Pollen storages in nests of bees of the genera *Partamona*, *Scaura* and *Trigona* (Hymenoptera, Apidae)

André Rodrigo Rech[1] & Maria Lúcia Absy[2]

[1]Programa de Pós-Graduação em Ecologia (PPGECO), Instituto de Biologia (IB), Universidade Estadual de Campinas (UNICAMP), Rua Monteiro Lobato 970, Caixa Postal 6190, 13083–970 Campinas–SP, Brasil. arech2003@yahoo.com.br.
[2]Coordenação de Pesquisa em Botânica (CPBO), Instituto Nacional de Pesquisas da Amazônia (INPA), Avenida André Araújo 2936, Caixa Postal 478, 69060–001 Manaus-AM, Brasil.

ABSTRACT. Pollen storages in nests of bees of the genera *Partamona*, *Scaura* and *Trigona* (Hymenoptera, Apidae). Bees and angiosperms established a mutualistic relationship along the evolutionary time. The aim of this study is to contribute for the understanding of this relation analyzing pollen stored by stingless bees colonies distributed along the Rio Negro. Fourteen species of Meliponini from the genera *Partamona*, *Scaura*, and *Trigona* were studied with regard to the content of pollen pots. The pollen material was removed from the pollen pots, homogenized, and prepared according to the usual acetolysis technique. The overlap of the trophic niche and the grouping of species by similarity of niches was calculated. The identification revealed 78 pollen types belonging to 36 families, being 37 types attractive and 16 considered as promoters of a temporary specialization event. With the results, it was possible to indicate a list of important plants for meliponiculture in the Amazon.

KEYWORDS. Pollination, pollinic resource, stingless bee

RESUMO. Pólen estocado nos ninhos de abelhas dos gêneros *Partamona*, *Scaura* e *Trigona* (Hymenoptera, Apidae). Abelhas e plantas estabeleceram ao longo do tempo evolutivo uma relação mutualística. Buscando contribuir para o entendimento dessa relação, foi analisado o pólen estocado por colônias de abelhas-sem-ferrão distribuídas ao longo do rio Negro. Foram estudados potes de pólen de 14 espécies de Meliponini dos gêneros *Partamona*, *Scaura* e *Trigona*. O material polínico foi retirado dos potes de pólen, homogeneizado e preparado segundo técnica usual de acetólise. Foram calculados a sobreposição de nicho trófico e o agrupamento das espécies pela similaridade de nichos. Foi identificado o total de 78 tipos polínicos, pertencentes a 36 famílias, sendo 37 destes, considerados atrativos, enquanto 16 foram promotores de eventos de especialização temporária. Com os resultados obtidos foi possível indicar uma lista de plantas de importância para a meliponicultura na Amazônia.

PALAVRAS-CHAVE. Abelhas-sem-ferrão, polinização, recurso polínico.

The perpetuation of angiosperms occurs largely due to pollination mechanisms, especially in tropical environments, where most species of flowering plants depend on biotic pollen vectors that promote gene flow, contributing for the formation of viable seeds (Bawa *et al.* 1985a, b; Bawa 1990; Ennos 1994). In this context, bees stand out as the major group of potential pollinators (Simpson & Neff 1981). The relationship between bees and angiosperms is very close because pollen and nectar are vital resources for the survival and reproduction of the bees and thus require them to constantly visit flowers throughout their entire lives.

Considering the interaction networks that are established between plants and bees, the study of the identity of each species involved in the interaction may determine a pathway that adds to our understanding of the dynamics of earth's ecosystems (Biesmeijer *et al.* 2005; Ebeling *et al.* 2008). One way to access identities in a plant-pollinator interaction network is to make direct observations in the natural conditions of the floral visitors of a given group of plants (Pedro & Camargo 1991; review in Biesmeijer *et al.* 2005). However, given the large number of plant species and the geographical breadth of environments such as rainforests, the use of indirect methods becomes more relevant. Pollen analysis is one such indirect method, and it has been shown to provide a fairly consistent means of identifying the plants visited by bees (Ramalho *et al.* 1991; Imperatriz-Fonseca *et al.* 1993). In spite of the usefulness and versatility of this method, only a few studies of this nature have been conducted to date in the Amazon region (Absy & Kerr 1977; Absy *et al.* 1980, 1984; Engel & Dingemans-Bakels 1980; Kerr *et al.* 1986, Marques-Souza *et al.* 1995, 1996, 2002, 2007; Thiele & Inouye 2007; Marques-Souza 2010).

Once the floral visitors of a given plant species are known, it becomes possible to test their effectiveness in the pollination process and thus increase fruiting or reduce the risk of extinction of endangered species (Kevan & Imperatriz-Fonseca 2002). For the bees, an understanding of their main pollen sources may allow us to establish plantations that provide them with pollen and consequently lead to the stability and productivity of colonies (Kerr *et al.* 1986). Furthermore, the knowledge and understanding of the local flora capable of supporting beekeeping activities decreases the need to introduce exotic species and makes beekeeping (with native bees) a practice that is both ecologically correct and potentially sustainable.

Thus, the aim of this study was to utilize the pollen analysis method to identify the plants used by fourteen species of Meliponini that occur along the Rio Negro channel in Amazonas, Brazil.

MATERIAL AND METHODS

The pollen material used in this study was collected and kindly provided for this study by a team (M. Mazucato and S. R. M. Pedro) led by Dr. João Maria Franco de Camargo (*in memoriam*) during a collection expedition held between July 15 and August 15, 1999 (rainy season). The natural nests from which the samples were obtained (pollen pots) were located along an approximately 1600 km stretch of the Rio Negro and its tributaries located between the Amazonian municipalities of Manaus and São Gabriel da Cachoeira (Fig. 1). The species studied, the locations for the collection of pollen pots, their geographical coordinates and the number of pots used for each species are listed in Table I.

Each pollen pot was considered as one sample. Pollen samples were extracted directly from storage closed pots collected in the natural nests of the bee species listed in Table I. Pollen extraction from pollen storage pots was done using 5 mm diameter sterile straws. The whole content of the pollen pots were homogenized with spatulas in Petri dishes, afterwards the samples were weighed and 0.5 g of each sample was stored in a test tube containing 3 ml Acetic Acid. After sufficient time, the samples were chemically processed via acetolysis (Erdtman 1960). Slides were prepared by mounting the samples in glycerin-gelatin and sealing them with paraffin. Three slides were prepared for each sample. For some bee species, different sample weights were taken from each pollen pot. Test results indicated no significant difference in the richness of pollen types weighing 0.5g or above. Furthermore, when new types were found in samples with heavier weights, they were characterized by an extremely low abundance of pollen. For this reason, we decided to use the sample weight of 0,5 g for each pollen pot.

Pollen types were determined by comparing them to slides from the pollen collection of the Palynology Laboratory of the Instituto Nacional de Pesquisas da Amazônia (INPA) and by consulting the specialized literature. Six hundred pollen grains were counted per sample to figure out their relative abundance. We followed Ramalho *et al.* (1985) in defining a minimum representation of 10% to consider a plant as attractive to a given bee species. To define the occurrence of

