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Comparative palynology of food provisions of Tetragonisca angustula (Apidae, Meliponini) from the Lower Amazon (N Brazil) and caatinga (NE Brazil)

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Abstract: Tetragonisca angustula is a stingless bee species widely distributed in Brazil. Past studies have shown a rich native flora supplying this meliponine with pollen and nectar. The aim of this study was to compare, by a cluster analysis performed with published pollen spectra, the food provisions of T. angustula in two areas in the Lower Amazon mesoregion in the state of Pará and two areas of caatinga vegetation in the state of Bahia, Brazil. We used a data set of 57 samples of honey and 46 samples of pollen stocked in colonies of T. angustula. The honeys from the Lower Amazon and from the caatinga displayed 23 and 16 pollen types with frequency higher than >10%, respectively, with emphasis on the families Fabaceae, Solanaceae and Urticaceae. In the pollen stocked samples, 18 and 11 pollen types were found, respectively. Cluster analyses (Dice similarity) performed with these published pollen spectra of the honeys grouped the samples from each geographic region with higher similarity than the analyses performed with the pollen spectra of the stocked pollen.

Response to Reviewers: Dear Editor,

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We have followed your suggestion and clarified that the data set has been previously published but not statistically compared.

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we cannot state if these populations are genetically distinct. This was not the aim of the study. We do not have palynological data sets available for communities of stingless bees elsewhere. If we take into account the extension of the Brazilian Amazonia, for instance, most of the published datasets reflect only the region near Manaus (AM State).

Unfortunately, it is hard to carry out any attempt of study to cover all Brazilian ecosystems where T. angustula can be found. Only inside Amazonia we have a mosaic of ecosystems and ecotones areas. However, in the manuscript we have tried to drive efforts in order to provide new dataset for areas poorly studied on a palynological view, including a qualitative statistical approach. Most of the pollen analyses of bee products performed in Brazil present their pollen spectra, but do not provide any statistical discussion or comparison between different ecosystems or biomes.

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The manuscript has been translated by AJE.

Reviewer 3:
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All minor corrections suggested by the reviewers were made along the text.

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Comparative palynology of food provisions of *Tetragonisca angustula* (Apidae, Meliponini) from the Lower Amazon (N Brazil) and *caatinga* (NE, Brazil)

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Short title: Melissopalynology of Amazon and *caatinga*

Abstract – The Amazon Forest and the *caatinga* (dry forest) are two Brazilian biomes that are rich in meliponine species. *Tetragonisca angustula* is a stingless bee species...
widely distributed in Brazil. Past studies have shown a rich native flora supplying this meliponine with pollen and nectar. The aim of this study was to compare, by a cluster analysis performed with published pollen spectra based on palynology, the food provisions of *T. etragonisca angustula* in four areas of Brazil: two areas in the Lower Amazon mesoregion in the state of Pará and two areas of caatinga vegetation in the state of Bahia, Brazil. We analysed 103 samples, consisting of a data set of 57 samples of honey and 46 samples of pollen stocked in colonies of *T. angustula*. The honeys from the Lower Amazon and from the caatinga displayed 23 and 16 pollen types (with frequency higher than >10%), respectively, with emphasis on the families Fabaceae, Solanaceae and Urticaceae. In the pollen stocked samples, 18 and 11 pollen types were found, respectively. Cluster analyses (Dice similarity) performed with these published pollen spectra of the honeys grouped the samples from each geographic region with higher similarity than the analyses performed with the pollen spectra of the stocked pollen.
1. INTRODUCTION

The tribe Meliponini includes more than 500 bee species known as natives or stingless indigenous species, distributed especially through the tropical and subtropical regions (Michener 2007, 2013). In the Neotropics, Brazil stands out as one of the countries containing the greatest diversity of bee species, due to its vast territorial expanse and to the floristic richness that supports such insects by providing them food and shelter.

With a territory of more than 8 million km², Brazil displays six continental biomes. Of these biomes, the Amazon Forest and the caatinga (dry forest) together form more than 5 million km², equivalent to approximately 60% of the national territory (IBGE 2004). The Amazon Forest, extending over eight Latin-American countries in addition to Brazil, is the largest tropical rainforest of the planet, with a high precipitation level irregularly distributed in time and space (Fisch et al. 1998). In contrast, the seasonally dry forests of the caatinga encompass different mosaics of vegetation subjected to a rigorous precipitation deficit (Prado 2003). According to Giulietti et al. (2004), the caatinga can be considered the only genuinely Brazilian biome, although it is still modestly studied in comparison to the remaining biomes of the country. Disturbances in both of these biomes have threatened native bee populations and hindered the environmental services provided by them (Freitas et al. 2009; Maia-Silva et al. 2012).

