-	-	-	-	31.92	-	-	-
11		Iriartella type	-	5.79	-	-	-	-	-	-
12	Asteraceae	Tribe Eupatorieae	0.86	-	-	-	-	-	-	-
13	Bixaceae	Bixa orellana	-	-	-	-	-	-	0.08	-
14	Burseraceae	Protium type	0.72	-	0.08	-	0.42	-	-	-
15	Cannabaceae	Trema micrantha	0.31	-	-	-	-	-	-	-
16		Trema type	-	0.08	-	-	0.42	-	-	-
17	Cyperaceae	Scleria type	-	-	28.41	-	-	-	-	-
18	Dichapetalaceae	Tapura lanceolata	0.06	-	-	-	-	-	-	-
19	Euphorbiaceae	Alchornea type	-	-	-	0.67	-	-	-	-
20		Anomalocalyx type	-	-	0.16	-	0.33	-	-	-
21		Croton cajucara	-	-	54.77	-	-	-	-	-
22		Mabea nitida	-	-	-	-	12.53	-	-	-
23		Mabea type	-	-	-	-	-	-	-	-
24		Sapium type	0.78	-	-	-	-	-	-	-
25		Acacia type	-	-	-	7.83	-	-	-	-
26		Aldina latifolia	0.03	-	-	-	2.28	-	-	-
27		Bowdichia type	-	-	0.69	-	-	-	-	-
28		Cassia alata	-	0.92	-	-	-	-	-	-
29	Cassia occidentalis	-	-	-	-	1.17	-	-	-	
30	Cassia type	-	0.25	-	-	-	-	-	-	
31	Copaifera langsdorffii	-	-	0.13	-	-	-	-	-	
32	Cynometra marginata	-	-	-	-	-	83.0	-	-	
33	Cynometra type	-	-	14.61	-	-	14.8	-	-	
34	Desmodium type	-	-	-	-	5.61	-	-	1.0	
35	Dicorynia paraensis	-	1.29	0.11	-	-	-	-	-	
36	Dinizia excelsa	-	-	-	-	-	-	0.14	-	
37	Mimosa type	-	-	0.02	4.0	-	-	0.06	-	
38	Phaseolus type	-	0.08	-	-	-	-	-	-	
39	Schizolobium amazonicum	0.44	-	-	34.67	-	-	0.03	-	
40	Sclerolobium type	-	0.04	0.05	0.65	0.50	-	0.33	-	
41	Swartzia type	13.72	-	-	-	-	-	-	-	
42	Hypericaceae	Vismia type	1.47	-	0.55	5.17	0.58	-	-	-
43	Lamiaceae	Hyptis type	-	-	0.05	-	-	-	-	-
44	Lecythidaceae	Lecythis type	-	-	-	-	0.03	-	-	-
45	Loranthaceae	Phthirusa micrantha	-	0.17	-	-	0.53	-	-	-
46	Malpighiaceae	Byrsonima chrysophylla	-	0.75	-	-	-	-	-	-
47		Byrsonima type	0.03	0.83	-	-	2.39	-	-	-
48	Malvaceae	Pseudobombax munguba	0.03	-	-	-	-	-	-	-
49	Melastomataceae	Bellucia type	0.39	0.63	0.08	-	0.03	-	0.44	-
50	Meliaceae	Guarea type	-	-	-	-	0.22	-	-	-
51	Moraceae	Artocarpus type	-	-	0.02	-	-	-	-	-
52	Myrtaceae	Eugenia type	0.11	-	0.13	-	-	-	-	-
53		Myrtaceae type	0.03	-	-	-	-	-	-	-
54	Passifloraceae	Passiflora coccinea	-	-	-	-	-	-	0.14	-
55		Passiflora type	0.28	-	-	-	-	-	0.08	-
56		Turnera ulmifolia	-	0.04	-	-	-	-	-	-
57	Primulaceae	Cybianthus type	0.08	-	-	-	-	-	-	-
58	Rubiaceae	Psychotria type	0.14	-	-	-	-	-	-	-
59	Salicaceae	Ryania speciosa	-	-	-	-	37.44	-	-	-
60		Ryania type	1.47	-	-	-	-	-	-	-
61	Sapindaceae	Matayba type	-	0.54	-	-	-	-	-	-
62	Sapotaceae	Pouteria type	-	0.04	-	-	-	-	-	-
63	Solanaceae	Solanaceae type	-	0.04	-	-	-	-	-	-
64	Urticaceae	Cecropia type	78.58	58.96	-	34.67	-	1.7	-	-
65		Pourouma type	-	-	-	11.83	-	-	-	-



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**Table 3.** Relative frequency (%) of pollen types (per pot) found inside the nests of *Frieseomelitta flavicornis*, *Frieseomelitta* sp., *F. portoi* and *F. trichocerata* found along Rio Negro riverside, Amazonas, Brazil. Bee species in the columns are numbered according to Table 1, and the plant species in the rows are numbered according to Table 2. Sites are coded as follows: SI – Santa Isabel do Rio Negro; CUR – Curicuriari; IA – Igarapé Açu; PC – Ponta do Cumucuri and IP – Ilha do Pinto.