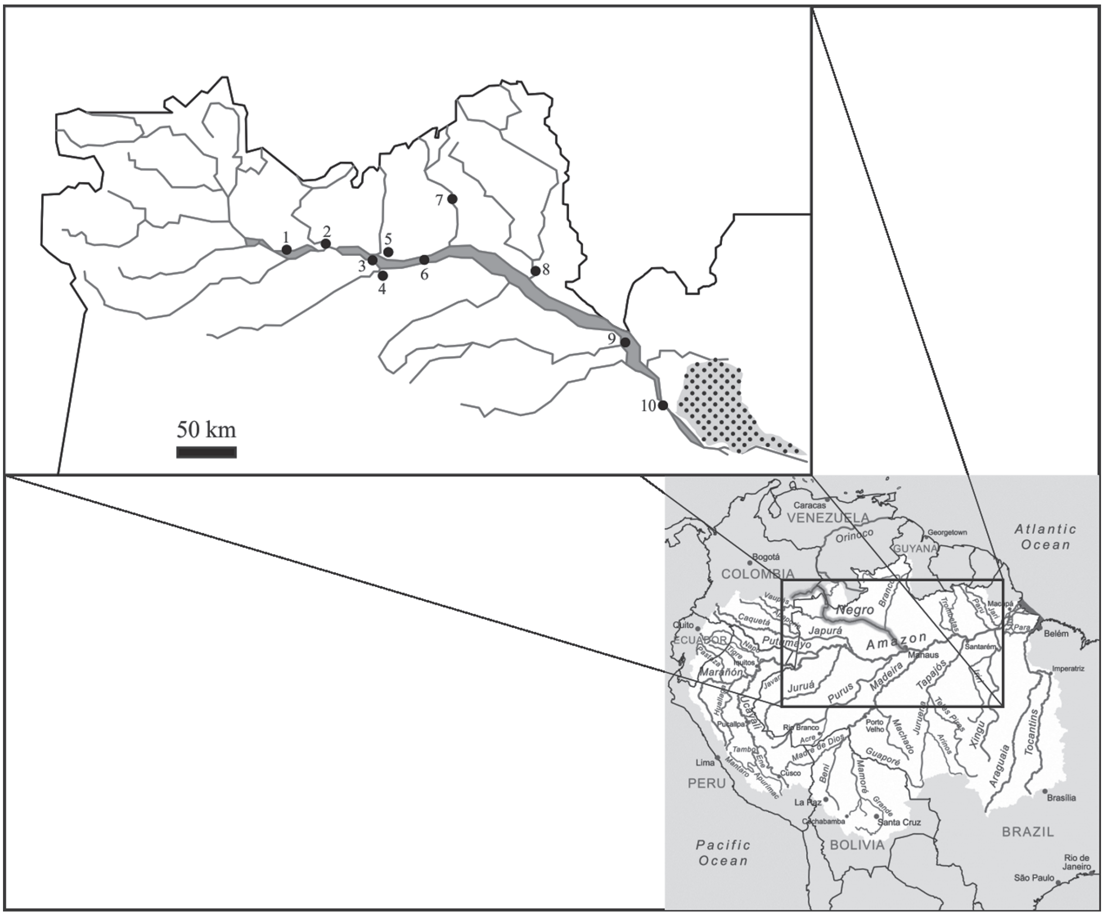

Fig. 1. Schematic map of sample sites along the Rio Negro channel, Amazonas – Brazil. Black dots correspond to sample sites (1. Tapurucuara-Mirim, 2. Ponta Camucuri, 3. Tabocal-Rio Uneiuxi, 4. Nazaré do Rio Negro, 5. Sta. Isabel do Rio Negro-Igarapé do Dará, 6. Samauma-Rio Dará, 7. Foz do Padauari, 8. Rio Demeni-"Pai Raimundo", 9. Lago Caurés and 10. Igarapé Açu-São Francisco) and the dotted area correspond to Manaus city.

Table I. Bee species, location and geographical coordinates of studied nests and the number of pollen pots studied in Amazonas, Brazil.

Nest	Species	Locality	Coordinate	Pollen pots
1	*Partamona ailyae* Camargo, 1980	Lago Caurés	01º18'59"S, 62º11'02"W	1
2	*Partamona ferreirai* Pedro & Camargo, 2003	Idem	Idem	1
3	*Partamona ferreirai* Pedro & Camargo, 2003	Nazaré do rio Negro	0º31'22"S, 65º04'07"W	6
4	*Partamona mourei* Camargo, 1980	Idem	Idem	6
5	*Partamona ferreirai* Pedro & Camargo, 2003	Ponta Camucuri, Margem Direita	0º20'02"S, 65º59'20"W	3
6	*Partamona mourei* Camargo, 1980	Rio Demeni, "Pai Raimundo"	0º24'01"S, 62º53'41"W	6
7	*Partamona pearsoni* (Schwarz, 1938)	Samauma, rio Daraá	0º27'7"S, 64º45'35"W	1
8	*Partamona ailyae* Camargo, 1980	Santa Helena, Ponta do Gavião, rio Negro	01º23'33"S, 61º47'06"W	6
9	*Partamona mourei* Camargo, 1980	Santa Izabel do Rio Negro, Igarapé Dará	0°25'04"S, 65°01'07"W	1
10	*Partamona epiphytophila* Pedro & Camargo, 2007	Tapurucuara-Mirim	0°25'17"S, 66°24'22"W	5
11	*Partamona ailyae* Camargo, 1980	Idem	Idem	6
12	*Partamona ferreirai* Pedro & Camargo, 2003	Idem	Idem	5
13	*Partamona vicina* Camargo, 1980	Idem	Idem	6
14	*Scaura* sp. group *tenuis* (Ducke, 1916)	Igarapé Açú, São Francisco, rio Negro	02º49'58"S, 60º46'51"W	1
15	*Scaura* sp. group *latitarsis* (Friese, 1900)	Santa Isabel do rio Negro, Igarapé Dará	0°25'04"S, 65°01'07"W	2
16	*Scaura tenuis* (Ducke, 1916)	Tabocal, rio Uneiuxi	0º34'45"S, 65º05'57"W	1
17	*Scaura* sp. group *tenuis* (Ducke, 1916)	Tapurucuara-Mirim	0º25'17"S, 66º24'22"W	6
18	*Scaura tenuis* (Ducke, 1916)	Idem	Idem	4
19	*Trigona branneri* Cockerell, 1912	Foz do Padauari, Rio Negro	2°06'27"S, 61°13'10"W	4
20	*Trigona branneri* Cockerell, 1912	Idem	Idem	4
21	*Trigona cilipes* (Fabricius, 1804)	Idem	Idem	6
22	*Trigona cilipes* (Fabricius, 1804)	Tabocal, rio Uneiuxi	0°24'45"S, 65°05'57"W	6
23	*Trigona dalatorreana* Friese, 1900	Idem	Idem	2
24	*Trigona* sp. group *recursa* Smith, 1863	Tapurucuara-Mirim	0º25'17"S, 66º24'22"W	6
25	*Trigona* sp. group *recursa* Smith, 1863	Lago Caurés	1º18'59"S, 62º11'02"W	3
26	*Trigona williana* Friese, 1900	Foz do Padauari, Rio Negro	2°06'27"S, 61°13'10"W	6

"temporary specialization" events (concentrated collection from a specific pollen source), we established a minimum representation of 90% of a single pollen type in one sample. Data on the flowering phenophase of the species present on the pollen spectra were obtained from the information found on the labels of specimens from the INPA Herbarium.

The patterns of trophic overlap between bee species were evaluated according to the Schoener Index (1968), which is given by the following formula: $S = 1 - 0.5\ \Sigma(Pxi - Pyi)$, where S = diet overlap; Pxi = proportion of food item *i* in the diet of species *x*; Pyi = proportion of food item *i* in the diet of species *y*. This index varies from 0 to 1. The overlap is considered to be biologically significant when S is equal to or greater than 0.6 (Zaret & Rand 1971; Wallace 1981). We also calculated the niche overlap indexes for the allopatric species. While the values we obtained do not have real biological value, they indicate the potential of such species to compete in cases of co-occurrence. The data for the abundance of pollen types were used to perform a cluster analysis for pairing based on Bray Curtis Index. The resulting graph is shown in an UPGMA format.

Voucher specimens of the bees taken from the analyzed nests were deposited in the "Camargo" Collection – RPSP of the Biology Department of the Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, Universidade de São Paulo. Pollen slides were deposited in the Palinoteca of the Instituto Nacional de Pesquisas da Amazonia (INPA). João M. F. Camargo identified the bee species according to the classification proposal of Camargo and Pedro (2008). The plant nomenclature follows Tropicos (Missouri Botanical Garden – MOBOT) and the classification proposal APGII.

RESULTS

An analysis of 104 pots of pollen led to the identification of 78 pollen types, with 47 of those being identified at species level belonging to 36 botanical families (Table II). Of the total number of recorded plants, 39.7% had a confirmed flowering phenophase during the months of June, July and August. On average, the pollen pots samples contained between one and five pollen types. The bee species with the broadest pollen spectrum were *Trigona williana* and *Trigona cilipes* (nest 22), each one with fifteen pollen types, while the narrowest pollen spectrum was recorded for *Scaura* sp. gr. *tenuis* (nest 14), with only two pollen types. The lowest average of pollen type per spectrum was recorded among *Scaura* species (4.4). For this genus, fewer bee species and an equally low number of pollen pots (14) were evaluated; however, when we evaluated the con-

Table II. Plant species represented in the pollen pots from nests of the genera *Partamona* Schwarz, 1939, *Scaura* Schwarz, 1938 and *Trigona* Jurine, 1807, and their relative occurrence in the total samples of each bee genus analyzed and for all the samples studied (104) from the Rio Negro in Amazonas, Brazil.