Tetragonisca angustula (Latreille, 1811) is one of the most known and managed native bees found in Brazil. The small quantity of honey produced by T. angustula is highly valued, especially in rural communities, for use in the treatment of cataracts,
pterygium, stomach and liver diseases, wounds and ulcers (Iwama and Melhem 1979; 
Dardón et al. 2013).

Recently, in independent palynological studies, we investigated the pollen spectra of 
samples of honey and pollen of *T. angustula* obtained in areas of the Lower Amazon, in 
the west of the state of Pará (north region of Brazil) (Novais and Absy 2013; Novais 
and Absy, in press), and of the *caatinga* in the centre-north of the semiarid region of the 
state of Bahia (northeast region of Brazil) (Novais et al. 2013, 2014).

- The aim of this manuscript was to perform a comparative palynological analysis of 
the food provisions of *T. angustula* between different biomes in Brazil based on the 
published data described above of *T. angustula* from these same areas in the Lower 
Amazon and in the Bahian *caatinga*. The data on the pollen types found has been 
previously published but not statistically compared. With this study, we compiled the 
data set of plants foraged by *T. angustula* in two different biomes (Amazon and 
*caatinga*) and also perform a cluster analysis aiming to better understand the similarity 
of pollen diet of this species in different regions in Brazil, one wet and another dry, we 
expect to further comprehend the feeding habits of *T. angustula* in different 
environments, contributing to the ecological studies of the communities of this native 
pollinators, especially in the Amazonian region and in poorly studied xeric areas.

2. MATERIAL AND METHODS

Study sites
We used data obtained from four study sites: two located in the west of the state of Pará, in the Lower Amazon mesoregion (N Brazil), and two areas in the central-north semiarid zone of the state of Bahia (NE Brazil) (Figure 1).

In the Amazonian region, the study was performed in the municipalities of Belterra and Santarém, located in the Lower Amazon geographic mesoregion, state of Pará (IBGE 1990) (Figure 1). In this mesoregion, the rainy season usually lasts five to six months, beginning in December and with a peak of precipitation in April, when the Intertropical Convergence Zone acts locally with more intensity (Albuquerque et al. 2010). The mean annual precipitation is approximately 2,000 mm, and the mean annual temperature is 25 ºC (Carvalho et al. 1986; EMBRAPA 2013). According to Forzza et al. (2010), the most diverse families of angiosperms in the Amazon Forest are Fabaceae, Orchidaceae, Rubiaceae, Melastomataceae and Poaceae. In a study of the floristic composition of a secondary forest of the plateau in Belterra, Carvalho et al. (1986) identified Bignoniaceae, Combretaceae, Melastomataceae and Myrtaceae as the most abundant families, which together accounted for more than 67% of the vegetation studied.

In the caatinga, the sampling was performed in the municipalities of Itaberaba and Ruy Barbosa, belonging to the geographic mesoregion of the Centre North of Bahia (IBGE, 1990) (Figure 1). According to Prado (2003), the semiarid caatingas display extreme meteorological characteristics compared to the remaining Brazilian biomes. In these areas, the precipitation is low and irregular, frequently not exceeding 700 mm per year and limited to a short period in the year (Nimer 1972; Prado 2003). This climate directs an extremely adapted vegetation, including approximately 318 species endemic to the northeast region of Brazil, although this selective climate does not imply
physiognomic or floristic uniformity (Giulietti et al. 2004). The seasonally dry shrub or tree forests of the caatinga usually display deciduous, small plant species with twisted trunks, bearing prickles, thorns and other modified structures to minimize water loss (Prado 2003; Giulietti et al. 2004). According to Forzza et al. (2010), the most diverse angiosperm families in the caatinga include Fabaceae, Poaceae, Asteraceae, Euphorbiaceae and Rubiaceae.

[FIGURE 1]

Collection, laboratory processing and palynological analysis

In total, 103 samples were studied: 57 samples of honey and 46 samples of pollen stocked by *T. angustula*. The samples were collected monthly in between September 2010 and January 2012 in the study sites of the Lower Amazon [Belterra (16 and 15 samples of honey and pollen, respectively) and Santarém (14 and 8 samples of honey and pollen, respectively)] and of the caatinga [Itaberaba (13 and 10 samples of honey and pollen, respectively) and Ruy Barbosa (14 and 13 samples of honey and pollen, respectively)] (Novais and Absy 2013; Novais and Absy, in press; Novais et al. 2013, 2014).

The protocol for the collection of material, the laboratory procedures adopted and the qualitative and quantitative palynological analysis performed were previously described by Novais and Absy (2013) and Novais et al. (2013). The technique of acetolysis (Erdtman 1960) was used to process all the samples. For the purpose of this study, a sample consists of 5 mL of honey or 2-3 g of stocked pollen, collected from one colony.
of *T. angustula* in each study site. After chemical processing, four glass slides were prepared and, subsequently, at least 500 pollen grains per sample were identified and quantified. From these data, the following frequency classes were established, as proposed by Louveaux et al. (1978): predominant pollen (>45% of the grains counted in a sample), secondary pollen (16 – 45%), important minor pollen (3 – 15%) and minor pollen (<3%).

