Neotrop Entomol (2020) 49:595–603
https://doi.org/10.1007/s13744-019-00756-8

INSECT POLLINATORS

# Stingless Bees (*Melipona subnitida*) Overcome Severe Drought Events in the Brazilian Tropical Dry Forest by Opting for High-Profit Food Sources

C Maia-Silva[1,2], AAC Limão[1], CI Silva[3,4], VL Imperatriz-Fonseca[1,3], M Hrncir[1,3]

[1]Univ Federal Rural do Semi-Árido, Mossoró, RN, Brasil
[2]Univ Federal do Ceará, Fortaleza, CE, Brasil
[3]Univ de São Paulo, São Paulo, SP, Brasil
[4]Univ do Estado de São Paulo, Rio Claro, SP, Brasil

**Keywords**

Meliponini, melittopalynology, Caatinga, jandaíra, pot-pollen, pot-honey

**Correspondence**
Camila Maia-Silva, Univ Federal do Ceará, Fortaleza, CE, Brasil; maiasilvac@gmail.com

Edited by Márcia M Maués – Embrapa

Received 2 August 2019 and accepted 20 December 2019

**Abstract**

In the Brazilian Tropical Dry Forest, the Caatinga, stingless bees (Apidae, Meliponini) need to adjust their foraging behavior to a very short and unpredictable blooming period. *Melipona subnitida* Ducke 1910 is one of the few meliponine species adapted to the environmental peculiarities of this biome. To get an insight into how these highly eusocial bees are able to maintain their perennial colonies despite extended periods of food scarcity, we asked the following questions: (1) At which plant species do colonies of *M. subnitida* collect their food during the rainy season? And (2) are there any plant species during the dry season, from which the colonies may profit for replenishing their food stores? During 1 year, we collected monthly honey and pollen samples from recently built storage pots of five colonies of *M. subnitida* and identified the botanical origin of the collected resources. In the course of our study, the colonies foraged at native trees, shrubs, and herbaceous species, demonstrating the importance of all plant strata for the bees' diet. Profitable plants, which bloom mainly during the rainy season and usually produce a great number of flowers, were frequently sampled in new pots throughout the entire study, even during the dry season. From our results, we compiled a list of the most important plant species providing floral resources for bees throughout the year, including periods of drought. We recommend these plants for restoration areas to improve the conservation of native bee species and local beekeeping in the Brazilian Tropical Dry Forest.

## Introduction

The Tropical Dry Forest in north-eastern Brazil, the Caatinga, is characterized by a semiarid climate, with elevated annual temperatures and extended periods of drought. Average annual rainfall varies from 240 to 1500 mm, and, in about half of this ecoregion, does not exceed 700 mm (Prado 2003; Andrade *et al* 2017). Moreover, most of the precipitation is concentrated in three to four consecutive months, which results in an elevated water deficit over a long period of the year (Vasconcellos *et al* 2010; Andrade *et al* 2017). Despite these harsh climate conditions for plants, the Brazilian Tropical Dry Forest hosts an important flora biodiversity with significant levels of endemism (Albuquerque *et al* 2012). The Caatinga is a mosaic of different forest types, characterized by trees and shrubs adapted to the periodic drought, such as deciduous species and succulent plants (Prado 2003; Moro *et al* 2014). Blooming of the vast majority of trees, shrubs and herbaceous species, occurs during the very short, irregular, and unpredictable rainy season (Reis *et al* 2006; Santos *et al* 2013; Quirino and Machado 2014). Thus, the foraging activity of flower visitors, which depend to a high degree on floral resources, is tightly synchronized to the annual flowering cycle of plants (Zanella & Martins 2003; Maia-Silva *et al*. 2015; Maia-Silva *et al*. 2018).

An important group of flower visitors in the Brazilian tropical dry forest are the stingless bees (Apidae, Meliponini), a highly diverse and abundant group of eusocial bees with perennial colonies in tropical and subtropical regions of the globe, where they play a central role in the pollination of many plant species (Michener 1974; Roubik 1989). Only few meliponine species have adapted to the environmental challenges of the Caatinga (Zanella 2000). The most probable explanation for the limited diversity of these bees in the Brazilian Tropical Dry Forest is the reduced availability of floral resources during the long dry spells (Araújo *et al* 2007; Maia-Silva *et al* 2015; Maia-Silva *et al*. 2018) that can last for up to 10 months (Prado 2003; Andrade *et al* 2017). For maintaining their perennial colonies during these extended periods of drought, meliponine species have to hoard large amounts of food in their nests during the very short rainy season (Maia-Silva *et al*. 2015; Maia-Silva *et al* 2018; Hrncir *et al* 2019). However, in these wet months as well, the occurrence and quantity of rainfall determines the amount of flowering plants, particularly of herbaceous species and shrubs (Araújo *et al* 2007), which are important food sources for bees in the Caatinga (Maia-Silva *et al* 2015; Maia-Silva *et al* 2018).

*Melipona subnitida* Ducke 1910 is one of the few stingless bee species adapted to the environmental peculiarities of the Caatinga (Zanella 2000). The survival strategies of this species include the preferential collection at highly profitable resources during the short rainy season, and the reduction of the colony population and, thus, of food requirement, throughout the dry months (Maia-Silva *et al* 2015; Maia-Silva *et al* 2016). To get an insight into how these highly eusocial bees are able to maintain their perennial colonies despite extended periods of food scarcity, we asked the following questions: (1) At which plant species do colonies of *M. subnitida* collect their food during the rainy season? And (2) are there any plant species during the dry season, from which the colonies may profit for replenishing their food stores? The answers to these questions provide an important contribution to the conservation of this and other meliponine species of the Brazilian Tropical Dry Forest because they highlight those plant species that are indispensable for these bees to survive extended periods of drought.

## Material and Methods

### *Study site*

The study was conducted from January to December 2012 at the Experimental Field Station Rafael Fernandes of the Brazilian Federal University at Mossoró, Rio Grande do Norte (Universidade Federal Rural do Semi-Árido; 5°03′54.45″S, 37°24′03.64″W, altitude 79 m). The field station, located close to large agricultural areas and rural settlements, comprises approximately 400 ha, including experimental crop plantations surrounded by native vegetation typical for the Brazilian tropical dry forest. On average, the annual cumulative rainfall in the study region is around 700 mm. Yet, in dry years, the total precipitation can drop below 200 mm and it can exceed 1200 mm in wet years (Espínola Sobrinho *et al* 2011).