	Plant family	Pollen type	Relative occurrence in the pollen pots (%)			
			Scaura	*Trigona*	*Partamona*	Total
1	Anacardiaceae	*Tapirira guianensis* Aubl.	–	–	1.89	0.97
2		*Spondias mombin* L.	–	–	5.66	2.91
3		*Thyrsodium* Salzm ex Benth.	–	–	1.89	0.97
4	Apocynaceae	Tipo	–	–	1.89	0.97
5		*Couma utilis* (Mart.) Müll. Arg.	–	11.11	–	3.88
6		*Geissospermum* Allemão	–	13.89	–	4.85
7	Aquifoliaceae	*Ilex divaricata* Martius ex Reisseck	–	8.33	–	2.91
8	Araliaceae	*Schefflera morototoni* (Aubl.) Mag. Stey. & Frod.	–	22.22	–	7.77
9	Arecaceae	*Astrocaryum* G. Mey	–	–	30.19	15.53
10		*Attalea maripa* (Aubl.) Mart.	–	25.00	5.66	11.65
11		*Bactris gasipaes* Kunth	–	2.78	3.77	2.91
12		*Cocos nucifera* L.	–	–	1.89	0.97
13		*Euterpe precatoria* Mart.	7.14	13.89	11.32	11.65
14		*Elaeis guineenses* Jacq.	–	–	18.87	9.71
15		*Leopoldinia pulchra* Mart.	–	2.78	5.66	3.88
16		*Mauritia flexuosa* L. f.	14.29	–	9.43	6.80
17		*Socratea exorrhiza* (Mart.) H. Wendl.	–	–	3.77	1.94
18	Asteraceae	Tipo 1	–	13.89	1.89	5.83
19	Boraginaceae	*Cordia nodosa* Lam.	–	–	1.89	0.97
20	Bromeliaceae	*Pepinia sprucei* (Baker) G.S. Varad. & Gilmartin	–	–	1.89	0.97
21	Burseraceae	*Protium* Burm. f.	–	13.89	3.77	6.80
22	Cucurbitaceae	*Gurania bignoniacea* (Poepp. & Endl.) C. Jeffrey	–	–	1.89	0.97
23	Cyperaceae	*Lasiacis* (Griseb.) Hitchc	–	8.33	–	2.91
24		*Scleria* P.J. Bergius	14.29	5.56	–	3.88
25	Euphorbiaceae	*Alchornea* Sw.	7.14	16.67	–	6.80
26		*Aparisthmium cordatum* Rich ex A. Juss.	14.29	2.78	–	2.91
27		*Sapium*	50.00	8.33	3.77	11.65
28	Fabaceae: Caesalpinioideae	Tipo	–	–	1.89	0.97
29		*Bauhinia* L.	–	5.56	–	1.94
30		*Cassia* L.	–	16.67	–	5.83
31		*Cassia tora* L.	–	–	5.66	2.91
32		*Cassia undulata* Benth.	–	5.56	–	1.94
33		*Copaifera multijuga* Hayne	–	–	22.64	11.65
34		*Peltogine venosa* (Vahl.) Benth.	–	–	1.92	0.97
35		*Tachigali hypoleuca* (Benth.) Zarucchi & Herend.	–	25.00	11.32	14.56
36	Fabaceae: Mimosoideae	*Mimosa* L.	7.14	–	7.55	4.85
37		*Parkia panurensis* Benth. ex. H. C. Hopkins	–	2.78	–	0.97
38	Fabaceae: Papilionoideae	Tipo *Phaseolus*	–	–	1.89	0.97
39		*Aldina latifolia* Spruce ex Benth	14.29	–	9.43	6.80
40		*Desmodium* Desv.	21.43	–	–	2.91
41		*Dioclea* Kunth	–	16.67	1.89	6.80
42		*Macrolobium multijugum* (DC.) Benth.	–	8.33	1.89	3.88
43		*Swartzia pendula* Spruce ex Benth.	–	–	9.43	4.85
44		*Tephrosia brevipes* Benth.	7.14	–	–	0.97
45	Humiriaceae	*Humiriastrum cuspidatum* (Benth.) Cuatrec.	–	11.11	–	3.88
46	Hipericaceae	*Vismia* Vand.	–	36.11	11.32	18.45
47	Lacistemataceae	*Lacistema grandifolium* Schnizl.	–	2.78	–	0.97
48	Lamiaceae	*Vitex triflora* Vahl	–	30.56	9.43	15.53

Continue

Table II. Continued.

	Plant family	Pollen type	Relative occurrence in the pollen pots (%)			
			Scaura	*Trigona*	*Partamona*	Total
49	Loranthaceae	*Phthirusa rufa* (Mart.) Eichler	–	11.11	–	3.88
50	Malpighiaceae	*Banisteriopsis* C. B. Rob.	–	2.78	–	0.97
51		*Burdachia prismatocarpa* A. Juss.	–	19.44	–	6.80
52		*Byrsonima* Rich. ex Kunth	14.29	25.00	16.98	19.42
53	Malvaceae: Bombacoideae	*Catostemma sclerophyllum* Ducke	–	–	1.89	0.97
54	Malvaceae: Sterculioideae	*Teobroma grandiflorum* (Will. ex Spreng.) Schum.	–	2.78	–	0.97
55	Melastomataceae	*Bellucia imperialis* Saldanha & Cogn.	14.29	16.67	–	7.77
56		*Miconia* Ruiz & Pav.	35.71	2.78	18.87	15.53
57	Meliaceae	*Carapa guianensis* Aubl.	–	5.56	–	1.94
58	Moraceae	*Trymatococcus amazonicus* Poepp. e Endl.	–	27.78	1.89	10.68
59	Myrsinaceae	*Conomorpha spicatus* (Kunth) Mez	–	–	1.89	0.97
60	Myrtaceae	Tipo	7.14	8.33	50.94	30.10
61	Olacaceae	*Aptandra liriosmoides* Spruce ex Miers	–	–	5.66	2.91
62	Passifloraceae	*Passiflora* Killip	7.14	–	–	0.97
63	Piperaceae	*Piper* L.	–	11.11	–	3.88
64	Poaceae	Tipo *Pariana*	7.14	11.11	–	4.85
65	Polygalaceae	*Securidaca longifolia* Poepp.	–	2.78	1.89	1.94
66	Rubiaceae	*Amaioua corymbosa* Kunth	–	–	1.89	0.97
67		*Spermacoce* L.	–	2.78	–	0.98
68		*Isertia hypoleuca* Benth.	–	33.33	–	11.65
69	Rutaceae	*Zanthoxylum rhoifolium* Lam.	7.14	–	5.66	3.88
70	Salicaceae	*Casearia* Jacq.	–	2.78	–	0.97
71		*Laetia suaveolens* (Poepp.) Benth.	–	–	5.66	2.91
72		*Lindackeria paludosa* (Benth.) Gilg	7.14	25.00	1.89	10.68
73		*Ryania speciosa* Vahl.	–	5.56	–	1.94
74	Sapindaceae	*Matayba* Aubl.	–	–	1.92	0.97
75		*Toulicia* Aubl.	–	–	3.77	1.94
76	Urticaceae	*Cecropia* Loefl.	–	8.33	13.21	9.71
77		*Pourouma* Aubl.	–	8.33	–	2.91
78	Verbenaceae	*Citharexylum macrophyllum* Poir.	14.29	–	–	1.94

tent of each pollen pot, we noticed the same average amount of the other species from the other two genera (*Trigona* and *Partamona*) that were studied.

The most commonly pollen type was Myrtaceae, which was present in 30.1% of the pollen samples analyzed. The species considered attractive (frequency > 10%) were the following: *Alchornea* sp., *Aptandra liriosmoides*, *Astrocaryum* sp., *Attalea maripa*, *Bactris gasipaes*, *Bellucia imperialis*, *Burdachia prismatocarpa*, *Byrsonima* sp., *Cassia* sp., *Cecropia* sp., *Citharexylum macrophylum*, *Coco nucifera*, *Copaifera multijuga*, *Desmodium* sp., *Dioclea* sp., *Elaeis guineenses*, *Euterpe precatoria*, *Isertia hypoleuca*, *Laetia suaveolens*, *Lasiacis* sp., *Leopoldinia pulchra*, *Lindackeria paludosa*, *Mauritia flexuosa*, *Miconia* sp., *Piper* sp., *Pourouma* sp., *Ryania speciosa*, *Sapium* sp., *Schefflera morototoni*, *Scleria* sp., *Spondias mombin*, *Swartzia pendula*, *Tachigali hypoleuca*, *Trymatococcus amazonicus*, *Vismia* sp., *Vitex triflora* and *Zanthoxylum rhoifolium* (Table III). Among these species, *Alchornea*, *Astrocaryum*, *Ba. gasipaes*, *Byrsonima*, *Cassia*, *C. multijuga*, *E. guineenses*, *E. precatoria, L. corymbulosa*, *L. paludosa*, *M. flexuosa*, *Miconia*, *Pourouma*, *Scleria*, *T. hypoleuca* and *Z. rhoifolium* triggered temporary specialization events (frequency > 90% in one given pot).