**Statistical analysis**

Statistical analysis was performed with the pollen spectra obtained, considering only the pollen types with frequencies higher than 10% in at least one of the samples analysed because these types represent the most significant floral resources for the bees (Ramalho et al. 1985). We have not included in this analysis pollen types which frequencies were lower than 10% in all samples.

We performed a cluster analysis, using the Dice similarity coefficient (McCune and Grace 2008), to evaluate the formation of groups among the samples studied based on the pollen types identified in the samples. For the honeys, the 57 samples were considered objects, and the 36 pollen types identified were considered variables. Similarly, for the stocked pollen, the 46 samples were considered objects, and the 29 pollen types identified were considered variables. Therefore, we evaluated the presence of structured patterns, considering the period of collection and the different sampling areas. This analysis considered only the presence or absence of the pollen types in the individual samples, disregarding the absence of a given pollen type as an indication of similarity.
The similarity analysis was performed with the software PAST – *PAlaeontological STatistics*, version 2.16 (Hammer et al. 2001). The climatic data of the study sites were obtained from the Brazilian National Institute of Meteorology (Instituto Nacional de Meteorologia, INMET 2013), except for the municipality of Ruy Barbosa, Bahia, where there is no meteorological station to record such data. A given month was considered dry when the total monthly precipitation, in milimeters, was equal to or lower than double the mean monthly temperature, expressed in degrees Celsius (P ≤ 2T) (Bagnouls and Gaussen 1962).

3. RESULTS

General considerations of the pollen spectra and the most representative pollen types

The honey samples revealed a higher number of representative pollen types (those with a frequency higher than 10% in at least one sample) than the pollen stocked samples. In decreasing order, the highest number of pollen types in the honey samples was recorded in Santarém, PA (17 pollen types), followed by Ruy Barbosa, BA (14), Belterra, PA (12) and Itaberaba, BA (10) (Table I). For the pollen stocked samples, the municipality with the highest number of representative pollen sample types was Belterra, PA (11), followed by Santarém, PA (10), Itaberaba, BA (9) and Ruy Barbosa, BA (7) (Table II).

In total, the honeys from the Amazonian study sites displayed 23 pollen types, representing 15 botanical families. In decreasing order, *Warszewiczia coccinea*
(Rubiaceae), Microtea (Phytolaccaceae), Byrsonima (Malpighiaceae), Cecropia (Urticaceae) and Borreria verticillata (Rubiaceae) were the most common pollen types and occurred in more than 50% of the samples (Figure 2a). In the honeys from the study sites in the caatinga, 16 pollen types and 11 botanical families were recorded, from which Prosopis juliflora (Fabaceae), Solanum (Solanaceae), Heteropterys (Malpighiaceae) and Schinus (Anacardiaceae) were the most commonly observed pollen types (Figure 2b).

The pollen stocked samples from the Amazonian study sites, in contrast, displayed 18 pollen types, representing 17 botanical families. The pollen types Cecropia and Borreria verticillata occurred in more than 50% of the samples (Figure 3a). The pollen stocked samples from the study sites in the caatinga revealed 11 pollen types and seven botanical families. Of these types, the most frequent were Prosopis juliflora, Solanum, Senna macranthera (Fabaceae), Brosimum (Moraceae) and Heteropterys (Figure 3b).

In general, the families Anacardiaceae, Bignoniacae, Euphorbiaceae, Fabaceae, Malvaceae, Myrtaceae and Rubiaceae displayed two to four distinct pollen types per study site (Figures 2 and 3).

The honey samples from the Lower Amazon displayed eight pollen types classified as "predominant pollen": Borreria verticillata (69.27%), Byrsonima (68.55%, 68.32%, 60.34% and 47.12%), Cecropia (54.51% and 50.66%), Chamaecrista (Fabaceae) (62.59%), Clidemia hirta (Melastomataceae) (54.12%, 47.86% and 46.30%), Diodia (Rubiaceae) (89.53%), Solanum (93.39%) and Warszewiczia coccinea (54.64%) (Table I). Of these pollen types, Byrsonima (4), Clidemia hirta (3) and Cecropia (2) stood out because they were more frequent (into the predominant class) in the studied samples predominant in four, three and two samples, respectively (Table I). In contrast,
the honeys from the caatinga revealed five predominant pollen types: *Cecropia* (93.02%), *Gomphrena demissa* (Amaranthaceae) (63.84%), *Prosopis juliflora* (68.59% and 48.76%), *Schinus* (93.21%, 74.39%, 69.49%, 55.30% and 47.95%) and *Solanum* (85.52%, 60.58% and 59.33%) (Table I). Of these, *Schinus* (5), *Prosopis juliflora* and *Solanum* (3) and *Prosopis juliflora* (2) were predominant in two and three samples, respectively, and *Schinus* was predominant in five samples (Table I).