### *Environmental parameters*

For each month of our study, we calculated the following environmental variables (EV): $T_{AVG}$, average ambient temperature (°C); $T_{MAX}$, maximum ambient temperature (°C); $T_{MIN}$, minimum ambient temperature (°C); and RAIN, total precipitation (mm). The data were obtained from a nearby weather-station of the National Institute of Meteorology (Instituto Nacional de Meteorologia, INMET; weather-station number A318).

### *Bee species*

For our study, we used five queenright colonies of the stingless bee species *Melipona subnitida* Ducke 1910 (Apidae, Meliponini), popularly known as jandaíra, whose geographic distribution is restricted to the Brazilian north-east (Zanella 2000). The colonies were maintained in wooden observation hives installed in an area of native caatinga vegetation approximately 1 year prior to our study.

### *Floral origin of pot-honey and pot-pollen*

Monthly from January through December 2012, we collected pot-honey and pot-pollen samples from the bee colonies. In order to avoid repeated sampling of the same material, we collected honey and pollen only from new pots, built between two subsequent sampling events, identified by mapping the colonies' food stores. Pollen samples were extracted from the pots with a plastic drinking-straw (2–3 g of pollen per colony) and the honey samples with a disposable syringe (10 ml of honey per colony). In case a colony had not built a new pot since the last sampling event, we did not collect the respective material from the nest. In total, we obtained 23 samples of pot-pollen and 30 samples of pot-honey.

Samples were acetolysed following the methods described by Erdtman (1960), and the pollen grains were identified through comparison with reference material from university's pollen collection (Coleção ASA-Abelhas Semiárido). In order to evaluate the composition of the potentially mixed pollen content in the storage pots, we counted between 400 and 800 pollen grains per sample and calculated the relative abundance ($A$) of each pollen type:

$$A = \frac{n_i \times 100}{\sum_{j=1}^{p} n_j}$$

where $n$ is the number of grains counted for a specific pollen type ($i$, $j$) in a sample, and $p$ the number of different pollen types in a sample.

Due to the great size variation between pollen grains from different plant species, abundance obtained by simple counting may not represent the real contribution in weight or volume of each plant in the samples (Silveira 1991). Consequently, we determined the relative importance of each pollen source performing a volumetric correction ($Q$) of the grains for pot-pollen samples (Silveira 1991):

$$Q_i = \frac{(\text{average diameter of pollen type } i)^3}{(\text{average diameter of smallest pollen type in sample})^3}$$

where $Q_i$ is the volumetric correction coefficient for pollen type $i$ present in a sample. The average diameters of differently shaped pollen grains (sphere, ellipsoid, triangular) were obtained following the equations indicated in Silveira (1991).

To estimate the relative importance of each pollen source in each pot-pollen sample, we calculated its $Q$-corrected volumetric contribution ($Q$-corrected abundance $A_C$):

$$A_C = \frac{n_i \times Q_i \times 100}{\sum_{j=1}^{p} n_j \times Q_j}$$

where $n$ is the number of grains counted for a specific pollen type ($i$, $j$) in a sample, $Q$ the volumetric correction coefficient, and $p$ the number of different pollen types in a sample.

For pot-pollen samples, this volumetric correction is important because it considers that different-sized pollen grains contribute differently to the amount of protein available for the bees (Silveira 1991). Volumetric correction was not performed on the pot-honey samples, given that the protein content has only marginal importance for this kind of bee-food, and pollen grains only accidentally end up in the honey storage pots (Barth 2004).

## Results

### *In dry months, colonies reduced the construction of new storage pots*

The year 2012 was a very dry year for the study region, with a total precipitation of 226.6 mm from January through December. Most of the rainfall occurred between January and April (Fig 1). February was the most humid month with 25.9% of the annual precipitation. The monthly average, minimum, and maximum temperatures showed little variation in the course of 2012 (Fig 1). Probably owing to the low precipitation in the second half of the study year, and the concomitant decline in food source availability, the colonies of *M. subnitida* did not build new storage pots (Fig 1) and we were not able to collect pot-honey and/or pot-pollen samples for our analyses (June, and August through November: no new honey pots; September through December: no new pollen pots).

### *Floral composition of pot-honey and pot-pollen*

In total, we identified 18 pollen types collected by *M. subnitida* in the course of our study (17 pollen types in pot-honey; 12 pollen types in pot-pollen). Of these, the mass-flowering tree species *Pityrocarpa moniliformis* was the most abundant nectar source contributing to the pot-honey (51.5% of total grains counted). The most abundant pot-pollen sources were shrub species with poricidal flowers, *Chamaecrista* spp. (20.8% of total grains counted) and *Senna obtusifolia* (22.3%), as well as the mass-flowering tree species *P. moniliformis* (25.1%) (Figs 2 and 3, Table 1). We identified pollen of only two exotic species (*Eucalyptus* sp. and *Leucaena leucocephala*) and of one cultivated plant (*Psidium guajava*, common name: guava) in our samples.

In the course of the year, we observed a variation concerning the floral composition of the food stored by *M. subnitida*. Some pollen types were present in both pot-honey and pot-pollen samples throughout the entire study (in case new pots were available for sampling), whereas others were only found in specific periods. Pollen of *P. moniliformis*, *Mimosa arenosa*, and *M. caesalpiinifolia* occurred in all samples collected from January through August and in December 2012, regardless of the fact that these mass-flowering trees bloom mainly in the rainy period. Other species frequent in pot-pollen and pot-honey throughout the year were *Borreria verticillata*, *Chamaecrista* spp., *M. tenuiflora*, *Psidium guajava*, and *Senna obtusifolia* (Figs 2 and 3, Table 1). By contrast, *Croton sonderianus*, a mass-flowering tree that blooms in the rainy months, and *Myracrodruon urundeuva*, a mass-flowering tree that blooms in the dry season, contributed to the pot-honey and pot-pollen samples according to their flowering period