	<i>F. flavicornis</i>										<i>Frieseomelitta</i> sp.						<i>F. portoi</i>						<i>F. trichocerata</i>							
	SI				CUR						SI						SI			IA	SI						PC	IP		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
1	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	87	0.66	-	6	-	-
3	72.81	4.18	0.34	5.69	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	15	6.83	12.17	83.52	51.5	37.17	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	19.33	-
6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	79.18	-
7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.66	-	2.5	-	1.66
8	7	14.83	-	-	-	-	-	-	-	0.39	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	-	-	12.1	1.66	-	-	-	0.7	-	-	-	-	-	-	-	-	-	0.16	-	-	0.16	-	85	90.33	-	13.83	46.5	53.5	-	-
10	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	54.33	57.7	16.7	37.7	25.16	-	-	-	-	-	-	-	-	-
11	11.6	6.5	5.2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	5.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-
14	-	-	-	-	-	1.67	2.67	-	-	0.16	-	-	-	0.17	0.16	-	4.16	-	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	-	-	1.85	-	-	-	-	-	-	-	-	-	-	-	-	2.5	-	-	-	-	-	-	-	-	-	-	-
16	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-	0.5	83.34	72.16	14.85	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
18	-	-	-	-	-	-	-	-	0.32	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
19	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.66	-	-	-	-	-	-	-	-
20	-	-	-	-	-	-	-	-	-	-	-	-	0.16	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-
21	-	-	-	-	-	-	-	-	-	96.3	15.67	24.27	-	95.5	97.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
22	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	47	12.5	0.67	3.33	6.67	4.33	-	-	-	-	-	-	-	-	-
23	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.33	0.83	8.67	2.16	9.5	-	-	-	-	-	-	-	-	-
24	-	-	-	-	-	4.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
25	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.83	-	-	-	-	-	-	0.16	0.16
26	-	-	-	-	-	-	-	-	0.16	-	-	-	-	-	-	6.83	6.83	-	-	-	-	-	-	-	-	-	-	-	-	-
27	-	-	-	-	-	-	-	-	-	0.16	0.5	2.1	-	-	1.33	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-
28	2.5	0.83	0.16	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
29	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-	-	-
30	-	0.83	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
31	-	-	-	-	-	-	-	-	-	0.83	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
32	-	-	-	-	-	-	-	-	-	-	-	-	84.83	2.67	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	82.85



Pollen sources used by *Frieseomelitta* Ihering 1912 (Hymenoptera: Apidae: Meliponini) bees along the course of the Rio Negro, Amazonas, Brazil

Table 3. Cont.