We registered 41 events of temporary specialization (frequency > 90%); six among 37 analyzed pots of *Trigona*, six among 14 pots of *Scaura* and 29 among 53 pollen pots of *Partamona*. The cluster analysis indicated that the closest associations were not based on the taxonomic proximity of the bee species (Fig. 2). None species had pollen spectra from all pots grouped together. For the overlap of the pollen niche (Table IV), only one pair of allopatric species, namely *Partamona pearsoni* and *Partamona ferreirai* (nest 12), and two nests of *P. mourei* (nests 6 and 9) showed a biologically significant overlap (greater than 0,6). However, one species from each pair had only one pot of pollen analyzed.

Table III. Relative frequency (per pot) of pollen types found in the pollen pots of the Meliponini nests from the Rio Negro channel in Amazonas, Brazil. Bee species (columns) are numbered according to Table I and plant species (rows) are numbered according to Table II.

Nests	*Partamona*													*Scaura*					*Trigona*							
	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
1	–	6.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
2	–	–	–	14	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
3	–	–	–	–	–	–	–	4.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
4	0.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.1	–	–	–	–	–
6	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1
7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3	–	0.7	–	–	–	–
8	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9.0	–	0.4	–	27	–	–
9	–	–	–	22	–	93	–	–	84	46	25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
10	–	–	–	26	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	–	–	–	–	–	28
11	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–	–	–	–	–	–	17	–	–
12	87	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
13	–	0.7	–	4.9	–	–	–	–	–	–	17	0.1	–	–	–	4.5	–	–	–	1.2	–	2.5	42	–	–	–
14	–	–	–	–	–	–	–	–	–	53	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
15	–	–	–	–	31	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–	–
16	–	–	–	–	–	–	–	1.4	–	–	–	0.1	47	–	–	–	–	21	–	–	–	–	–	–	–	–
17	0.9	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
18	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1
19	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
20	–	–	–	–	–	–	–	1.0	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
21	–	–	–	–	–	–	–	–	–	0.1	1.2	–	–	–	–	–	–	–	–	–	–	0.1	–	0.1	–	0.1
22	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
23	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	–	–
24	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	–	–	–	–	–	–	–	0.5	–
25	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	95	–	–	–	–	–	45	–	–	0.1	–
26	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	6.1	–
27	–	73	–	–	–	–	3.2	–	–	–	–	–	–	1.0	35	–	–	47	–	18	–	–	–	15	–	–
28	–	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
29	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1
30	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	53	–	–	–	–	–	0.1
31	–	–	–	–	–	0.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
32	–	–			–	–		–	–	–	–	–		–	–	–	–	–	–	–	–	6.0	–	–	–	–
33	–	–	33	0.9	–	–	93	–	–	–	–	81	17	–	–	–	–	–	–	–	–	–	–	–	–	–
34	–	–	–	–	–	–	2.3	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
35	–	–	–	–	–	–	–	–	–	–	–	0.2	36	–	–	–	–	–	43	–	29	–	–	–	–	–
36	–	4.3	–	0.2	2.4	–	–	–	–	–	–	–	–	–	–	–	2.6	–	–	–	–	–	–	–	–	–
37	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2.0	–	–	–	–
38	–	–	–	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
39	–	–	–	–	–	0.1	–	–	–	–	8.2	–	–	–	1.2	–	–	–	–	–	–	–	–	–	–	–
40	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	30	–	–	–	–	–	–	–	–
41	5.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	20	–	–	–	–	–
42	–	–	–	–	–	–	0.7	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3	–	–	–	–
43	–	–	–	–	–	–	–	–	–	–	–	18	–	–	–	–	–	–	–	–	–	–	–	–	–	–
44	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–
45	–	–	–	–	–	–	–		–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.3
46	–	14	–	–	–	–	–	0.1	–	–	2.0	–	–	–	–	–	–	–	–	0.2	29	–	–	–	19	1.1
47	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1.3	–	–	–	–	–	–
48	4.5	–	–	–	–	–	–	15	–	–	3.5	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	2.3

Continue

Table III. Continued.

Nests	*Partamona*													*Scaura*					*Trigona*							
	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
49	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	9.5	–	–	–	–
50	2.5	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–	–
51	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	5.4	–	18	–	–	–	–	–
52	–	–	67	19	–	–	–	–	–	–	–	–	–	–	0.3	–	–	–	2.8	–	–	8.6	–	–	4.2	0.4
53	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
54	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1
55	–		–	–	–		–	–	–	–	–	–	–	–	37.8	–	–	–	–	–	–	–	–	–	–	66
56	–	0.7	–	–	7.3	0.2	–	–	0.2	–	18	–	–	–	–	–	63.1	1.0	–	–	–	–	–	0.3	–	–
57	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5
58	–	–	–	–	–	–	–	1.1	–	–	–	–	–	–	–	–	–	–	–	–	–	0.2	0.6	5.4	18	–
59	–	–	0.4	–	–		–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
60	–	–	0.1	0.2	2.3	3.1	–	5.9	–	–	5.4	0.3	–	–	0.58	–	–	–	–	–	0.1	–	–	–	0.3	–
61	–	–	–	–	3.4	–	–	–	–	–	11	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
62	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–
63	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	15	–	–
64	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.5	–	–	–	–	–	–	–	4.7	–	–
65	–	–	–	–	–	–	–	–	–	–	0.2	–	–	–	–	–	–	–	–	–	–	0.4	–	–	–	–
66	–	–	–	–	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–
67	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–		–	–	–	0.1
68	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	16	–	–	3.2	0.5
69	–	–	–	–	–	–	–	32	–	–	–	–	–	–	–	–	14	–	–	–	–	–	–	–	–	–
70	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	0.9	–	–	–	–	–
71	–	–	–	–	54	3.4	–	–	–	–	–	–	–		–	–	–	–	–	–	–		–	–	–	–
72	–	–	–	–	–	–	–	–	–	0.2	–	–	–	99	–	–	–	–	31	–		8.1	–	–	–	–
73	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	18	–	0.2	–	–	–	–	–
74	–	–	–	–	–	–	–	0.1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
75	–	0.8	–		–	–	–	–	–	–	2.2	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
76	–	–	–	13	–	–	–	39	15	–	4.4	–	0.1	–	–	–	–	–	–	–	–	–	–	–	47	–
77	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	57	–	1.5	–
78	–	–	–	–	–	–	–	–	–	–	–	–	–	–	25	–	–	–	–	–	–	–	–	–	–	–

DISCUSSION

The clustering pattern of the nests did not reveal any pollen collection pattern that was characteristically inter- or intra-specific. These findings are in contrast to much of the previous literature regarding utilization of pollen resources by bees, in which the phylogeny (degree of relationship among *taxa*) and especially the phylogenetic/location association of nests were found to be the main determinants in the composition of the pollen spectra (Sommeijer *et al.* 1983; Biesmeijer & van Nieuwstadt 1997; Nagamitsu *et al.* 1999; Biesmeijer and Slaa 2004). In a study of three *Trigona* species (*sensu stricto*), for instance, was found a greater overlap in intraspecific pollen niches than among species of the same genus (Eltz *et al.* 2001).

Considering that the analysis presented here is based on naturally occurring nests, we believe that an explanation for the clustering pattern we found could be related to the following two factors: the location of the nests and the sharing of resources. Because the frequency of Meliponini nests inside the forest is usually low (Michener 1946; Hubbell & Johnson 1977; Oliveira *et al.* 1995), we hypothesize that some nests may be just as isolated from the others in the same sampling area as from others located in different sampling areas. In this way, the succession of massive and rapid flowering events at the various locations where the bees are present would explain the existence of pots of distinct nests being grouped in one set and pots from the same nests not being grouped (Fig. 2).

The second factor relates to nests located in such a way that there would be an overlap in the different bees' collection areas. In this case, there is the possibility of shared resources among the different species of bees, which would make it possible to find some species of plants being shared among nests in the same sampling point regardless of the bee species, while the main pollen type in the spectra of each

Table IV. Index of the overlap of the pollen trophic niche between pairs of bee nests. Column and row numbers indicate bee nests as listed in Table I.