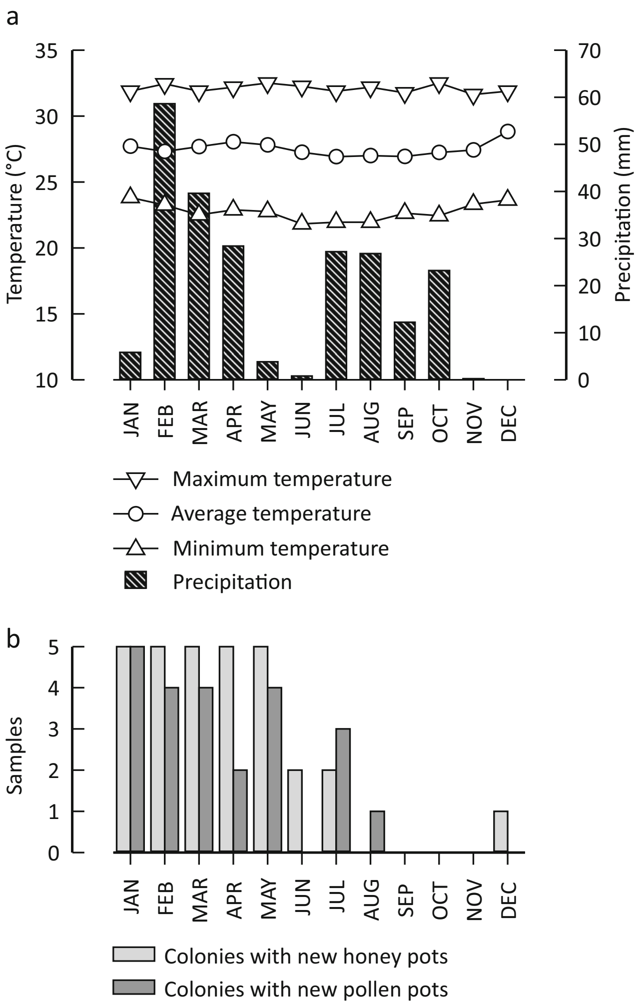

Fig 1 Reduction of storage pots in dry months. **a** Variation of environmental parameters in the course of the study period (January 2012 to December 2012). Given are monthly temperatures (upright triangle: maximum temperature; down-pointing triangle: average temperature; circle: minimum temperature) and total precipitation (shaded bars). **b** Number of colonies of *Melipona subnitida* ($N_{\text{total}} = 5$) that had built new storage pots (honey pots: light gray bars; pollen pots: dark gray bars) in a given month.

(*C. sonderianus*: February through June 2012; *M. urundeuva*: June, July, and December 2012) (Figs 2 and 3, Table 1).

In pot-honey samples, we identified a significant number of pollen grains from non-nectar flowers. *Chamaecrista* spp. and *S. obtusifolia*, both plants with flowers that have poricidal anthers and produce high amounts of pollen, do not produce nectar. Nevertheless, pollen grains of these species were highly abundant and frequent in pot-honey samples throughout the year (21% of identified pollen grains; Table 1). Similarly, the cultivated fruit tree *P. guajava*, whose flowers also only produce pollen as floral reward, contributed 1.4% to the total amount of pollen grains identified in the pot-honey samples (Table 1).

For pot-pollen, in addition to the relative abundance of pollen types (*A*), we estimated the relative importance of each pollen source by calculating its *Q*-corrected volumetric contribution (*Q*-corrected abundance, $A_C$) to the samples. Here, pollen sources with big grains gained whereas those with small grains lost in importance. According to simple counting, the most abundant pollen source during our study was *Pityrocarpa moniliformis* (average diameter = 20.6 µm; frequency in samples = 100%; *A* = 25.1%). However, after volumetric correction, the pollen of this mass-flowering tree contributed only 8.8% to the analyzed pot-pollen (Fig 3, Table 1). Similarly, other pollen sources with small-sized grains, such as *Mimosa arenosa/M. caesalpiinifolia* (average diameter = 14.3 µm; frequency in samples = 100%; *A* = 15.9%, $A_C$ = 1.9%) and *Mimosa tenuiflora* (average diameter = 19.5 µm, frequency in samples = 57%; *A* = 10.1%, $A_C$ = 3.0%) lost in relative importance after calculating their *Q*-corrected volumetric contribution to the stored pollen (Fig 3, Table 1). On the other hand, a pollen source that increased significantly in relative importance was *Senna obtusifolia* (average diameter = 40.4 µm). Pollen grains of this plant were found in 85.7% of the pot-pollen samples with a relative abundance of 22.3%. Yet, after volumetric correction, we found that this pollen source contributed by more than half ($A_C$ = 59.2%) to the annual pot-pollen storage (Fig 3, Table 1).

## Discussion

The year of 2012 marked the onset of a supra-annual drought in the Brazilian tropical dry forest that lasted until 2016 (Marengo *et al* 2017). In the study region, the cumulative rainfall of less than 250 mm in that year remained far below the annual average of 700 mm (Andrade *et al* 2017), turning 2012 into the driest year of the twenty-first century so far (Espínola Sobrinho *et al* 2011; Salimon & Anderson 2018). These severe drought conditions surely influenced the phenology of the plants, reducing the amount of resources available to the bees. Yet, albeit all climatic adversity, *M. subnitida* was able to collect resources at flowers of native trees, shrubs, and herbaceous species, demonstrating the importance of all plant strata in the habitat for the maintenance of the perennial colonies of this meliponine species in the Brazilian Tropical Dry Forest. Furthermore, our results demonstrate that the bees obtained most of their food from a rather small number of plant species, preferentially visiting profitable food sources.