	<i>F. flavicornis</i>										<i>Frieseomelitta</i> sp.						<i>F. portoi</i>						<i>F. trichocerata</i>						PC	IP		
	SI				CUR						SI						SI			IA			SI									
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28			29	30
33	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	14.83
34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	32	-	1.66	-	-	-	-	-	-	-	-	-	
35	-	1	-	4.16	-	-	-	-	-	-	0.5	-	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1.33	
36	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.83	-	-	-	-	-	
37	-	-	-	-	-	-	-	-	-	-	-	-	-	0.16	-	-	-	-	-	-	-	-	4	-	-	-	0.33	-	-	-	-	
38	-	-	-	0.34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
39	-	-	-	-	-	2.16	-	-	0.17	0.16	-	-	-	-	-	-	-	-	-	-	-	-	34.3	-	0.17	-	-	-	-	-	-	
40	-	-	0.16	-	-	-	-	-	-	-	0.16	-	0.16	-	-	-	-	-	-	-	2.67	0.16	0.67	-	-	-	-	2	-	-	-	
41	-	-	-	-	82.34	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
42	-	-	-	-	8	0.5	0.33	-	-	-	0.5	0.33	0.16	0.16	1	1.09	-	-	-	0.3	2.67	0.5	5.17	-	-	-	-	-	-	-	-	
43	-	-	-	-	-	-	-	-	-	-	-	0.16	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
44	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	
45	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	1.6	0.15	-	-	0.16	-	0.67	-	-	-	-	-	-	-	-	
46	3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7.5	5.67	1.16	-	-	-	-	-	-	-	-	-	-	-	-	
47	2.1	1.17	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
48	-	-	-	-	-	-	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
49	-	-	2.34	-	-	1.33	-	-	-	1	0.5	-	-	-	-	-	0.16	-	-	-	-	-	-	-	2.67	-	-	-	-	-	-	
50	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.67	3	0.16	-	-	-	-	-	-	-	-	0.5	
51	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
52	-	-	-	-	-	-	-	0.5	-	1.5	-	-	0.83	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
53	-	-	-	-	-	-	-	-	0.17	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
54	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.83	-	-	-	
55	-	-	-	-	-	1.67	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	0.5	-	-	-	-	
56	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
57	-	-	-	-	-	-	0.5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
58	-	-	-	-	-	0.83	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
59	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	36.91	14.03	39.48	35.67	37.97	58.37	-	-	-	-	-	-	-	-	-	
60	-	-	-	-	8.83	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
61	-	2.16	-	-	-	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
62	-	-	-	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
63	0.16	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	
64	0.83	68.5	79.38	87.17	0.83	79	96.5	98.8	99.5	96.7	-	-	-	-	-	-	-	-	-	-	-	-	-	34.6	-	-	-	-	-	-	-	
65	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	11.87	-	-	-	-	-	-	-	-



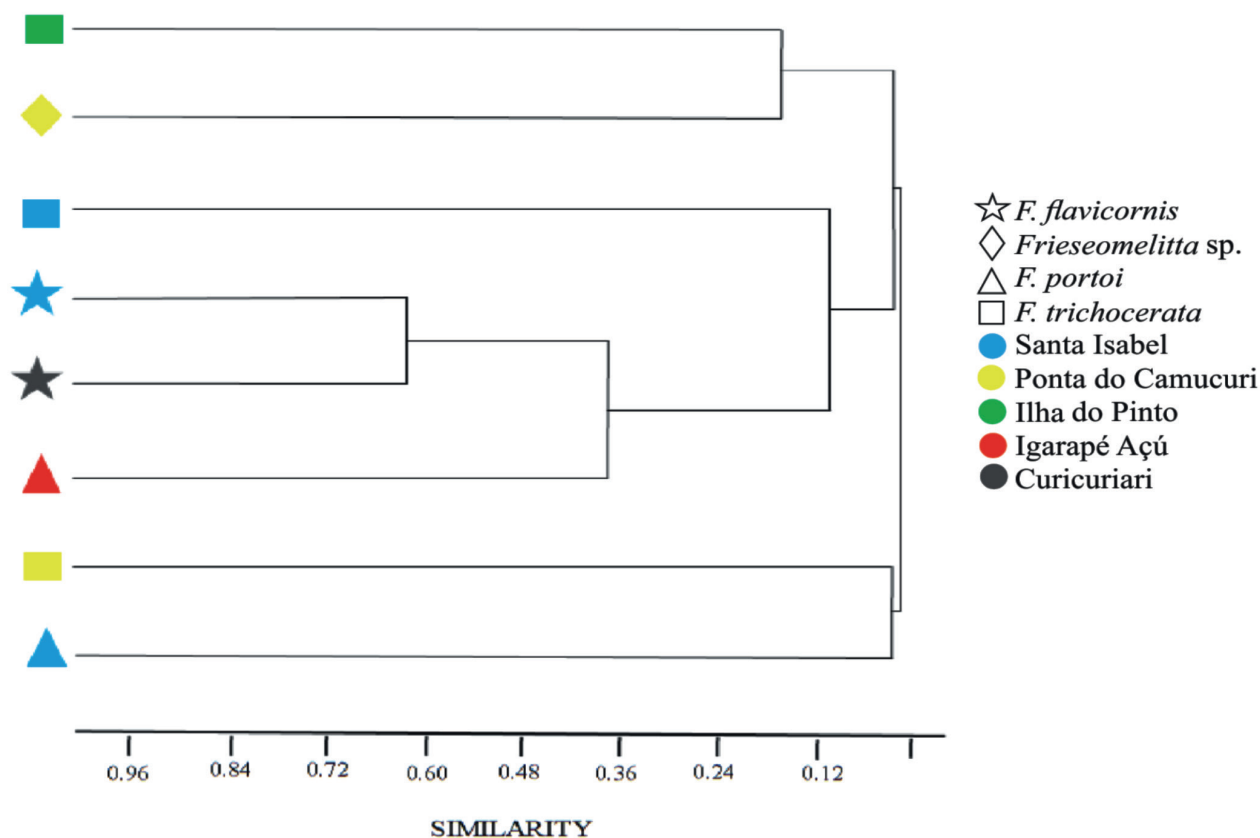
with *Croton cajucara* (~55 %), *Scleria* type (~28 %) and *Cynometra* type (15 %) being commonest in the sample. For *F. trichocerata*, a species found at three locations, the pollen spectrum was dominated by palms. At Santa Isabel, *Euterpe* type pollen occurred in 48 % of the studied samples, with *Schefflera* type (~35 %) and Araliaceae type (~15 %) being the other commonest pollen types (Tab. 2).