Furthermore, we emphasise that the pollen types *Cecropia* and *Solanum* were part, as predominant pollen types, of the foraging behaviour of *Tetragonisca angustula* in both the Lower Amazon and the Bahian caatinga (Table I and Figure 2). In addition to the families Solanaceae and Urticaceae, the family Fabaceae had different representatives occurring as the predominant pollen in these two regions (Table I).

The pollen stocked samples of *T. angustula* from the Lower Amazon revealed the following predominant pollen types: *Byrsonima* (92.10%, 82.68%, 73.96%, 55.56% and 49.06%), *Cecropia* (99.60%, 97.03%, 82.02%, 76.78%, 60.71%, 58.00% and 49.08%), *Clidemia hirta* (98.31%, 90.65% and 74.41%), *Davilla kunthii* (Dilleniaceae) (83.11%), *Eriope* (Lamiaceae) (74.07%), *Myrcia* (Myrtaceae) (88.27%) and *Vismia guianensis* (Hypericaceae) (72.44%) (Table II). *Cecropia* (7), *Byrsonima* (5) and *Clidemia hirta* (3) stood out for being predominant in seven, five and three of the analysed pollen stocked samples, respectively (Table II). The pollen stocked samples from the caatinga revealed seven predominant pollen types: *Brosimum* (73.01%, 50.95% and 50.00%).
Caesalpinioideae (Fabaceae) (90.57%), *Prosopis juliflora* (85.11%, 81.06%, 80.74%, 80.53%, 76.66%, 71.01%, 54.91%, 53.41%, 49.33% and 46.98%), *Schinus* (47.96%), *Senna macranthera* (84.56%), *Solanum* (83.55%, 60.39%, 57.12% and 54.88%) and *Waltheria* (Malvaceae) (60.62%) (Table II). Of these types, *Prosopis juliflora* (10), *Solanum* (4) and *Brosimum* (3) were predominant in 10, five and three samples, respectively (Table II). No predominant pollen type occurred simultaneously in the pollen stocked samples from both of the biomes.

**Pollen groups based on the cluster analysis**

The groups obtained by the cluster analysis of the pollen spectra of the honey samples were more homogeneous than those obtained with the pollen spectra of the pollen stocked samples (Figures 4 and 5).

The first phenogram obtained (cophenetic coefficient 0.94, Figure 4) initially formed two distinct groups, gathering all the samples from the Lower Amazon in group A and all samples from the caatinga in group B. However, the level of similarity of group A was lower than that of group B (Figure 4).

The cluster analysis also revealed the formation of subgroups within the wider groups (A and B), gathering the samples per municipality (Figure 4). In crescent order of similarity, the following subgroups were formed: C (gathering the samples from Belterra), D (Santarém), E (Ruy Barbosa) and F (Itaberaba) (Figure 4). Of the subgroups, F was the most consistent, the last with a level of similarity higher than 0.70 (Figure 4).
In group A, the predominant and/or secondary pollen types shared by subgroups C and D were *Byrsonima*, *Cecropia*, *Microtea*, *Tapirira guianensis* (*Anacardiaceae*) and *Warszewiczia coccinea* (Figure 4). Of these types, only *Tapirira guianensis* was not among the most frequent pollen types in the honey samples from the Lower Amazon (Figure 4). The pollen types *Heteropterys*, *Prosopis juliflora*, *Schinus* and *Solanum* were shared as predominant and/or secondary pollen types in the samples gathered in group B, thus characterising this cluster (Figure 4). These same pollen types were among those with the highest occurrence in the honey samples from the *caatinga* (Figure 2).

The second phenogram (cophenetic coefficient 0.96, Figure 5), obtained from the cluster analysis with the data from the pollen stocked samples, shows less-consistent groups than those obtained from the cluster analysis with the data from the honey samples (Figure 4). Two main groups can be observed: group A, gathering the samples from the Lower Amazon; and group B, gathering the samples from the *caatinga* (Figure 5). However, these groups showed a low similarity level (<0.4), especially group A (<0.1) (Figure 5).