During periods in which floral food is abundant, colonies of stingless bees intensify their foraging activity and store large amounts of pollen and nectar to ensure a constant food supply and, consequently, increase the colonies' chances of survival during events of resource scarcity (Hrncir & Maia-Silva 2013; Maia-Silva *et al* 2015; Maia-Silva *et al* 2016; Hrncir *et al* 2019). In the Brazilian Tropical Dry Forest, floral food is available mainly during

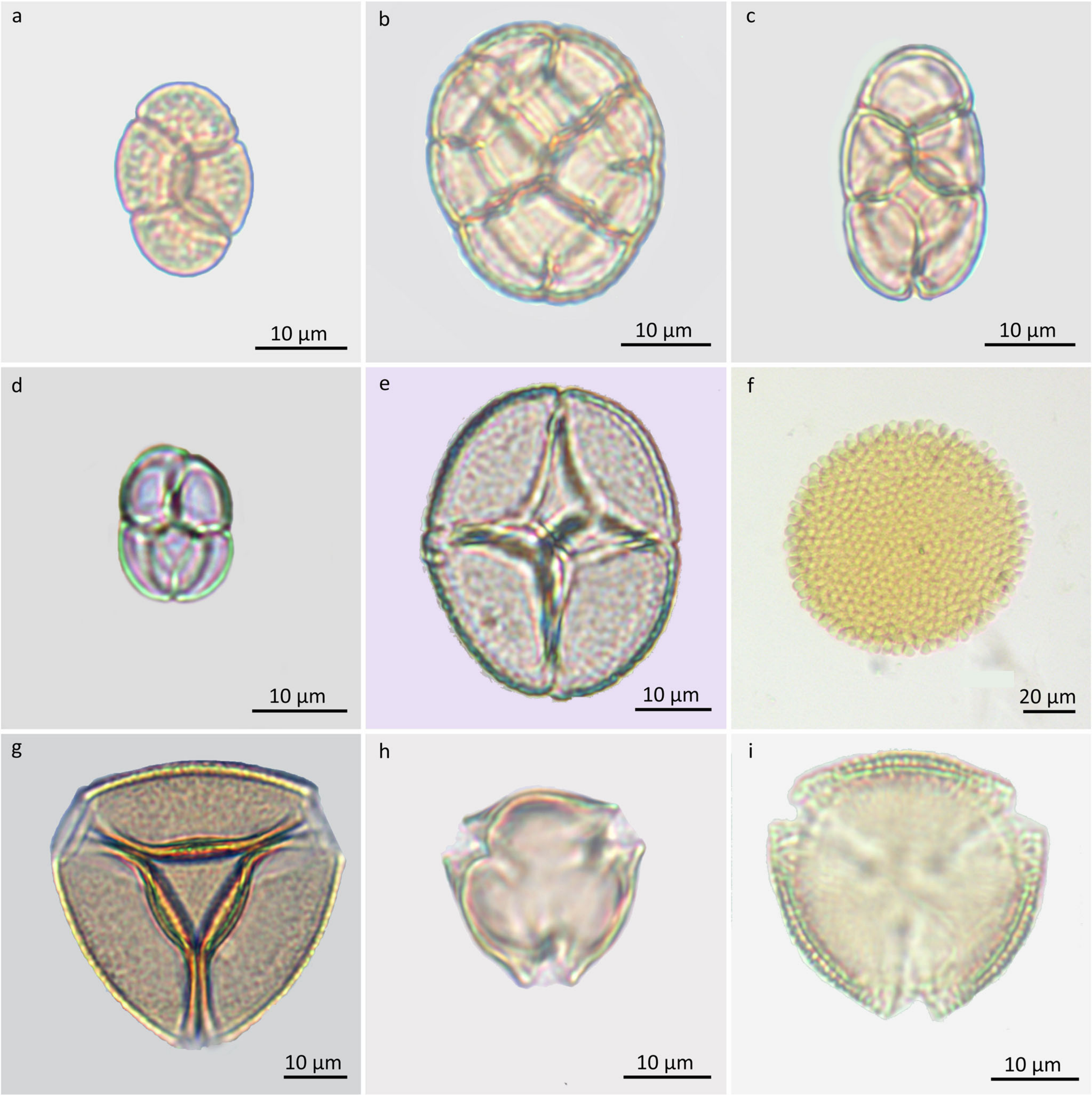

Fig 2 Mainly pollen types harvested by *Melipona subnitida* in the Brazilian Tropical Dry Forest. **a** *Mimosa tenuiflora.* **b** *Anadenanthera colubrina.* **c** *Pityrocarpa moniliformis.* **d** *Mimosa arenosa.* **e** *Mimosa quadrivalvis*. **f** *Croton sonderianus.* **g** *Senna obtusifolia.* **h** *Chamaecrista duckeana.* **i** *Myracrodruon urundeuva.*

short, irregular rainy periods that last between 2 and 5 months (Prado 2003; Andrade *et al* 2017). To profit of the ephemeral resource abundance, colonies of *M. subnitida* preferentially explore highly profitable food sources, such as mass flowering trees and plants with poricidal flowers (Maia-Silva *et al*. 2014; Maia-Silva *et al* 2015). These plants provide large quantities of pollen and nectar and, consequently, are excellent resources that allow stingless bees to build up large food reserves in a short period of time (Wilms *et al* 1996; Ramalho 2004). Although mass flowering trees that bloom in the dry season, like *M. urundeuva* and *Anadenanthera colubrina*, allow social bees to replenish part of their food stores, the colonies of *M. subnitida* did not built new storage pots during the hottest and driest months of our study. This result indicates that the key resources for the