At Ponta do Camucurí, a single collection was carried out with six pots of the same nest of *F. trichocerata*, which yielded only three pollen types. Of these types, two were the palms: *Bactris gasipaes* (79 %) and *Bactris brongniartii* (20 %). On Pinto Island, only one sample was collected and only four pollen types were found. In contrast to Ponta do Camucurí, this sample had a small percentage (~1 %) of palm pollen (*Euterpe* type), while Fabaceae was dominant and represented by *Cynometra marginata* (83 %) and *Cynometra* type (~14 %) (Tab. 2).

Dominance analysis showed a clear pattern of high values in most analysed samples. Two locations, Ponta do Camucurí (PC) and Ilha de Pinto (IP), showed high dominance values and a reduced number of pollen types per sample (Fig. 3). Per pot profile for *F. flavicornis* revealed a consistent pattern, with high dominance being found in all analysed pots from the two study areas, but this species also had a broad pollen

spectrum. *Frieseomelitta* sp. showed high dominance (above 0.9) in three of the six pots analyzed, with *Croton cajucara* as the dominant species in all samples. For *F. portoi* from Igarapé Açú (IA) and Santa Isabel, dominance was low (averages of 0.2 and 0.3, respectively), with the species having pots containing up to ten pollen types. For *F. trichocerata*, four of the six samples analyzed from Santa Isabel showed high dominance, with *Euterpe* being the commonest pollen in these samples. The same pattern was observed in samples at two other communities (Ponta do Camucurí and Ilha de Pinto), where dominance was high. In both of these sites, only one sample from each bee species was analyzed, and both showed greatly reduced pollen spectra, with three and four types, respectively.

Cluster analysis was performed, and partitioned the pollen profile in two ways: (i) separating all pots for each species (Fig. 3) and (ii) by grouping pots from the same bee nest at the species/site level (Fig. 4). The analysis showed that, for the same species, diet similarity between bee colonies was low. The only species where the diet was similar between different sample locations was *F. flavicornis*, which concentrated its collection on *Cecropia* type pollen at both sample localities. Both *F. trichocerata* and *Frieseomelitta* sp. from different localities formed distinct clusters based



**Figure 3.** Cluster analysis of the pots of each nest of *Frieseomelitta flavicornis*, *Frieseomelitta* sp., *F. portoi* and *F. trichocerata* along the Rio Negro, Amazonas, Brazil, using pollen spectra identity per colony and a cluster method based on Bray-Curtis Index similarity. Different symbols relate to different species, and colours are associated to the sampling site.