From these two main groups (A and B), two additional sub-groups were formed (Figure 5); however, these sub-groups did not show a significant geographic discrimination, in contrast to the first phenogram (Figure 4). In crescent order of similarity level, the subgroups C and D were generated for the Lower Amazon, and the subgroups E and F were generated for the *caatinga* (Figure 5). Subgroup C gathered, with low similarity (<0.3), only three pollen stocked samples from Santarém, in which the predominant pollen types were *Clidemia hirta* and *Davilla kunthii*. Subgroup D gathered samples from Belterra and Santarém. Within this subgroup, smaller clusters
were generated, gathering, for example, samples exclusive to Santarém (clusters G and J) and to Belterra (H and I). Subgroup E gathered pollen stocked samples from the two caatinga areas, whereas subgroup F gathered only the sample collected in Itaberaba in January 2011, with Caesalpinioideae as the predominant pollen type (Figure 5). Within subgroup E, cluster K stood out for gathering 10 samples exclusively from Ruy Barbosa at a similarity level higher than 0.7. The predominant pollen types in this cluster (K) were *Prosopis juliflora*, *Schinus* and *Solanum* (Figure 5). Clusters L and M gathered samples from both Itaberaba and Ruy Barbosa, with emphasis on the pollen type *Brosimum* (Figure 5).

The predominant and/or secondary pollen types shared by the majority of the more than one subgroups of group A were *Byrsonima* (G and H), *Cecropia* (G, H and I) and *Clidemia hirta* (C and G) (Figure 5). Of these types, *Cecropia* was among the most frequent pollen types in the pollen stocked samples from the Lower Amazon (Figure 3). In contrast, *Brosimum* (K, L and M), *Heteropterys* (K and M), *Prosopis juliflora* (K, L and M), *Schinus* (K and M) and *Solanum* (K, L and M) were the pollen types most shared by subgroups of group B (Figure 5). Of these, only *Schinus* was not among the pollen types with the highest occurrence in the pollen stocked by *Tetragonisca angustula* in the caatinga (Figure 3).

With the analysis of the climatic data from the study sites, we noted that in Belterra, five months were considered dry (September and November 2010; August, September
In Santarém, only October 2010 and September 2011 were dry. In contrast, in Itaberaba, all the months of 2011 were dry except November (Figure 6). However, there was no evident relationship between the groups shown in the phenograms and the meteorological data. In the honey samples from Santarém, the cluster formed by the samples collected between February and April 2011 represents the peak of precipitation in this region (Figures 4 and 6) and the period of dominance of the pollen type *Clidemia hirta* (Online Resource 1). In contrast, the pollen stocked samples from Belterra in the months of September and October 2010, in addition to those of June, August and September 2011, formed a cluster representing the months that were dry or had low precipitation (Figures 5 and 6), and these samples were dominated by the pollen types *Byrsonima*, *Borreria verticillata*, *Cecropia*, *Schefflera morototoni* (Araliaceae) and *Tabebuia* (Bignoniaceae) (Online Resource 2).

[FIGURE 6]

4. DISCUSSION AND CONCLUSION

Despite the high number of pollen types identified in both the honey and pollen stocked samples, few pollen types effectively contributed to the composition of the majority of the pollen spectra obtained. This finding corroborates previous palynological studies performed in areas of the Central Amazon involving other species of meliponines. Marques-Souza et al. (1996) identified 56 pollen types, representing 23 botanical families, in the pollen collected over a one year period from the corbiculae spectrum of *Trigona williana* Friese, 1900 in the municipality of Manaus, state of
However, only the families Araliaceae, Arecaceae, Bignoniaceae, Caricaceae, Fabaceae, Malpighiaceae, Melastomataceae, Moraceae and Myrtaceae were attractive to *T. williana*, with pollen types present at a frequency equal to or higher than 10% in the samples. Similarly, Marques-Souza et al. (2002) identified seven to 37 pollen types per meliponine, representing four to 22 botanical families, when investigating the pollen collected by species of *Frieseomelitta*, *Melipona* and *Scaptotrigona* in the Central Amazon. However, only 18 pollen types were considered by these authors to be the most representative of the composition of the samples studied. These pollen types belonged to families Anacardiaceae, Euphorbiaceae, Fabaceae, Lythraceae, Melastomataceae, Myrtaceae, Portulacaceae, Rubiaceae, Rutaceae and Sapindaceae. Additionally, in a study performed with corbicular pollen of *Frieseomelitta varia* Lepeletier, 1836, Marques-Souza (2010) obtained a pollen spectrum containing 79 identified pollen types, from 37 botanical families. However, only the families Araliaceae, Combretaceae, Euphorbiaceae, Fabaceae, Melastomataceae, Moraceae, Myrtaceae, Sapotaceae, Urticaceae and Verbenaceae had representatives with a frequency equal to or higher than 10% in the samples.