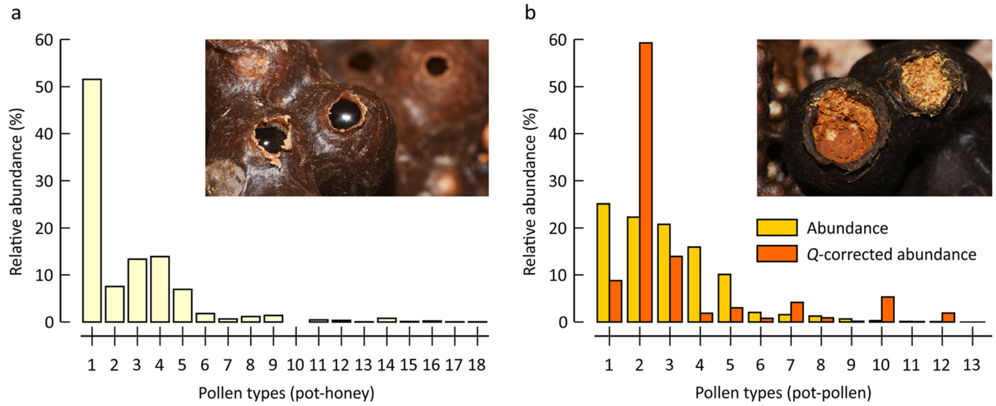

Fig 3 Pollen types identified in food stores of *Melipona subnitida.* **a** Relative abundance of pollen types in pot-honey. **b** Pollen types in pot-pollen; given are the relative abundance of pollen types throughout the study period without volumetric correction (yellow bars) and after volumetric correction (*Q*-corrected abundance, orange bars). (1) *Pityrocarpa moniliformis*; (2) *Senna obtusifolia*; (3) *Chamaecrista* spp.; (4) *Mimosa arenosa*/ *Mimosa caesalpiinifolia*; (5) *Mimosa tenuiflora*; (6) *Borreria verticillata*; (7) *Mimosa quadrivalvis*; (8) *Myracrodruon urundeuva*; (9) *Psidium guajava*; (10) *Leucaena leucocephala*; (11) *Eucalyptus* sp.; (12) *Croton sonderianus*; (13) *Sida cordifolia*; (14) *Alternanthera ficoidea*; (15) *Anadenanthera colubrina*; (16) *Waltheria* sp.; (17) *Ipomoea asarifolia*; (18) *Senegalia polyphylla.*

maintenance of perennial colonies in this meliponine species are profitable plants heavily exploited during the rainy season.

In our study, we identified pollen grains from mass flowering trees and plants with poricidal flowers that bloom exclusively in the rainy season throughout the entire year in newly built pots. This, on the one hand, highlights the large amounts of nectar and pollen from these food sources collected during the rainy period. On the other hand, the lack of association between the flowering period of plants and their occurrence in the food stores suggests the reallocated of resources from old into newly built storage pots. This transfer of old pollen together with non-pathogenic microorganisms present in the pots may induce fermentation processes that facilitate the preservation of the stored food (Gilliam *et al*. 1990; Menezes *et al*. 2013).

A further indicator for the reallocation of resources from old to new pots is the occurrence of pollen grains from non-nectar flowers in the honey pots. Plants with poricidal anthers offer only pollen as floral reward (Buchmann 1983; Dafni 1992). Also, nectar production by *Mimosa* species is an exception rather than the rule (Vogel *et al*. 2012). Consequently, the observed occurrence of pollen of these plants in the honey pots of *M. subnitida* cannot be attributed to nectar foraging but may be due to resource recycling between storage pots. An additional explanation for the occurrence of pollen from non-nectar flowers in pot-honey could be a contamination effect (Maia-Silva *et al*. 2018). Pollens of both plants with poricidal anthers and *Mimosa* species were abundant in the pot-honeys sampled in several months of our study. The incidence of these pollen types in the honey pots, particularly of pollen from poricidal flowers, trended to increase with increasing occurrence in the pollen pots (Table 1). *Melipona* nests, usually, present fewer pollen storage pots than honey pots (Alves *et al*., 2012; Nascimento and Nascimento 2012; Maia-Silva *et al*. 2016). Thus, when pollen foraging activity suddenly increases, as is the case during mass flowering or when flowers with poricidal anthers become available, pollen collectors may not find appropriate storage space and, consequently, deposit their load in any available pot. The consequence is a mixture of pollen grains from nectar and pollen plants in the pot-honey, as observed in our study.

Whereas pollen grains end up only occasionally and often accidentally in pot-honey and contribute only little to its nutritional value (Barth 2004), their proteins constitute the main nutrient of pot-pollen. Given that different-sized pollen grains contribute differently to the amount of protein available for the bees, analyzing the mere abundance of pollen grains overestimates the importance of small and abundant grains in pollen samples (Silveira 1991). Hence, for determining the relative importance of each pollen type, it is crucial to include the grain volume in the analysis of pot-pollen samples (Roubik 1989; Buchmann and O'Rourke 1991; Silveira 1991; Biesmeijer *et al*. 1992; Malagodi-Braga and Kleinert 2009). In our study, the comparison between simple pollen counts and volume-corrected abundance revealed considerable differences between these two approaches. In particular, *Senna obtusifolia* (large pollen) gained in importance as protein source. Pollen grains of this shrub with poricidal flowers had a relative abundance of 22.3% after simple pollen counts, yet accounted for 59.2% of the samples after volumetric correction. Although *S. obtusifolia* is considered an invasive species in agricultural crops, our results highlight the importance of this shrub species as key protein source for *M. subnitida.*

Our study underlines the importance of melittopalynological surveys for the elaboration of management plans for the

Table 1 Botanical origin of floral resources collected by *Melipona subnitida* in the Brazilian Tropical Dry Forest. Given are the relative abundance (H, honey; P, pollen) and the volume-corrected abundance (Q; for pollen data only) of monthly samples of pot-honey and pot-pollen collected from five colonies of *Melipona subnitida* between January and December 2012 (percentage of pooled samples). No data were available from August to November (absence of pot-honey) and in June, and September to December (absence of pot-pollen), owing to low storage in these months.