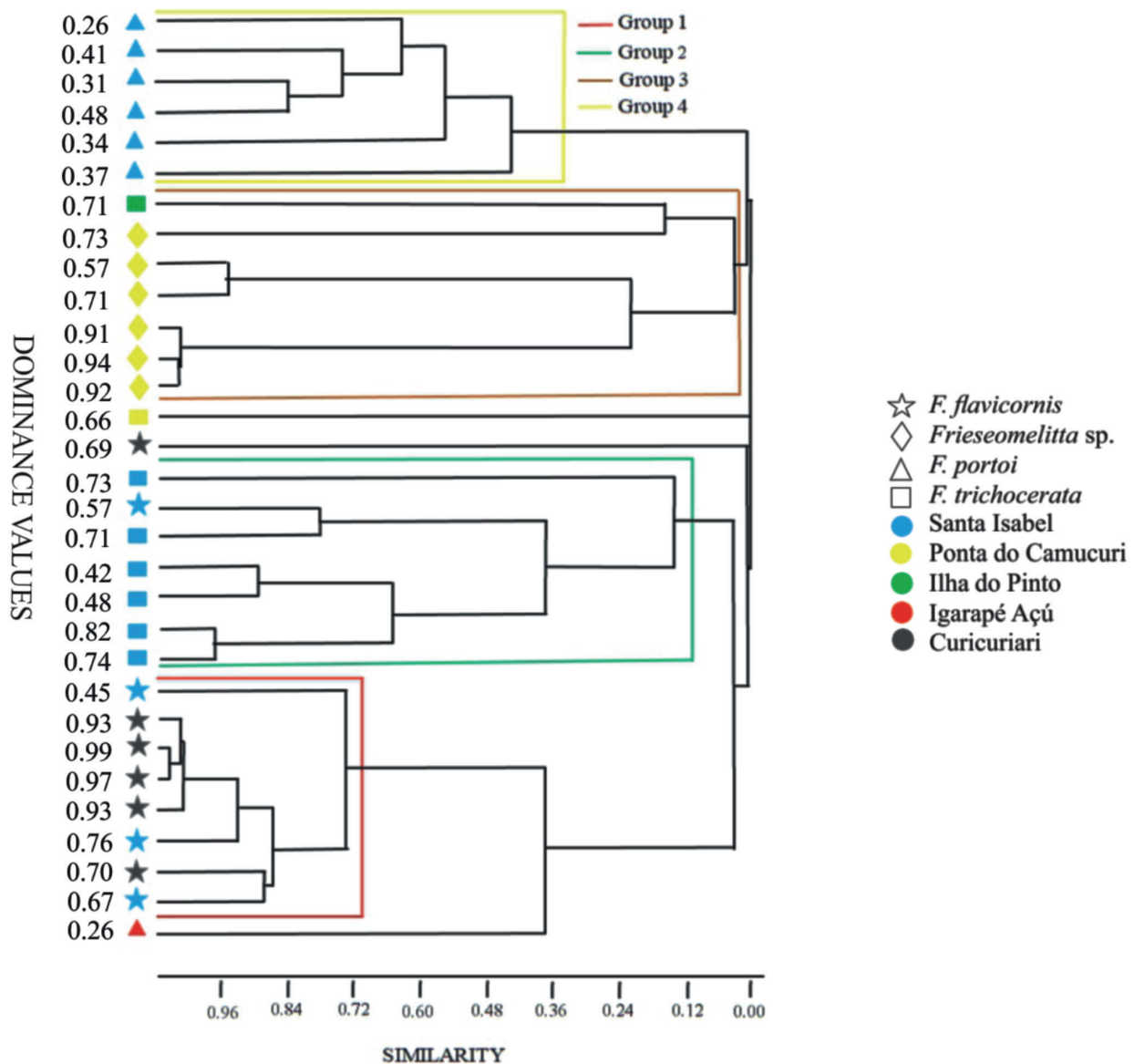


Pollen sources used by *Frieseomelitta* Ihering 1912 (Hymenoptera: Apidae: Meliponini) bees along the course of the Rio Negro, Amazonas, Brazil

on their collections, and between-collection similarity was low. Although the species *F. trichocerata* and *F. portoi* grouped together, similarity between them was almost zero, indicating their diets were strongly dissimilar (Fig. 4).

In general, collection pot cluster analysis found an internal consistency for pots from the same nests. This led to the creation of four groups: Group 1 was formed by *F. flavicornis*, even though the species was sampled at different locations (Curicuriari and Santa Isabel), and characterized by high similarity (above 0.6). This group also containing a single *F. portoi* pot, which like those of *F. flavicornis*, was dominated by *Cecropia* type pollen. However, the similarity of *F. portoi* within the group was low; Group 2

was composed almost entirely of *F. trichocerata*, which showed high between-pot similarity. Sampled pots all came from the same locality; pots from the same species, but from different localities, showed distance-related variation in diet content (Fig. 4); Group 3 was formed by *Frieseomelitta* sp., collected at Ponta do Camucuri, plus a single pot of *F. trichocerata* from Ilha do Pinto. Although the latter placed in this group analytically, it showed a low similarity with the other pots. Finally, Group 4 was composed only of *F. portoi* pots collected at Santa Isabel, which showed a consistent pattern of having *Ryania speciosa* and *Iriartella setigera* as the main pollen types. However, the single pot collected for *F. portoi* at another community (Igarapé Açú),



**Figure 4.** Dominance values (left side numbers) and cluster analysis of the pots of each nest of *Frieseomelitta flavicornis*, *Frieseomelitta* sp, *F. portoi* and *F. trichocerata* along the Rio Negro, Amazonas, Brazil, using pollen spectra identity per pot and a cluster method based on Bray Curtis Index similarity. Different symbols relate to different species, and colours are associated to the sampling site. Pots were represented by the same symbols and colours.



showed a different pattern, dominated by *Cecropia* type and *Schizolobium amazonicum*, so having greater similarity to *F. flavicornis* pot composition.