N.	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
1	1																								
2	–	1																							
3	0.03	–	1																						
4	0.02	0.01	0.20	1																					
5	–	0.03	*	0.01	1																				
6	–	*	*	0.23	0.03	1																			
7	–	0.03	0.33	0.01	–	–	1																		
8	0.05	*	*	0.13	0.02	0.03	–	1																	
9	0.01	*	–	0.35	*	0.85	–	0.15	1																
10	–	–	–	0.22	–	0.46	–	–	0.46	1															
11	0.04	0.04	*	0.31	0.13	0.26	–	0.13	0.30	0.25	1														
12	–	*	0.33	0.01	*	*	0.81	*	–	–	*	1													
13	–	–	0.17	0.01	–	–	0.17	*	*	–	*	0.17	1												
14	–	0.01	–	–	–	–	0.01	–	–	–	–	–	–	1											
15	*	0.35	*	0.01	0.01	0.01	0.03	0.01	–	–	0.02	*	–	0.01	1										
16	–	0.01	–	0.05	–	–	–	–	–	–	0.05	*	–	–	–	1									
17	–	0.03	–	*	0.10	*	–	0.14	*	–	0.18	–	–	–	–	–	1								
18	–	0.48	–	–	0.01	*	0.03	0.01	*	–	0.01	*	0.21	0.01	0.35	–	0.01	1							
19	0.03	–	0.03	0.03	–	–	–	*	–	*	*	*	0.36	0.31	*	–	–	–	1						
20	–	0.19	–	0.17	*	–	0.03	*	–	–	0.01	*	–	0.01	0.19	–	–	0.19	–	1					
21	0.05	0.14	*	*	*	*	–	*	–	–	0.02	*	0.29	–	*	–	–	–	0.35	*	1				
22	0.11	0.01	0.07	0.09	*	–	0.01	*	–	*	0.02	*	–	0.07	0.10	0.39	–	–	0.10	0.02	–	1			
23	–	0.01	–	0.05	–	–	–	0.01	–	–	0.17	*	–	–	–	0.05	–	–	–	0.01	–	0.02	1		
24	–	0.15	–	–	*	*	0.03	0.01	*	*	*	–	*	0.15	0.15	0.01	*	0.15	–	0.24	–	0.01	0.01	1	
25	0.03	0.14	0.04	0.18	*	*	–	0.42	0.15	–	0.07	*	*	–	*	–	*	–	0.03	*	0.19	0.12	*	0.05	1
26	0.05	0.05	*	0.26	*	–	–	0.02	–	*	0.03	–	–	–	0.38	–	–	–	*	0.16	0.09	0.09	–	*	0.02

* Overlap lower than 0.01.

bee species would be different (Ramalho *et al.* 2007). This pattern was clearly observed among the *Trigona* species from the Foz do Padauari sampling point (nests 19, 20, 21 and 26), among which some pollen types were shared with antagonic abundances (Table III). Another example was found at the Tapurucuara-mirim sampling point between the species *P. ferreirai* and *Partamona vicina*. *P. ferreirai* focused its foraging activity on *Copaifera multijuga,* with the pollen spectrum of all pots showing the prevalence of this plant, apart from one single pot. On the other hand, for *P. vicina* we observed the prevalence of the same plant, *C. multijuga,* in only one pot, suggesting that the both species could have succeeded in collecting this resource.

Sharing of pollen resources among different species of bee has been reported in several studies on Atlantic vegetation. However, it is rare to find the same flower as the major source of pollen for the different species of bees being compared (Ramalho *et al.* 2007). A vast niche overlap was reported for the pollen sources of Meliponini and *Apis mellifera* L. 1758 in the studies performed in the Atlantic forest. Such overlap was attributed to very productive flowering, where the chances of competition are lower (Ramalho 1990; Ramalho *et al.* 1991, 2007). Given the speculative nature of the explanations offered here, we suggest that additional systematic research is needed to address the issue of the sharing of pollen resources in the natural environment of the Amazon region.

The biologically significant overlap in the pollen niches reported here have no real biological value because the bee species with overlapping niches did not occur in the same locations. However, it may be important to consider the potential characteristics of the plants involved in the overlap (in this particular case, *Astrocaryum* sp. and *C. multijuga*) for beekeeping initiatives and to fully realize the importance of these plant species for bees. It is also noteworthy that the four species whose niches overlapped belong to the genus *Partamona*; the nests of one pair were found in Igapó vegetation (wetland) and the other in Terra firme vegetation (land).

The data obtained here for *Trigona williana* confirm those from Marques-Souza *et al.* (1996), who, in their work with the same species, reported abundant pollen collection in species from the genera *Attalea* and *Bellucia*. Besides these two species, the authors identified 56 more pollen types collected by *T. williana* over a 1-yr period. They observed that the lowest total number of pollen types was collected during the rainy season. According to the authors, the competition for food intensifies during that season as the supply diminishes and,

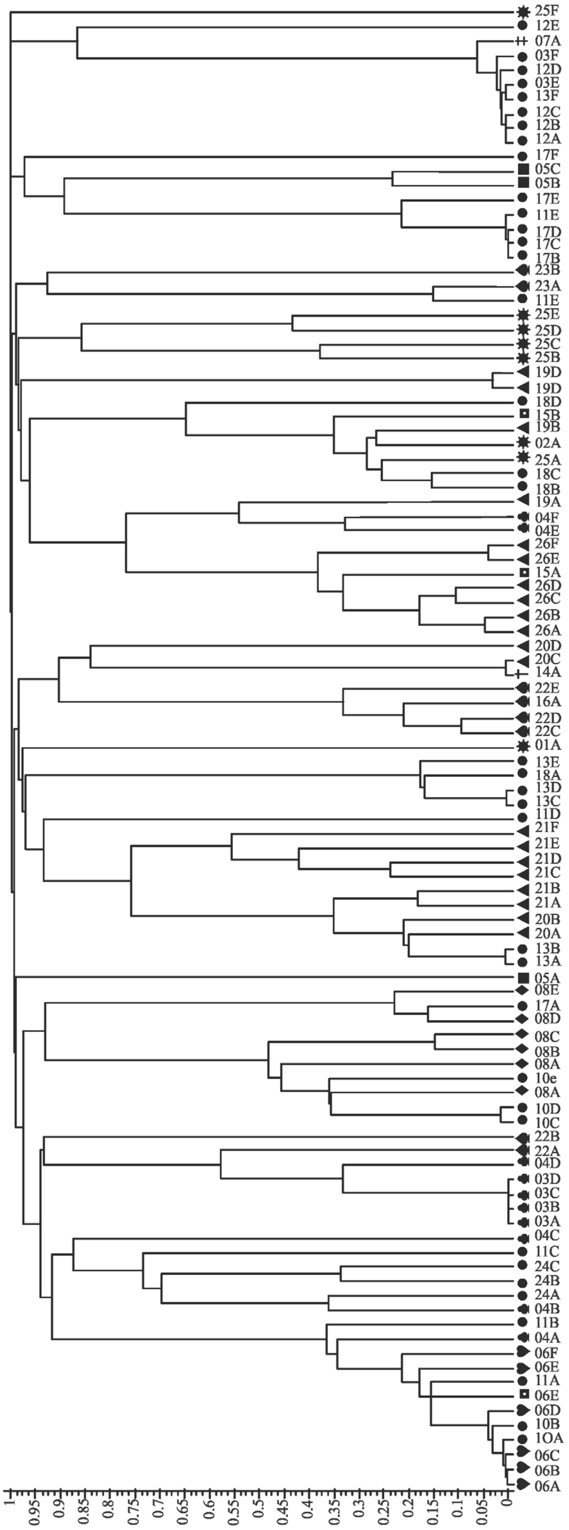

Fig. 2. Clustering of the Meliponini nests of *Partamona*, *Scaura* and *Trigona* according to the identity of the pollen spectra using the "pairing method" as a function of the Bray Curtis Index. Bee nests are numbered according to Table I and letters represent the different pots analyzed from the same nest. Each symbol represent different places as follow: ● Tapurucuara-Mirim, ■ Ponta Camucuri, ♠ Tabocal-Rio Uneiuxi, ♣ Nazaré do Rio Negro, ◘ Sta. Isabel do Rio Negro-Igarapé do Dará, ‡ Samauma-Rio Dará, ▲ Foz do Padauari, ♥ Rio Demeni-"Pai Raimundo", ✹ Lago Caurés, and † Igarapé Açu-São Francisco, ♦ Santa Helena, Ponta do Gavião, Rio Negro.

in this case, the strategy of mass collection associated with aggression may lead to an increase in the pollen spectrum. In the present study, however, the amplitude of the pollen spectrum per pot of pollen analyzed was not greater for *Trigona* than for any other genera analyzed.