| Families | Pollen types | | Jan/12 | | Feb/12 | | Mar/12 | | Apr/12 | | May/12 | | Jun/12 | Jul/12 | | Aug/12 | Dec/12 | Total | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Stratum | H | P (Q) | H | P (Q) | H | P (Q) | H | P (Q) | H | P (Q) | H | H | P (Q) | P (Q) | H | H | P (Q) |
| Amaranthaceae | *Alternanthera tenella* Colla | Herb | 4.5 | | 1.5 | | | | | | | | | | | | | 0.8 | |
| Anacardiaceae | *Myracrodruon urundeuva* Allemão | Tree | | | | | | | 0.1 | | | | 3.0 | 5.8 | 9.6<br>(7.8) | | 5.9 | 1.2 | 1.3<br>(0.9) |
| Convolvulaceae | *Ipomoea asarifolia (*Desr.) Roem. & Schult. | Herb | | | 0.1 | | | | | | | | | | | | | 0.01 | |
| Euphorbiaceae | *Croton sonderianus* Müll.Arg. | Tree | | | 0.1 | | 1.5 | 0.2<br>(16.8) | 0.1 | 0.3<br>(13.3) | 0.1 | | 0.2 | | | | | 0.3 | 0.05<br>(1.9) |
| Fabaceae, Caesalpinioideae | *Chamaecrista* spp. | Shrub | 50.8 | 62.6<br>(70.3) | 14.2 | | 1.1 | 2.2<br>(3.7) | 4.0 | 3.8<br>(3.8) | 2.6 | 5.4<br>(3.3) | 7.0 | 22.7 | 22.4<br>(17.3) | 60<br>(53.2) | 15.3 | 13.4 | 20.8<br>(13.9) |
| | *Senna obtusifolia* (L.) H.S.Irwin & Barneby | Shrub | 0.6 | 3.3<br>(14.7) | 50.6 | 86.8<br>(98.5) | | 0.4<br>(2.6) | 0.3 | | 0.04 | 25.6<br>(61.5) | | 8.9 | 11.2<br>(34.3) | 11.5<br>(40.4) | | 7.5 | 22.3<br>(59.2) |
| Fabaceae, Mimosoideae | *Anadenanthera colubrina* (Vell.) Brenan | Tree | 0.2 | | 0.3 | | 0.1 | | 0.1 | | 0.04 | | | | | | | 0.1 | |
| | *Leucaena leucocephala* (Lam.) de Wit | Tree | | | | | | | | 1.1<br>(35.0) | | 0.9<br>(17.2) | | | | | | | 0.3<br>(5.3) |
| | *Mimosa arenosa/M. caesalpiinifolia* * | Tree | 9 | 17.85<br>(3.5) | 4.3 | 3.9<br>(0.2) | 0.5 | 17.9<br>(5.4) | 44.3 | 6.9<br>(1.2) | 23.5 | 33.8<br>(3.6) | 6.4 | 3.9 | 6.3<br>(0.8) | 22<br>(3.4) | 12.4 | 13.9 | 15.9<br>(1.9) |
| | *Mimosa quadrivalvis* L. | Herb | | 0.8<br>(3.6) | | | | | | | 1.0 | 2.1<br>(5.0) | 2.4 | 2.1 | 7.8<br>(24.0) | | | 0.6 | 1.5<br>(4.2) |
| | *Mimosa tenuiflora* (Willd.) Poir. | Tree | 2.9 | 12.3<br>(6.1) | 1.6 | 2.8<br>(0.4) | | | 0.8 | | 4.4 | 18.8<br>(5.0) | 26.5 | 23.6 | 28.3<br>(9.7) | | 8.4 | 6.9 | 10.1<br>(3.0) |
| | *Pityrocarpa moniliformis* | Tree | 28.8 | 3.2<br>(1.9) | 26.4 | 6.6<br>(1.0) | 96.7 | 78.4<br>(70.9) | 47.3 | 84.4<br>(45.1) | 60.9 | 4.3<br>(1.4) | 51.4 | 28.8 | 9.7<br>(3.9) | 6.5<br>(3.0) | 44.1 | 51.6 | 25.1<br>(8.8) |
| | *Senegalia polyphylla* (DC.) Britton & Rose | Tree | | | 0.1 | | | | | | | | | | | | | 0.01 | |
| Malvaceae, Byttnerioideae | *Waltheria* sp. | Shrub | 0.9 | | | | | | | | | | 0.2 | 0.6 | | | | 0.2 | |
| Malvaceae, Malvoideae | *Sida cordifolia* L. | Shrub | 0.1 | | | | | | | | | | | | | | | 0.01 | |
| Myrtaceae | *Eucalyptus* sp. | Tree | 0.7 | | 0.5 | | | | 0.2 | 0.8<br>(0.7) | 0.3 | 0.2<br>(0.1) | | | | | 3.6 | 0.4 | 0.1<br>(0.1) |
| | *Psidium guajava* L. | Tree | 1.7 | | 0.5 | | 0.2 | 1.1<br>(0.6) | 1.2 | 2.9<br>(1.0) | 1.5 | 1<br>(0.2) | 0.7 | 0.2 | | | 10.9 | 1.4 | 0.6<br>(0.1) |
| Rubiaceae | *Borreria verticillata* (L.) G.Mey. | Herb | 0.2 | | 0.1 | | | | 1.8 | | 5.7 | 7.9<br>(2.7) | 2.5 | 3.4 | 4.8<br>(2.1) | | | 1.8 | 2.0<br>(0.8) |

*Given that flowering of the tree species *M. arenosa* and *M. caesalpiniifolia* occurred simultaneously and due to the high similarity between the pollen types, it was impossible to separate these two species in the samples. We, therefore, referred to these pollen samples as *M. arenosa/M. caesalpiniifolia*.

conservation of native pollinator populations. In the Brazilian Tropical Dry Forest, just as in most other terrestrial ecosystems, social bees are important pollinators of native plants and agricultural crops (Aguiar 2003; Freitas and Bomfim 2017). In addition, some of them, including *M. subnitida*, are traditionally used for honey production by local beekeepers, providing an extra income for rural communities (Jaffé *et al*. 2015). Thus, declines of bee populations associated with habitat destruction and regional climate changes predicted for the coming decades may have severe ecologic and socioeconomic consequences (Potts *et al*. 2016; Giannini *et al*. 2017). Melittopalynological studies are a helpful tool to indicate suitable plant species for habitat restoration and habitat improvement programs aiming at the conservation of native bee biodiversity and the increase of productivity of local meliponiculture. Especially in semiarid regions, the use of native flora, which is adapted to the challenging ambient conditions, is crucial for the success of restoration programs. Our results highlight the contribution of native species of all plant strata (trees, shrubs, and herbaceous species) for the diet of *M. subnitida* colonies. Of particular importance are profitable food sources, such as mass-flowering plants or species with poricidal flowers, and species that bloom in the dry season. From our results, we strongly recommend the following plant species for composing suitable foraging areas of *M. subnitida*: (1) mass-flowering in the dry season: *A. colubrina*, *M. urundeuva*; (2) mass-flowering in the rainy season: *C. sonderianus*, *M. arenosa*, *M. caesalpiinifolia*, *P. moniliformis*, and *S. polyphylla*; (3) mass-flowering in the transition between rainy and dry season: *M. tenuiflora*; (4) flowers with poricidal anthers: *Chamaecrista* spp. and *S. obtusifolia*. These plants could be used in areas of habitat restoration and habitat improvement to increase the success of conservation programs for native bee populations and, also, to improve the productivity of stingless beekeeping.