## Discussion

The current study adds a new set of data to a series of investigations on Negro river region Meliponini species pollen sources (Rech & Absy 2011a; b). Here we focused on the *Frieseomelitta* genus, and found it to be a generalist group of species, a result in agreement with previous studies in the Amazon region (Marques-Souza 2010), as expected for this study. Even compared to other already known *Frieseomelitta* species, the Amazonian species seem to have broader pollen profiles (Teixeira 2003). Moreover, apart from *Frieseomelitta flavicornis* the sampling site was the main pollen profile driver, thus partially corroborating our first prediction.

In a bibliographical survey of the genus *Frieseomelitta* Teixeira (2003) analysed 19 studies covering eight species of the genus and found that, though 36 botanical families were visited during the studied period (1967-2001), the bees tended to visit three botanical families in particular: Fabaceae, Malpighiaceae and Anacardiaceae. Although only five studies included in the survey were from the Amazon region, our results partially agree with the pattern reported, with the families Arecaceae, Urticaceae, Araliaceae and Fabaceae being the most important floral resources among the 29 botanical families recorded. The *Frieseomelitta* species recorded by Teixeira (2003) visited, on average, nine species of plants, while in the current study each bee species visited an average of 16 species of plant. It is important to point out that 80 % of the studies collated by Teixeira (2003) and collaborators were carried out in the Cerrado and Caatinga. In these environments, not only does more open landscape show high spatial structuring, but species diversity and specially species density are both lower than in the Amazonian Biome (MMA 2012). Hypothetically, this could be one of the reasons for the observed bee pollen spectra disparity.

In the same area and period as covered by the current study work, Rech & Absy (2011a) analysed collections made by members of the genera *Partamona*, *Scaura* and *Trigona*, and recorded 78 pollen types. However, it should be noted that these authors analyzed many more species of bees (26 species, and 104 samples) than did the current study (four species, and 32 samples). However, the issue of sample size disappears when the amount of pollen types per pot is taken into account; Rech & Absy (2011a) recorded one to five pollen types per pot, while the current study found between three and 12, reinforcing that observation that *Frieseomelitta* stored more pollen types per pot than larger-bodied forms such as *Partamona*, *Scaura* and *Trigona*.

Both *Partamona* and *Trigona* are classified as medium-sized monopolist bees, and thus have advantages over *Frieseomelitta* (classified as small-sized by Silveira *et al.*

2002). Bees such as *Partamona* and *Trigona* usually dominate good food sources while *Frieseomelitta* tend to avoid competition, and will generally switch to other available resources (Marques-Souza *et al.* 2002).

Studying *Tetragonisca*, *Nannotrigona* and *Plebeia* from the same region as the current study Rech & Absy (2011b) noted that these too have a form of “avoidance behavior”. The consequences of different behavior strategies also clearly reflected in the number of temporary specializations events (39 %) recorded by Rech & Absy (2011a), which contrasts with the 26 % of the pollen pots recorded in the current study.

The species of bee where temporary specialization was most common was *F. flavicornis*, which had more than 90 % of *Cecropia* type in four of the total ten pots, followed by *Frieseomelitta* sp., (3) where *Croton cajucara* prevailed, and *F. trichocerata* where one pot was dominated by *Euterpe* type pollen. It should be noted, however, that since no analysis exists of the availability of each plant species at the study sites, it is not possible to differentiate the effect of preferences from that resulting from limited collection options, a phenological scenario that would also generate an event classified as ‘temporary specialization’ (though one arising out of necessity rather than choice). Finally, should be noted that those plants collected intensively may be important species for bee management.

*Cecropia* is a wind-pollinated species and that may be one reason for less competitive bees such as *Frieseomelitta* to collect its pollen when resources are scarce or disputed intensively. Moreover, Silveira (1991), who investigated the relationships between pollen grains and their importance to bees, emphasized that one load of pollen carried by a bee may contain much more pollen grains than another species of equal mass or volume, but made up of pollen of a greater diameter. As a result, to obtain an equivalent mass or volume sufficient to fill a corbicula (or pollen basket), small pollen types such as *Cecropia* pollen grains ( $\pm 10 \mu\text{m}$ ) needs to be collected in greater quantity than, for example, *Croton* pollen grains which are five times larger (average  $\pm 51 \mu\text{m}$  in size). Thus, enumeration of pollen grains, may give a misleading indication of their proportional contribution, which is better estimated by factoring gain number and volume.