Although the pollen grain type Myrtaceae was found in 30.1% of the pollen pots, its frequency was not sufficiently high for it to be considered attractive. We believe that this fact may be related to the onset of the flowering phenophase of some widely distributed Myrtaceae species, because pollen from plants of this family is usually intensively collected when available (Absy *et al.* 1984; Marques-Souza *et al.* 1993, 2007; Ramalho *et al.* 1989, 2007). Moreover, there are many reports of the pollination of Myrtaceae being attributed to the Meliponini (Gressler *et al.* 2006; Cortopassi-Laurino & Ramalho 1988).

Two types of pollen from Cyperaceae (*Scleria* and *Lasiacis*), collected only by *T. recursa*, *Trigona* sp. gr. *recursa* and *Scaura tenuis*, were considered attractive. This is particularly interesting because the Cyperaceae family does not have flowers that are considered attractive to bees and its pollen is light and dry, consistent with anemophily pollination (Vogel 1954; Faegri & Pijl 1979; Fenster *et al.* 2004). One possible explanation for this finding may be pollen shortage, a phenomenon previously described in Meliponini by others (Ducke 1902; Adams *et al.* 1981; Terrell & Batra 1984). Alternatively, there may be floral traits that attract visitors to the flowers; studies on pollen morphology of the species *Pariana* (Poaceae) and the presence of insects in the flowers suggest possible involvement of insects in its pollination mechanisms (Salgado-Labouriau *et al.* 1993). The authors hypothesize that the graminoids in the understory of tropical forest may require the involvement of insects for pollination when anemophily is compromised by moisture.

Along the same lines, other pollen types from anemophilous plants have been recorded (*Alchornea*, *Cecropia*, *Pouroma* and *Piper*). Just as in Cyperaceae, these plants do not possess features obviously attractive to bees (Vogel 1954; Faegri & Pijl 1979). However, all the genera mentioned produce copious amounts of pollen and this might be a very important feature for bees that continuously need pollen in large quantities to replenish brood cells (Michener 2000). Furthermore, collection of anemophilous pollen may be further intensified in periods of pollen shortage; in the Amazon, this corresponds to the rainy season when there is a reduced number of species in the flowering phenophase, which makes pollen less available as a function of the high humidity and constant rainfall (Schaik *et al.* 1993; Bentos *et al.* 2008).

The species of Arecaceae corroborate the hypothesis of attractiveness due to resource abundance. In our study, only *C. nucifera*, *Euterpe precatoria* and *Leopoldinia pulchra* belong to the group of palm trees primarily pollinated by bees and, secondarily, by beetles (Listabarth 1996; Henderson *et al.* 2000). The other genera, namely *Astrocaryum*, *Bactris*, *Attalea, Mauritia* and *Elaeis,* belong to the cantharophilic group, in which bees are secondary pollinators (Storti 1993; Henderson *et al.* 2000; Tandon *et al.* 2001). Regardless of the effectiveness of bees as pollen vectors for palm trees, the abundance and constant supply of pollen throughout the year seems to make Arecaceae an especially important resource for Meliponini (Henderson 1986; Tomlinson 1990; Storti 1993; Henderson *et al.* 2000). In a study of *T. williana*, eleven species of palm trees were recorded, with of the majority of them making pollen available for more than two months, including some species such as *A. maripa* and *C. nucifera* that were recorded in the pollen spectra for more than ten months (Marques-Souza *et al.* 1996).

Although not as prolific in pollen production as the previously mentioned species, *C. macrophylum* and *Isertia hypoleuca* were considered attractive for the *Scaura* and *Trigona* species, respectively. The floral morphology of cogeneric species *Citharexylum myrianthum* Cham. is compatible with the phalenophily syndrome. Previous studies have reported moth visits and their effectiveness in this mechanism of pollination and these studies indicated that Meliponini acted as pollen robbers (Rocca & Sazima 2006). Likewise, the morphology of *I. hypoleuca* is consistent with ornithophily pollination syndrome, in that visits by hummingbirds have been recorded at an appropriate frequency to make them potential pollinators (Giacomini & Webber, unpublished data).

Among the species whose morphology is consistent with melittophily syndrome, many are not effectively pollinated by the Meliponini we studied here. This is mainly due to the small size of these bees, which does not allow for legitimate visits, and also to the destructive and robber habits of some species, especially of *Partamona* and *Trigona*. Among the pollen types of melittophilous plants that are not pollinated by Meliponini are those from species with poricidal anthers such as *Cassia* spp., *Miconia* sp. and *B. imperialis*, which require floral visitors capable of vibrating the anthers to remove the pollen ("buzz pollination") (Buchmann 1983; Renner 1983). Because the bees we studied are non-vibrating, it appears that *Trigona* spp. damage the anthers with their mandibles and then rob the pollen (Renner 1983), while the remaining bees either use the hole produced by *Trigona* spp. to collect pollen or act as "garbage collectors" by removing the pollen remaining after the collection by vibrating bees (Wille 1963).

Another group of melittophilous plants not pollinated by the bees we studied here includes Malpighiaceae (*Byrsonima* and *B. prismatocarpa*), two species of Fabaceae (*S. pendula* and *Dioclea* sp.) and one species of Salicaceae (*R. speciosa*), which are only pollinated by larger solitary bees. The Malpighiaceae flowers have oil glands in their sepals and are mainly pollinated by solitary bees (Centridini, Tapinotaspidini and Tetrapediini tribes) specialized in collecting oils, that they use as larval food and nest-construction material (Teixeira & Machado 2000; Machado 2004; Rêgo *et al.* 2006). The Fabaceae (*S. pendula* and *Dioclea* sp.) require floral visitors larger than the Meliponini for contact to occur with the fertile parts of the flower (Lopes & Machado 1996; Pinheiro & Sazima 2007; Dutra *et al.* 2009), in the same way that *R. speciosa* is only pollinated by Euglossini bees (Martiniano, unpublished data).

C. multijuga (Freitas & Oliveira 2002), *Vismia* sp. (Santos & Machado 1998), *S. mombin* (Nadia *et al.* 2007), *Z. rhoifolium* (Bawa 1985b), *L. paludosa* (Flores & Webber, unpublished data), *Desmodium* sp. (Willmer *et al.* 2009) and *T. hypoleuca* (Venturieri 1997) are among the species visited and potentially pollinated by the Meliponini we studied here. In addition to these species, the Meliponini are thought to influence the pollination mechanisms of *Vitex* spp., *L. suaveolens*, *S. morototoni* and *Sapium* spp. because, although no specific data is available in the literature, these species have a floral morphology consistent with pollination by insects, and they are frequently found in the pollen spectra of Meliponini from the Amazon (Absy *et al.* 1980, 1984; Engel & Dingemans-Bakels 1980; Marques-Souza *et al.* 1995, 1996).

Based on the results presented in this study and the studies by Absy *et al.* (1984) and Rech & Absy (*in press*.), and considering the large number of plants identified as pollen sources for bees, it is evident that further analyses are needed to verify the real need for artificial feeding of native bees in beekeeping in the Amazon. Although not all plants have a flowering phenophase that coincides with the rainy season, we show here that with proper planning, it may possible to define and cultivate plants that allow for the existence of pollen calendars convenient to the reality of each beekeeper. The species of *Copaifera*, *Bactris*, *Bellucia*, *Byrsonima*, *Astrocaryum*, *Euterpe*, *Mauritia*, *Pouroma* and *Spondias* may be especially interesting given the availability of pollen for bees and the possibility that they may be utilized further by human and animal populations for their fruits, seeds and oil. Moreover, species that usually grow spontaneously and are selectively removed by farmers, such as *Cecropia*, *Sapium*, *Schefflera* and *Vismia*, may also serve as pollen sources for bees if they are not eliminated.

ACKNOWLEDGEMENTS

This work is dedicated to the memory of Dr. João Maria Franco Camargo, in recognition of the brilliance of his career and the significant contributions he made in advancing our understanding of the biology of stingless bees. We thank Silvia Pedro and Caroline Scherer for reading this manuscript and making valuable suggestions, and Cleonice de Moura Oliveira, Ana Paula Moraes and Mauricio Fernandez Otarola for general helping. This work was financially supported by grants from CNPq, Processes 472563/2006–8 and 472246/2008–9, a scholarship to A. Rech, the primary author, and FAPESP process 1998/11605–9 that financially supported the Rio Negro collection expedition.