**Acknowledgments** This study was financially supported by scholarships of the Brazilian Ministry of Education (CAPES) to AACL and CMS as well as grants of the Brazilian Ministry of Education to MH (CAPES: 3168/2013) and the National Council for Scientific and Technological Development to VLIF (CNPq: 482218/2010-0, 406102/2013-9) and to MH (CNPq: 304722/2010-3, 309914/2013-2, 404156/2013-4).

**Author Contribution** All authors contributed to the study conception and design. Material preparation and data collection were performed by Camila Maia-Silva and Amanda Aparecida Castro Limão. Data were analyzed by Camila Maia-Silva, Amanda Aparecida Castro Limão, Cláudia Inês da Silva, and Michael Hrncir. The first draft of the manuscript was written by Camila Maia Silva and Michael Hrncir, and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

**Compliance with ethical standards** This study complies with current Brazilian laws.

## References

Aguiar CML (2003) Utilização de recursos florais por abelhas (Hymenoptera, Apoidea) em uma área de Caatinga (Itatim, Bahia, Brasil). Rev Bras Zool 20:457–467. https://doi.org/10.1590/S0101-81752003000300015

Albuquerque UP, Araújo EL, El-Deir ACA, Lima ALA, Souto A, Bezerra BM, Ferraz EMN, Freire EMX, Sampaio EVSB, Las-Casas FMG, Moura GJB, Pereira GA, Melo JG, Ramos MA, Rodal MJN, Schiel N, Lyra-Neves RM, Alves RRN, Azevedo-Júnior SM, Telino Júnior WR, Severi W (2012, 2012, 2012) Caatinga revisited: ecology and conservation of an important seasonal dry forest. Sci World J:205182. https://doi.org/10.1100/2012/205182

Alves RMO, Carvalho CAL, Faquinello P, Ledo CAS, Figueredo L (2012) Parâmetros biométricos e produtivos de colônias de Melipona scutellaris Latreille, 1811 (Hymenoptera: Apidae) em diferentes gerações. Magistra 24:105–111. https://doi.org/10.13140/RG.2.1.2447.9768

Andrade EM, Aquino DN, Chaves LCG, Lopes FB (2017) Water as capital and its uses in the Caatinga. In: Silva JMC, Leal IR, Tabarelli M (eds) Caatinga – the largest tropical dry forest region in South America. Springer International Publishing, Cham, pp 281–302

Araújo EL, Castro CCC, Albuquerque UP (2007) Dynamics of Brazilian Caatinga – a review concerning the plants, environment and people. Funct Ecosyst Commun 1:15–28

Barth OM (2004) Melissopalynology in Brazil: a review of pollen analysis of honeys, propolis and pollen loads of bees. Sci Agric 61:342–350. https://doi.org/10.1590/S0103-90162004000300018

Biesmeijer JC, van Marwijk B, van Deursen K, Punt W, Sommeijer MJ (1992) Pollen sources for *Apis mellifera* L (Hym, Apidae) in Surinam, based on pollen grain volume estimates. Apidologie 23:245–256. https://doi.org/10.1051/apido:19920308

Buchmann SL (1983) Buzz pollination in angiosperms. In: Jones CE, Little RJ (eds) Handbook of experimental pollination biology. Van Nostrand Reinhold, New York, pp 73–113

Buchmann SL, O'Rourke MK (1991) Importance of pollen grain volumes for calculating bee diets. Grana 30:591–595. https://doi.org/10.1080/00173139109427817

Dafni A (1992) Pollination ecology: a practical approach. Oxford University Press, Oxford, p 250

Erdtman G (1960) The acetolized method – a revised description. Sven Bot Tidskr 54:561–564

Espínola Sobinho J, Pereira VC, Oliveira AD, Santos WO, Silva NKC, Maniçoba RM (2011) Climatologia da precipitação no município de Mossoró - RN. Período: 1900-2010. In: Anais do XVII. Congresso Brasileiro de Agrometeorologia, Guarapari

Freitas BM, Bomfim IGA (2017) Meliponíneos e polinização: a abelha jandaíra e outros meliponíneos na polinização agrícola no semiárido. In: Imperatriz-Fonseca VL, Koedam D, Hrncir M (eds) A abelha jandaíra no passado, presente e futuro. Editora Universitária UFERSA, Mossoró, pp 213–226

Giannini TC, Maia-Silva C, Acosta AL, Jaffé R, Carvalho AT, Martins CF, Zanella FCV, Carvalho CAL, Hrncir M, Saraiva AM, Siqueira JA, Imperatriz-Fonseca VL (2017) Protecting a managed bee pollinator against climate change: strategies for an area with extreme climatic conditions and socioeconomic vulnerability. Apidologie 48:784–794. https://doi.org/10.1007/s13592-017-0523-5

Gilliam M, Roubik DW, Lorenz BJ (1990) Microorganisms associated with pollen, honey, and brood provisions in the nest of a stingless bee, *Melipona fasciata*. Apidologie 21:89–97. https://doi.org/10.1051/apido:19900201

Hrncir M, Maia-Silva C (2013) On the diversity of foraging-related traits in stingless bees. In P. Vit P, S. R. M. Pedro SRM, and D. W. Roubik DW (eds). Pot honey: a legacy of stingless bees. Springer, New York, pp 201–215

Hrncir M, Maia-Silva C, Teixeira-Souza VHS, Imperatriz-Fonseca VL (2019) Stingless bees and their adaptations to extreme environments. J Comp Physiol A 205:415–426. https://doi.org/10.1007/s00359-019-01327-3

Jaffé R, Pope N, Carvalho AT, Maia UM, Blochtein B, Carvalho CAL, Carvalho-Zilse GA, Freitas BM, Menezes C, Ribeiro MF, Venturieri GC, Imperatriz-Fonseca VL (2015) Bees for development: Brazilian survey reveals how to optimize stingless beekeeping. PLoS One 10: e0121157. https://doi.org/10.1371/journal.pone.0121157