In areas of *caatinga* in the northeast region of Brazil, a similar pattern was also observed in palynological studies with meliponines. Alves et al. (2006) analysed pot honeys of *Melipona mandacaia* Smith, 1863 from the *caatinga* of the municipality of São Gabriel, state of Bahia, and identified 26 pollen types, representing 11 botanical families. Of these families, the families Euphorbiaceae, Fabaceae and Myrtaceae were the only ones with pollen types with representative frequency in at least one sample. Also in the state of Bahia, Novais et al. (2006) analysed pot honeys of *Tetragonisca angustula* from the municipality of Canudos. These authors found 30 pollen types,
from 16 families of the local vegetation, of which Amaranthaceae, Fabaceae, Malvaceae, Myrtaceae, Rubiaceae and Rhamnaceae were the most significant for *T. angustula*, according to the set of honey samples analysed. Recently, Santana et al. (2011) analysed pot honeys of *Melipona* spp., *Scaptotrigona tubiba* Smith, 1863 and *T. tetragonisca angustula* from the municipalities of Andaraí, Itaberaba, Manoel Vitorino, São Gabriel and Santa Teresinha in the semi-arid zone of the state of Bahia. The most important families observed by these authors were Anacardiaceae, Convolvulaceae, Erythroxylaceae and Fabaceae.

Therefore, it can be concluded that families such as Euphorbiaceae, Fabaceae, Myrtaceae and Rubiaceae are commonly shared in the pollen spectra of products of meliponines in certain areas of the Amazon Forest and of the *caatinga*.

In general, several pollen types were recorded in both the pollen and honey samples, such as *Alternanthera*, *Byrsonima*, *Cecropia*, *Heteropterys*, *Prosopis juliflora* and *Solanum*; however, in a few cases, these genera oscillated in the order of abundance. A similar trend was also observed by Imperatriz-Fonseca et al. (1984), who analysed the food provisions (honey and pollen) of *Tetragonisca angustula* in the state of São Paulo, southeast region of Brazil, and by Sosa-Nájera et al. (1994), who conducted research in the south of Mexico.

According to our studies and to data from the literature previously cited, some plant species with representative pollen types in the pollen spectra are presumably preferred by meliponines for several months. However, additional studies are required to evaluate if is it real preference or is it according to phenology of the plants. In the case of *T. angustula*, Obregón et al. (2013) noted that the workers of a same colony usually tend to
be consistent, visiting the same species and showing preferences for certain nectar
sources, mainly for species with massive flowerings.

These preferences are related to the availability of food in the foraging radius of the
meliponines, determining the extension of their trophic niche.

-Absy et al. (1980) and Marques-Souza (2010) did not observe a direct relationship
between climatic factors and diversification in the search for floral resources. Our data,
in principle, corroborate such studies because the cluster analysis here performed did
not allow the establishment of well-defined groups based only on the climatic data from
the study sites.

However, assuming that the beginning, duration and synchronisation of the flowering
process are related, although not exclusively, to climatic factors (Opler et al. 1976;
Murphy and Lugo 1986), it is possible to state that there is an indirect
participation of climatic conditions in the composition of the pollen spectra. In arid and
semiarid ecosystems, this relationship between flowering and precipitation is striking
because, for most species, the flower buds generally start blossoming after the rains
(Machado et al. 1997), changing the physiognomy of the caatingas. For tropical
regions, Opler et al. (1976) state that factors such as the reduction of water stress and
the isolated decrease in temperature can break dormancy and, consequently, lead to the
synchronised anthesis of several plant species. This synchronisation favours cross
pollination, providing flower rewards that attract several pollinators (Opler et al. 1976).

Both plants with seasonal flowering and plants that flower through the entire year are
important for bees. In the Amazon forest, species with the flowering peak during the
rainy season maintain a pollen and/or nectar supply for bees in a period usually
considered characterised by food scarcity (Marques-Souza 2010). Furthermore, genera
such as *Cecropia, Clidemia, Miconia* and *Myrcia* provide floral resources practically throughout the entire year (Absy et al. 1984; Marques-Souza 2010). Conversely, in the *caatinga*, few species maintain flowering during the long months of drought (Freitas and Silva 2006). Therefore, predominant species, such as *Prosopis juliflora* (Sw.) DC., that flower during several months become fundamental for bee populations in arid and semiarid ecosystems. It is also common to find species that share the same guild of pollinators but that display flowering periods that do not overlap. This pattern can result from selective pressures along the evolutive process toward avoiding or minimising interspecific competition for pollinators (Opler et al. 1976).

The botanical families with predominant pollen types in the samples from the Amazonian region were Dilleniaceae, Fabaceae, Hypericaceae, Lamiaceae, Malpighiaceae, Melastomataceae, Myrtaceae, Rubiaceae, Solanaceae and Urticaceae. Similar results were found by Rech and Absy (2011a, 2011b) when working with meliponines of the genera *Cephalotrigona, Partamona, Ptilotrigona, Scaura, Tetragonisca* and *Trigona* along the canal of the Negro River in the state of Amazonas. These results indicate the sharing of the same floral sources by different meliponines, although not necessarily during the same foraging period. A good example comes from plants with poricidal anthers, such as those of the genera *Clidemia* and *Solanum*, whose pollen grains are frequently found in the pollen and honey of meliponines (Rech and Absy 2011a; Novais and Absy 2013). These bees probably make use of the residual pollen released by the vibration of the anthers by larger bees (Rech and Absy 2011a; Novais and Absy 2013). Moreover, some meliponines are able to take pollen from poricidal anthers using their mandible (Roubik 1989).
In the samples from the *caatinga*, the families with predominant pollen types were Amaranthaceae, Anacardiaceae, Fabaceae, Malvaceae, Moraceae, Solanaceae and Urticaceae. These plant groups are cited in several studies of the bee flora in the semiarid region (Borges et al. 2006; Santos et al. 2006). Novais et al. (2006) characterised honeys of *T. angustula* produced in Bahia as composed of associations of pollen types related to the families Amaranthaceae, Fabaceae, Malvaceae, Myrtaceae and Rubiaceae. Similarly, Alves et al. (2006) included Anacardiaceae and Fabaceae among the most important families for *Melipona mandacaia* in an area of *caatinga*.