REFERENCES

Absy, M. L. & W. E. Kerr. 1977. Algumas plantas visitadas para obtenção de pólen por operárias de *Melipona seminigra merrilae* em Manaus. **Acta Amazonica 7**: 309–315.

Absy, M. L.; E. B. Bezerra & W. E. Kerr. 1980. Plantas nectaríferas utilizadas por duas espécies de Melipona da Amazônia. **Acta Amazonica 10**: 271–281.

Absy, M. L.; J. M. F. Camargo; W. E. Kerr & I. P. A. Miranda. 1984. Espécies de plantas visitadas por Meliponinae (Hymenoptera; Apoidea), para coleta de pólen na região do médio Amazonas. **Revista Brasileira de Biologia 44**: 227–37.

Adams, D. E.; E. Perkins & J. R. Estes. 1981. Pollination system in *Paspalum dilatatum* Poir (Poaceae): na example of insect pollination in temperate grass. **American Journal of Botany 68**: 389–394.

Bawa, K. S. 1990. Plant-Pollinator Interactions in Tropical Rain Forests. **Annual Review of Ecology and Systematics 21**: 399–422.

Bawa, K. S.; D. R. Perry & J. H. Beach. 1985a. Reproductive biology of tropical lowland rain forest trees. I. Pollination Systems and self-incompatibility mechanisms. **American Journal of Botany 72**: 331–345.

Bawa, K. S.; D. R. Perry; S. H. Bullock; R. E. Coville & M. H. Grayum. 1985b. Reproductive biology of tropical lowland rain forest trees. II. Pollinations mechanisms. **American Journal of Botany 72**: 346–356.

Bentos, T. V.; R. C. G. Mesquita & G. B. Williamson. 2008. Reproductive phenology of central amazon pioneer trees. **Tropical Conservation Science 1**: 186–203.

Biesmeijer, J. C. & E. J. Slaa. 2004. Information flow and organization of stingless bee foraging. **Apidologie 35**: 143–157.

Biesmeijer, J. C. & M. G. L. van Nieuwstadt. 1997. Colony foraging patterns of stingless bees in Costa Rica, with special reference to pollen, p. 35–57. *In*: **The organization of foraging in stingless bees of the genus *Melipona*.** Netherlands, Utrecht University, 261 p.

Biesmeijer, J. C.; E. J. Slaa; M. S. Castro; B. F. Viana; A. M. P Kleinert & V. L. Imperatriz-Fonseca. 2005. Connectance of brazilian social bee – food plant networks is influenced by habitat, but not by latitude, altitude or network size. **Biota Neotropica 5**: 1–8.

Buchmann, S. L. 1983. Buzz Pollination in Angiosperms. p. 73–114. *In*: Jones, C. E. & Little, R. J. (eds.) **Handbook of experimental pollination biology.** New York, Reinhold Company, 558 p.

Camargo, J. M. F. & S. R. M. Pedro. 2008. Meliponini Lepeletier, 1836. *In*: Moure, J. S., Urban, D.; Melo, G. A. R. (Orgs). **Catalogue of Bees (Hymenoptera, Apoidea) in the Neotropical Region** – online version. Available from http://www.moure.cria.org.br/catalogue (accessed 13 August 2008).

Cortopassi-Laurino, M. & M. Ramalho. 1988. Pollen harvest by africanized *Apis mellifera* and *Trigona spinipes* in São Paulo. Botanicals and ecological views. **Apidologie 19**: 01–24.

Ducke, A. 1902. Beobachtungen über blütenbesuch, erscheinungszeit etc. der bei Pará vorkommenden Bienen. II. **Allgemeine Zoologie Entomologie 7**: 321–326 [325].

Dutra, V. F.; M. F. Vieira; F. C. P. Garcia & H. C. Lima. 2009. Fenologia reprodutiva, síndromes de polinização e dispersão em espécies de Leguminosae dos Campos Rupestres do Parque Estadual do Itacolomi, Minas Gerais, Brasil. **Rodriguésia 60**: 371–387.

Ebeling, A.; A. M. Klein; J. Schumacher; W. W. Weisser & T. Tscharntke. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? **Oikos 117**: 1808–1815.

Eltz, T.; C. A. Bruhl; S. van der Kaars; V. K. Chey; K. E. Linsenmair. 2001. Pollen foraging and resource partitioning of stingless bees in relation to flowering dynamics in a Southeast Asian tropical rainforest. **Insectes Sociaux 48**: 273–279.

Engel, M. S. & F. Dingemans-Bakels. 1980. Nectar and pollen resources for stingless bees (Meliponinae, Hymenoptera) in Surinam (South America). **Apidologie 11**: 341–350.

Ennos, R. A. 1994. Estimating the relative rates of pollen and seed migration among plant populations. **Heredity 72**: 250–259.

Erdtman, G. 1960. The acetolysis method. A revided description. **Svensk Botanisk Tidskrift 54**: 561–564.

Faegri K. & L. van der Pijl. 1979. **The principles of pollination ecology.** Oxford, Pergamon Press, 244 p.

Fenster, C. B.; W. S. Armbruster; P. Wilson; M. R. Dudash & J. D. Thomson. 2004. Pollination syndromes and floral specialization. **Annual Review of Ecology Evolution and Systematics 35**: 375–403.

Freitas, C. V. & P. E. Oliveira. 2002. Biologia reprodutiva de *Copaifera langsdorffii* Desf. (Leguminosae, Caesalpinioideae). **Revista Brasileira de Botânica 25**: 311–321.

Gressler, E.; M. A. Pizo & L. P. C. Morellato. 2006.Polinização e dispersão de sementes em Myrtaceae do Brasil. **Revista Brasileira de Botânica 29**: 509–530.

Henderson, A. 1986. A Review of pollination studies in the Palmae. **The Botanical Review 52**: 222–255.

Henderson, A.; B. Fischer; A. Scariot; M. W. Pacheco & A. Pardini. 2000. Flowering phenology of a palm community in a central Amazon forest. **Brittonia 52**: 149–159.

Hubbell S. P. & L. K. Johnson. 1977. Competition and nest spacing in a tropical stingless bee community. **Ecology 58**: 949–963.

Imperatriz-Fonseca, V. L.; M. Ramalho & A. Kleinert-Giovannini. 1993. **Flores e Abelhas de São Paulo.** São Paulo, Edusp/FAPESP, 192 p.

Kerr, W. E.; M. L. Absy & A. C. M. Souza. 1986. Espécies nectaríferas e poliníferas utilizadas pela abelha *Melipona compressipes fasciculata* (Meliponinae-Apidae) no Maranhão. **Acta Amazonica 16–17**:145–156.

Kevan, P. & V. L. Imperatriz-Fonseca. 2002. **Pollinating bees: a conservation link between agriculture and nature.** Brasilia, Ministério do Meio Ambiente, 313 p.

Listabarth, C. 1996. Pollination of *Bactris* by *Phyllotrox* and *Epurea*. Implications of the palm breeding beetles on pollination at the community level. **Biotropica 28**: 69–81.

Lopes, A. V. F. E. & I. C. S. Machado. 1996. Biologia floral de *Swartzia pickelli* (Leguminosae-Papilionoideae) e sua polinização por *Eulaema* spp. (Apidae-Euglossinae). **Revista Brasileira de Botânica 19**: 17–24.

Machado, I. C. 2004. Oil-collecting bees and related plants: a review of the studies in the last twenty years and case histories of plants occurring in NE Brazil, p. 255–281. *In*: Freitas, B. M. & J. O. P. Pereira (eds.). **Solitary bees conservation, rearing and management for pollination.** Fortaleza, Imprensa Universitária, 285 p.

Marques-Souza, A. C. 2010. Ocorrência do pólen de *Podocarpus* sp. (Podocarpaceae) nas coletas de *Frieseomelitta varia* Lepeletier 1836 (Apidae: Meliponinae) em uma área urbana de Manaus, AM, Brasil. **Acta Botanica Brasilica 24**: 558–566.

Marques-Souza, A. C.; M. L. Absy; P. A. A. Condé & H. A. Coelho. 1993. Dados da obtenção de pólen por operárias de *Apis mellifera* no município de Ji-Paraná (RO), Brasil. **Acta Amazonica 23**: 59–76.