Whenever *Cecropia* type is collected by a particular bee species it generally appears in large numbers in any resulting samples. The reason may well have been provided by Radaeski & Bauermann (2016), who emphasized that pollen grain size is inversely proportional to pollen production. Accordingly, it is likely that *Cecropia* type pollen, because it has small pollen grains that are produced in large quantities, allows a large number of pollen grains to be collected. In addition, *Cecropia* type pollen grains are important bee diets because they have  $\beta$ -carotene, which is an antioxidant vitamin that cannot be synthesized by insects, and so is necessary as a supplement in bee diets (Pereira 2005; Melo *et al.* 2009). Finally, we cannot rule out the possibility that high *Cecropia*



pollen prevalence may also be a consequence of its being in flower when other species were not. In this scenario, this pollen source becomes highly attractive to bees as more profitable sources are absent.

Similarly, several other pollen types recorded here as important food items for the studied bees (*Astrocaryum* type, *Bactris brongniartii*, *Bactris gasipaes*, *Cocos nucifera*, *Euterpe precatoria*, *Euterpe* type, *Iriartella setigera* and *Iriartella* type) were all palms. A scientometric study by Souza *et al.* (2018) for the period between 2005 and 2017 found clear evidence that the Arecaceae family is one of the botanical families most often visited by bees. Such data agree with other studies (Aguiar 2003; Marques-Souza 2010), which have recorded palm pollen in *Frieseomelitta* collections.

Bee visitation to palm trees may occur principally because the large numbers of flowers grouped together in clusters allow extensive foraging (Barfod *et al.* 2003). According to Oliveira *et al.* (2003), although some palms have specific characteristics that favor visitation by beetles, their morphology also allows visitation by other insects, including bees, revealing a pattern of generalist interactions. In addition, in the Amazon, palm trees have both wide natural distributions and are commonly cultivated for their economic potential (which ranges from human and animal food to biodiesel production: Oliveira & Rios 2014). The resulting abundance of palms is good for bee-keeping and especially for Amazonian Meliponiculture.

With 16 collected species recorded, Fabaceae was another botanical family strongly represented in the studied *Frieseomelitta* bee collections. This corroborates several previous studies that found this family to be important in *Frieseomelitta* bee diets (Aguiar 2003; Teixeira 2003; Teixeira *et al.* 2007; Marques-Souza 2010; Aleixo *et al.* 2013). A review of 28 studies published between 1977 and 2013 (Freitas & Novais 2014) confirms this, reporting 610 types of pollen, from 94 botanical families, of which 129 types belong to the Fabaceae, the greatest contribution by a single family. Nationally, the dominance of Fabaceae was confirmed in the diets of bees through the work of Souza *et al.* (2019), who found it to be the family most strongly represented in palynological surveys published between 2005 and 2017.

The similarity analysis performed for bee nests examined in the current study showed a weak clustering between diets of the same bee species at different sites. In contrast, different pots of the same nest were frequently grouped together. Samples of *F. portoi* from two localities, for example, were located in different groups, while all pots from *F. trichocerata* clustered in Group 3. It is likely that local plant availability drove this pattern. For example, collections from Igarapé Açú concentrated mainly on *Cecropia* type pollen, while bees from Santa Isabel, had a preference for *Ryania* type pollen. Therefore, for *Frieseomelitta*, patterns of pollen resource composition supported the idea that locality has a stronger influence than species phylogenetic proximity

when explaining pollen resource profile of stingless bees, reinforcing the idea that this genus has a generalist, flexible and opportunist foraging behavioral strategy (Rech & Absy 2011a).

The present study showed that some plant species (*Cecropia* type, *Bactris gasipaes*, *Schefflera* type, *Schizolobium amazonicum*, *Cynometra marginata*, *Croton cajucara*, *Euterpe* type, *Ryania speciosa*, *Iriartella setigera* and *Scleria* type, in order of importance, based on relative frequency) are important for feeding colonies of the bees studied here, as well as showing such bees to be potential pollinators for these species (Fig. 5). These data also indicate that plants of these genera hold promise for use in areas where bee-keeping includes meliponary, and so deserve future studies of their interactions with pollinating stingless bees. The importance of local supply and behavior in the food profile of native bees combined with the importance of both a large number of cultivated palms and *Cecropia* type as pollen resource to *Frieseomelitta*, raise important questions about Meliponiculture and forest management in the Amazon region. These, however, will be a matter for future studies.