Roubik and Moreno (2013) state that the predominant pollen is often not an indication of the source of the nectar. This fact is evident when observing the presence of pollen types related to polleniferous species or genera (such as *Brosimum*, *Cecropia*, *Clidemia*, *Solanum* etc.) as the predominant pollen in honey samples. These pollen spectra should be interpreted in the sense of identifying plant species visited by bees to obtain floral resources, not only and necessarily nectar. For example, a honey sample with more than 90% of pollen grains of *Cecropia* in the pollen spectrum, as observed in Itaberaba in October 2010, certainly does not indicate a monofloral honey produced from nectar of this plant group. However, such data point to a very probable pollen source for this bee. Therefore, such information should not be disregarded in the pollen spectrum. Great care should be taken, therefore, with the labelling of honeys as monofloral based only on the quantification of the pollen grains present, without considering the real production of nectar and pollen by the plants that comprise the local bee pasture. This practice can lead to mistaken melissopalynological interpretations (Molan 1998).
Most bee and meliponine products are heterofloral or polyfloral, i.e., several plant species contribute to their elaboration, even if the plant species are underrepresented in the samples. The pollen niche varies with the availability of floral resources in the foraging radius of the bees as well as with other factors, such as intra- and interspecific competition and the feeding needs displayed by the colony (Heinrich 1976a, 1976b; Imperatriz-Fonseca et al. 1984).

The pollen spectra of the honey samples revealed a higher number of pollen types than the pollen spectra of the pollen stocked samples. This finding possibly reflects the higher number of plants that need to be foraged to supply the demand of *Tetragonisca angustula* for nectar, in both the Amazonian and the caatinga areas. Also, the extra plant species found in the honey samples could came from contamination after visiting nectar's flowers. In contrast, the protein need was supplied by a smaller array of plant species, although this pattern does not necessarily indicate a lower collection effort. The bees may have reduced foraging to a few species but visited a large number of flowers of those species in search of pollen.

We conclude that the data confirm the generalist habit of *T. angustula*, in both Amazonian and semiarid areas in Northeast Brazil. Based on the cluster analysis, we conclude the pollen data of the honey samples were more consistent in the grouping of samples analysed per geographic region than the pollen data of the pollen stocked samples. The climatic data did not allow a consistent grouping of the samples by study sites.

**ACKNOWLEDGMENTS**
We are extremely grateful to Carleandro Dias and Geancarlo Gouveia for authorising the collection of samples within their private meliponaries. We are also grateful to the regional management of the Company for Agricultural Development of the State of Bahia for providing logistic support during the samplings in Bahia; to the direction of the Mãe Jovina School of the Agricultural Family for allowing access to the meliponary in Ruy Barbosa; to the Municipal Secretariat of Education of Santarém for authorising the collections within the School of the Forest; to Bruno Henrique Andrade-Silva for contributing to the collections and to the processing of the samples; and to Leilton Damascena for providing the map shown here. We thank the Brazilian National Council for Scientific and Technological Development for partial funding of this research and for the scholarships granted to the authors of this study (processes 575747/2008-0, 143084/2009-7, 303557/2010-9 and 477127/2011-8).

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**FIGURE, TABLE AND ONLINE RESOURCE CAPTIONS:**

**Fig. 1** Location of the study sites in the Lower Amazon (map to the left) and in the *caatinga* (map to the right). In the map of the South America, in the centre, Brazil is coloured in grey, with emphasis on the states of Pará, in the north region, and Bahia, in the northeast region. The municipalities where the study was performed are represented by letters: A, Santarém; B, Belterra; C, Ruy Barbosa; D, Itaberaba.

**Fig. 2** Occurrence (%) of pollen types in 57 samples of honey produced by *Tetragonisca angustula* (Apidae, Meliponini) in Amazonian areas (2a) to the left in the figure and semiarid areas (2b) to the right of Brazil. Only the pollen types with a frequency equal to or higher than 10% in at least one of the samples analysed are represented in this diagram.