Marques-Souza, A. C.; M. L. Absy; W. E. Kerr & F. J. Aguilera-Peralta. 1995. Pólen coletado por duas espécies de meliponíneos (Hymenoptera: Apidae) da Amazônia. **Revista Brasileira de Biologia 55**: 855–864.

Marques-Souza, A. C.; M. L. Absy & W. E. Keer. 2007. Pollen harvest features of the Central Amazonian bee *Scaptotrigona fuvicutis* Moure 1964 (Apidae: Meliponinae), in Brazil. **Acta Botanica Brasilica 21**: 11–20.

Marques-Souza, A. C.; I. P. A. Miranda; C. O. Moura; A. Rabelo & E. M. Barbosa. 2002. Características morfológicas e bioquímicas do pólen coletado por cinco espécies de meliponíneos da Amazônia Central. **Acta Amazonica 32**: 217–229.

Marques-Souza, A. C.; C. O. Moura & B. W. Nelson. 1996. Pollen colected by *Trigona williana* Hymenoptera: Apidae) in Central Amazonia. **Revista de Biologia Tropical 44**: 567–573.

Michener, C. D. 1946. Notes on the habits of some Panamanian stingless bees (Hymenoptera, Apidae). **Journal of the New York Entomology Society 54**: 179–197.

Michener, C. D. 2000. **The Bees of the World.** Baltimore, John Hopkins University Press, 877 p.

Nadia, T. L.; I. C. Machado & A. V. Lopes. 2007. Polinização de *Spondias tuberosa* Arruda (Anacardiaceae) e análise da partilha de polinizadores com *Ziziphus joazeiro* Mart. (Rhamnaceae), espécies frutíferas e endêmicas da caatinga. **Revista Brasileira de Botânica 30**: 89–100.

Nagamitsu, T.; K. Momose; T. Inoue & D. W. Roubik. 1999. Preference in flower visits and partitioning in pollen diets of stingless bees in an Asian tropical rain forest. **Researches on Population Ecology 41**: 195–202.

Oliveira, M. L.; Morato, E. F. & Garcia, M. V. B. 1995. Diversidade de espécies e densidade de ninhos de abelhas sociais sem ferrão (Hymenoptera, Apidae, Meliponinae) em florestas de terra firme na Amazônia Central. **Revista Brasileira de Zoologia 12**: 13–24.

Pedro, S. R. M. & J. M. F. Camargo. 1991. Interactions on floral resources between the Africanized honey bee *Apis mellifera* L. and the native bee community (Hymenoptera: Apoidea) in a natural "cerrado" ecosystem in southeast Brazil. **Apidologie 22**: 397–415.

Pinheiro, M. T. & M. Sazima. 2007. Visitantes florais e polinizadores de seis espécies arbóreas de Leguminosae melitófilas na Mata Atlântica no sudeste do Brasil. **Revista Brasileira de Biociências 5**: 447–449.

Ramalho, M. 1990. Foraging by stingless bees of the genus, *Scaptotrigona* (Apidae, Meliponinae). **Journal of Apicultural Research 29**: 61–67.

Ramalho, M.; L. S. Guibu; T. C. Giannini & A. Kleinert-Giovannini. 1991. Ecologia nutricional de abelhas sociais, p. 225–252 *In*: Panizzi, A. R. & J. R. P. Parra (eds.) **Ecologia nutricional de insetos e suas implicações no manejo de pragas.** São Paulo, Ed. Manole Ltda. 359 p.

Ramalho, M.; A. Kleinert-Giovannini & V. L. Imperatriz-Fonseca. 1989. Utilization of floral resources by species of *Melipona* (Apidae: Meliponina): floral preferences. **Apidologie 20**: 185–195.

Ramalho, M.; M. D. Silva & C. A. L. Carvalho. 2007. Dinâmica de uso de fontes de pólen por *Melipona scutellaris* Latreille (Hymenoptera: Apidae): uma análise comparativa com *Apis mellifera* L. (Hymenoptera: Apidae), no Domínio Tropical Atlântico. **Neotropical Entomology 36**: 38–45.

Ramalho, M; V. L. Imperatriz-Fonseca & A.Kleinert-Giovannini. 1985. Exploitation of floral resources by *Plebeia remota* Holmberg (Apidae-Meliponinae). **Apidologie 16**: 307–330.

Rêgo, M. M. C.; P. M. C. Albuquerque; M. C. Ramos & L. M. Carreira. 2006. Aspectos da biologia de nidificação de *Centris flavifrons* (Friese) (Hymenoptera: Apidae, Centridini), um dos principais polinizadores do murici (*Byrsonima crassifolia* (L.) Kunth, Malpighiaceae), no Maranhão. **Neotropical Entomology 35**: 579–587.

Renner, S. 1983. The widespread occurrence of anther destruction by *Trigona* bees in Melastomataceae. **Biotropica 15**: 251–256.

Rocca, M. A. & M. Sazima. 2006. The dioecious, sphingophilous species *Citharexylum myrianthum* (Verbenaceae): Pollination and visitor diversity. **Flora 201**: 440–450.

Salgado-Labouriau, M. L.; S. Nilsson & M. Rinaldi. 1993. Exine sculpture in *Pariana* pollen (Gramineae). **Grana 32**: 243–249.

Santos, M. J. L. & I. C. Machado. 1998. Biologia floral e heterostilia em *Vismia guianensis* (Aubl.) Choisy (Clusiaceae). **Acta Botanica Brasilica 12**: 451–464.

Schaik, C. P.; J. W. Terborgh & S. J. Wright. 1993. The phenology of tropical forests: adaptative significance and consequences for primary consumers. **Annual Review of Ecology and Systematics 24**: 353–377.

Schoener, T. W. 1968. The Anolis lizards of Bimini: resource partitioning in a complex fauna. **Ecology 49**: 704–726.

Simpson, B. B. & J. L. Neff. 1981. Floral rewards: alternatives to pollen and nectar. **Annals of the Missouri Botanical Garden 68**: 301–322.

Sommeijer, M. J.; G. A. Rooy; W. Punt & L. L. M. Bruijn. 1983. A comparative study of foraging behavior and pollen resources of various stingless bee (Hym., Meliponinae) and honeybees (Hym., Apinae) in Trindad, West-Indies. **Apidologie 14**: 205–224.

Storti, E. F. 1993. Biologia floral de *Mauritia flexuosa* Lin. fil, na região de Manaus, AM, Brasil. **Acta Amazonica 13**: 371–381.

Tandon, R.; T. N.Manohara; B. H. M. Nijalingappa & K. R. Shivanna. 2001. Pollination and pollen-pistil interaction in oil palm, *Elaeis guineensis*. **Annals of Botany 87**: 831–838.

Teixeira, L. A. G. & I. C. Machado. 2000. Sistema de polinização e reprodução de *Byrsonima sericea* DC (Malpighiaceae). **Acta Botanica Brasilica 14**: 347–357.

Terrell, E. E. & S. W. T. Batra. 1984. Insect collect pollen of eastern wildrice *Zizania aquatic* (Poaceae). **Castanea 49**: 31–34.

Thiele, R. & B. D. Inouye 2007. Nesting Biology, Seasonality, and Mating Behavior of *Epicharis metatarsalis* (Hymenoptera: Apidae) in Northeastern Costa Rica. **Annals of the Entomological Society of America 100**: 596–602.

Tomlinson P. B. 1990. **The structural biology of palms.** Oxford, Claredon Press Oxford, 463 p.

Venturieri, G. C. 1997. Reproductive ecology of *Schizolobium amazonicum* Huber ex Ducke and *Sclerolobium paniculatum* Vogel (Caesalpiniaceae) and its importance in forestry management projects. *In:* The International Pollination Simposium, Lethbridge. **Acta Horticulturae 437**: 65–69.

Vogel, S. 1954. Blütenbiologische Typen als Elemente der Sippengliederung, dargestellt anhand der Flora Südafrikas. **Botanische Studien 1**:1–338.

Wallace, H. 1981. An assessment of diet overlap indexes. **Transactions of the American Fisheries Society 110**: 72–76.

Wille, A. 1963 Behavioral adaptations of bees for pollen collecting from *Cassia* flowers. **Revista de Biologia Tropical 11**: 205–210.

Willmer, P; D. Stanley; K. Steijven; I. Matthews & C. Nuttman. 2009. Bidirectional flower color and shape changes allow a second opportunity for pollination. **Current Biology 19**: 919–923.

Zaret T. M. & A. S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. **Ecology 52**: 336–342.

Received 24/8/2010; accepted 19/4/2011
Editor: Maria Cristina Gaglianone