Maia-Silva C, Imperatriz-Fonseca VL, Silva CI, Hrncir M (2014) Environmental windows for foraging activity in stingless bees, *Melipona subnitida* Ducke and *Melipona quadrifasciata* Lepeletier (Hymenoptera: Apidae: Meliponini). Sociobiology 61:378–385. https://doi.org/10.13102/sociobiology.v61i4.378-385

Maia-Silva C, Hrncir M, Silva CI, Imperatriz-Fonseca VL (2015) Survival strategies of stingless bees (*Melipona subnitida*) in an unpredictable environment, the Brazilian tropical dry forest. Apidologie 46:631–643. https://doi.org/10.1007/s13592-015-0354-1

Maia-Silva C, Hrncir M, Imperatriz-Fonseca VL, Schorkopf DLP (2016) Stingless bees (*Melipona subnitida*) adjust brood production rather than foraging activity in response to changes in pollen stores. J Comp Physiol A 202:723–732. https://doi.org/10.1007/s00359-016-1095-y

Maia-Silva C, Limão AAC, Hrncir M, Pereira JS, Imperatriz-Fonseca VL (2018) The contribution of palynological surveys to stingless bee conservation: a case study with *Melipona subnitida*. In: Vit P, Pedro SRM, Roubik DW (eds) Pot-pollen stingless bee melittology. Springer International Publishing, Cham, pp 89–101

Malagodi-Braga KS, Kleinert AMP (2009) Comparative analysis of two sampling techniques for pollen gathered by *Nannotrigona testaceicornis* Lepeletier (Apidae, Meliponini). Genet Mol Res 8: 596–606. https://doi.org/10.4238/vol8-2kerr014

Marengo JA, Torres RR, Alves LM (2017) Drought in Northeast Brazil – past, present, and future. Theor Appl Climatol 129:1189–1200. https://doi.org/10.1007/s00704-016-1840-8

Menezes C, Vollet-Neto A, Contrera FAL, Venturieri GC, Imperatriz-Fonseca VL (2013) The role of useful microorganisms to stingless bees and stingless beekeeping. In: Vit P, Pedro SRM, Roubik DW (eds) Pot honey: a legacy of stingless bees. Springer, New York, pp 153–171

Michener CD (1974) The social behavior of the bees – a comparative study. Harvard University Press, Cambridge, p 404

Moro MF, Lughadha EN, Filer DL, Araújo FS, Martins FR (2014) A catalogue of the vascular plants of the Caatinga phytogeographical domain: a synthesis of floristic and phytosociological surveys. Phytotaxa 160:1–118. https://doi.org/10.11646/phytotaxa.160.1.1

Nascimento DL, Nascimento FS (2012) Extreme effects of season on the foraging activities and colony productivity of a stingless bee (*Melipona asilvai* Moure, 1971) in northeast Brazil. Psyche 2012(267361):6. https://doi.org/10.1155/2012/267361

Potts SG, Imperatriz-Fonseca VL, Ngo HT, Aizen MA, Biesmeijer JC, Breeze TD, Dicks LV, Garibaldi LA, Hill R, Settele J, Vanbergen AJ (2016) Safeguarding pollinators and their values to human well-being. Nature 540:220–229. https://doi.org/10.1038/nature20588

Prado D (2003) As Caatingas da América do Sul. In: Leal IR, Tabarelli M, Silva JMC (eds) Ecologia e Conservação da Caatinga. Editora Universitária UFPE, Recife, pp 3–73

Quirino Z, Machado I (2014) Pollination syndromes in a Caatinga plant community in northeastern Brazil: seasonal availability of floral resources in different plant growth habits. Braz J Biol 74:62–71. https://doi.org/10.1590/1519-6984.17212

Ramalho M (2004) Stingless bees and mass flowering trees in the canopy of Atlantic Forest: a tight relationship. Acta Bot Bras 18:37–47. https://doi.org/10.1590/S0102-33062004000100005

Reis AMS, Araújo EL, Ferraz EMN, Moura AN (2006) Inter-annual variations in the floristic and population structure of an herbaceous community of "caatinga" vegetation in Pernambuco, Brazil. Braz J Bot 29: 497–508. https://doi.org/10.1590/S0100-84042006000300017

Roubik DW (1989) Ecology and natural history of tropical bees. Cambridge University Press, Cambridge, p 514

Salimon C, Anderson L (2018) How strong is the relationship between rainfall variability and Caatinga productivity? A case study under a changing climate. An Acad Bras Cienc 90:2121–2127. https://doi.org/10.1590/0001-3765201720170143

Santos JMFF, Santos DM, Lopes CGR, Silva KA, Sampaio EV, Araújo EL (2013) Natural regeneration of the herbaceous community in a semi-arid region in northeastern Brazil. Environ Monit Assess 185:8287–8302. https://doi.org/10.1007/s10661-013-3173-8

Silveira F (1991) Influence of pollen grain volume the estimation of the relative importance of its source to bees. Apidologie 22:495–502. https://doi.org/10.1051/apido:19910502

Vasconcellos A, Andreazze R, Almeida AM, Araujo HFP, Oliveira ES, Oliveira U (2010) Seasonality of insects in the semi-arid Caatinga of northeastern Brazil. Rev Bras Entomol 54:471–476. https://doi.org/10.1590/S0085-56262010000300019

Vogel S, Lopes AV, Cristina I (2012) Bat pollination in the NE Brazilian endemic *Mimosa lewisii*: an unusual case and first report for the genus. Taxon 54:693–700. https://doi.org/10.2307/25065426

Wilms W, Imperatriz-Fonseca VL, Engels W (1996) Resource partitioning between highly eusocial bees and possible impact of the introduced Africanized honey bee on native stingless bees in the Brazilian Atlantic rainforest. Stud Neotropical Fauna Environ 31:137–151. https://doi.org/10.1076/snfe.31.3.137.13336

Zanella FCV (2000) The bees of the Caatinga (Hymenoptera, Apoidea, Apiformes): a species list and comparative notes regarding their distribution. Apidologie 31:579–592. https://doi.org/10.1051/apido:2000148

Zanella FCV, Martins CF (2003) Abelhas da caatinga: biogeografia, ecologia e conservação. In: Tabarelli M, Silva JMC (eds) Leal IR. Ecologia e Conservação da Caatinga Editora Universitária UFPE, Recife, pp 75–134