**Fig. 3** Occurrence (%) of pollen types in 46 samples of pollen stocked by *Tetragonisca angustula* (Apidae, Meliponini) in Amazonian areas (3a) to the left in the figure and semiarid areas (3b) to the right of Brazil. Only the pollen types with a frequency equal to or higher than 10% in at least one of the samples analysed are represented in this diagram.
Fig. 4 Phenogram generated from the cluster analysis, using the Dice similarity coefficient, of the pollen spectra of 57 samples of honey produced by Tetragonisca angustula (Apidae, Meliponini) in areas of the Lower Amazon (Belterra and Santarém, state of Pará) and of the semiarid region (Itaberaba and Ruy Barbosa, state of Bahia) in Brazil. The main clusters obtained are emphasised (letters A–F) as well as the dominant pollen types (>45%) and accessory pollen types (16–45%) characteristic of the groups. Cophenetic coefficient: 0.9378.

Fig. 5 Phenogram generated from the cluster analysis, using the Dice similarity coefficient, of the pollen spectra of 46 samples of pollen stocked by Tetragonisca angustula (Apidae, Meliponini) in areas of the Lower Amazon (Belterra and Santarém, state of Pará) and of the semiarid region (Itaberaba and Ruy Barbosa, state of Bahia) in Brazil. The twelve clusters obtained are emphasised (letters A–M) as well as the dominant pollen types (>45%) and accessory pollen types (16–45%) characteristic of the groupings. Cophenetic coefficient: 0.9615.

Fig. 6 Climatic data obtained by INMET (2013) for the municipalities of Belterra (A), Santarém (B) and Itaberaba (C). A month was considered dry (emphasised in grey in the graphs) when the total precipitation (mm) was equal to or lower than twice the temperature (°C), according to Bagnouls and Gaussen (1962).
Table I. Pollen spectra indicative, based on the frequency class, of the number of samples in which the most representative pollen types occurred in honey samples of *Tetragonisca angustula* (Apidae, Meliponini) in the Lower Amazon, state of Pará (PA), north region, and in the *caatinga*, state of Bahia (BA), northeast region, Brazil. Only the pollen types with a frequency equal to or higher than 10% in at least one of the samples analysed were considered representative. Frequency classes: p, predominant pollen; s, secondary pollen; im, important minor pollen; m, minor pollen. =, total number of samples in which each pollen type was recorded, per locality.

Table II. Pollen spectra indicative, based on the frequency class, of the number of samples in which the most representative pollen types occurred in samples of pollen stocked by *Tetragonisca angustula* (Apidae, Meliponini) in the Lower Amazon, state of Pará (PA), north region, and in the *caatinga*, state of Bahia (BA), northeast region, Brazil. Only the pollen types with a frequency equal to or higher than 10% in at least one of the samples analysed were considered representative. Frequency classes: p, predominant pollen; s, secondary pollen; im, important minor pollen; m, minor pollen. =, total number of samples in which each pollen type was recorded, per locality.

Online Resource 1. Pollen spectra of the samples of honey produced by *Tetragonisca angustula* (Apidae, Meliponini) in Amazonian and semiarid areas of Brazil from September 2010 to January 2012. B, Belterra; S, Santarém; I, Itaberaba; R, Ruy Barbosa.
Online Resource 2. Pollen spectra of the samples of pollen stocked by *Tetragonisca angustula* (Apidae, Meliponini) in Amazonian and semiarid areas of Brazil from September 2010 to January 2012. B, Belterra; S, Santarém; I, Itaberaba; R, Ruy Barbosa.
Table I.

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<th>Itaberaba - BA</th>
<th>Ruy Barbosa - BA</th>
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Fig 3 - revised
Click here to download high resolution image
Similarity

**Predominant Pollen**
- Cecropia, Prosopis juliflora, Schinus, Solanum

**Secondary Pollen**
- Heteropterys, Myrcia, Prosopis juliflora, Schinus, Solanum, Syagrus coronata

**Predominant Pollen**
- Gomphrena demissa, Prosopis juliflora, Schinus, Solanum

**Secondary Pollen**
- Brosimum, Caesalpinioideae type, Euphorbia, Heteropterys, Prosopis juliflora, Schinus, Senna macranthera, Solanum

**Predominant Pollen**
- Byrsonima, Cecropia, Cladanthropis nitida, Clidemia hirta, Microtea, Myrcia, Protium, Senna, Solanum, Tapirira guianensis, Warszewiczia coccinea

**Secondary Pollen**
- Anacardium occidentale, Borreria verticillata, Byrsonima, Emilia fassbergii, Eriope, Microtea, Tapirira guianensis, Warszewiczia coccinea

Fig 4
Click here to download line figure: Fig4.eps
Fig 5
Click here to download line figure: Fig5.eps.eps
Online Resources 1 and 2

Click here to download Supplementary Material: ESM_1_and_2.xlsx