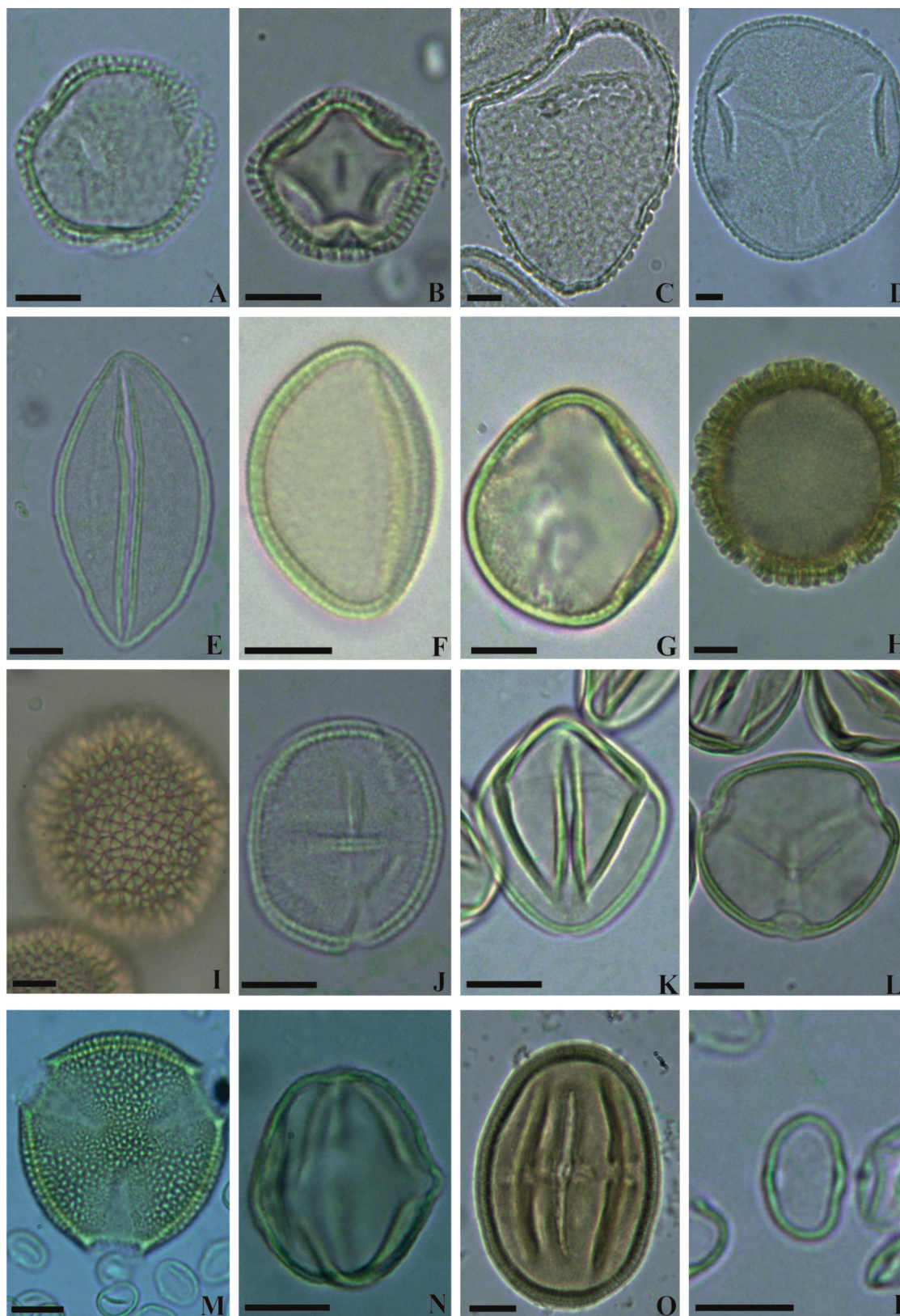
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**Figure 5.** Photomicrographs of the main pollen types collected by bees of the *Frieseomelitta* genus along the Rio Negro, Amazonas, Brazil. Araliaceae - Araliaceae tipo (A); *Schefflera* type (B); Arecaceae - *Bactris brongniartii* (C); *Bactris gasipaes* (D); *Euterpe* type (E); *Iriartella setigera* (F); Cyperaceae - *Scleria* type (G); Euphorbiaceae - *Croton cajucara* (H, I); *Mabea nitida* (J); Fabaceae - *Cynometra marginata* (K); *Cynometra* type (L); *Schizolobium amazonicum* (M); *Swartzia* type (N); Salicaceae - *Ryania speciosa* (O); Urticaceae - *Cecropia* type (P). Scale bars: 10  $\mu\text{m}$ .

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