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Species richness and activity pattern of bees (Hymenoptera, Apidae) in the restinga area of Lençóis Maranhenses National Park, Barreirinhas, Maranhão, Brazil

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ABSTRACT

The Apidae community structure was studied in a vegetated area of coastal dunes in Lençóis Maranhenses National Park. Collections were performed monthly from August 2009 to July 2010. The collection methods included the use of entomological nets on flowers and Moerike traps. In total, 1211 individuals belonging to 59 species were collected. The pattern of abundance and richness was similar to those found in Maranhão and other coastal areas of northeastern Brazil. The bees were present throughout the year, with an increase in the number of individuals during the rainy season. Constant and dominant species included *Trigona* sp. gr. *fulviventris*, *Apis mellifera*, *Plebeia alvarengai*, *Centris aenea*, *Xylocopa cearensis*, and *Centris caxiensis*.

Introduction

The exuberance and uniqueness of the landscape of Lençóis Maranhenses National Park (Parque Nacional dos Lençóis Maranhenses – PNLM), represented by dune fields surrounded by lakes, beaches, mangroves, and restingas (sandy coastal plains) and the high level of local biodiversity justified the creation of the Protected Area of PNLM in 1981 (Silva and Silva Filho, 2008). To improve the understanding of this ecosystem, species inventories have been performed at PNLM. Among the bees, several species of *Centris* and *Euglossa* were recorded using trap nests (Ramos et al., 2006). A more complete list of 14 of species of orchid bees (*Euglossa*, *Eulaema*, and *Eufriesea*) was obtained by baiting with aromatic fragrances (Silva et al., 2009). In a case study of murici pollinators (*Byrsonima crassifolia* (L.) Rich, Malpighiaceae), 21 species of Centridini were identified (Rêgo et al., 2006). Although these studies yielded first assessments of some species rich bee taxa, the knowledge regarding the bee species remained fragmentary because of the selectivity of the sampling methods used.

Sakagami et al. (1967) proposed the standardization of sampling, with the collection of bees on flowers using entomological nets, thus providing data on local diversity, relative abundance, habitat preference, and associated plants. This method allows comparisons among various ecosystems, enabling easier to compare patterns in the structure of bee communities in the Neotropical region (Aguiar and Zanella, 2005). Other methods of collecting bees are scent baiting, which is typically aimed at attracting Euglossini males (Nemésio and Silveira, 2007), the use of trap nests (Gazola and Garófalo, 2009), and more recently, sampling with coloured trays and bowls (Gonçalves and Oliveira, 2013). Without the use of complementary methods, 20% or 8% of the bee species would not have been recorded in recent inventories in Santa Catarina in southern Brazil (Krug and Alves-dos-Santos, 2008; Kamke et al., 2011, respectively).

As reported by Viana and Kleinert (2005), despite the variety of methods, little is known regarding the bee fauna of the coastal ecosystems of Brazil. Most surveys of bees in restinga areas have focussed on the southern region of the country, including studies in Paraná (Laroca, 1974; Zanella, 1991; Schwartz-Filho and Laroca, 1999), Santa Catarina (Mouga, 2004; Kamke et al., 2011), and Rio Grande do Sul (Alves-dos-Santos, 1999). Among the studies conducted in the northeastern region, we can cite Viana and Kleinert (2005), Silva et al. (2015) and Moreira et al. (2016) in Bahia and

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Madeira-da-Silva and Martins (2003) in Paraíba. Gottsberger et al. (1988) studied pollinating bees in the dune vegetation on São Luís Island (northern Brazil) and found that nine out of the 10 plant species studied were melittophilous, and in spite of the adverse conditions and the strong wind, 18 bee species were reported as flower visitors. In addition, the studies of Albuquerque (1998) and Oliveira et al. (2010) were conducted at the same location and resulted in inventories of 36 and 31 bee species, respectively.

The present study aims to evaluate, using different sampling methods, the species richness, and diversity of bees in PNLM to describe their activity pattern, and to compare the similarities with other coastal environments of northeastern Brazil.

Material and methods

Study area

This study was conducted in a restinga area measuring 200 ha located at the edge of PNLM in the municipality of Barreirinhas (2°43′22.5″ S–42°49′50″ W), Maranhão, Brazil. According to the Köppen (1948) classification, the regional climate is the Aw type, which is a tropical climate with high temperatures and two well-defined seasons, dry (July–December) and rainy (January–June), with approximately 1800 mm of rainfall (Maranhão, 2002).

The PNLM vegetation covers an area of 453.28 km^2, 405.16 km^2 (89%) of which are classified as restinga. There are also mangroves, riparian forests, and cerrados that cover a small portion of the total area (Ibama, 2003). According to studies conducted through the PNLM Management Plan (Ibama, 2003), the restinga of this region is composed of melittophilous plants that belong to the families Lythraceae, Malpighiaceae, Turneraceae, Asteraceae, and Ochnaceae.

Sampling

The collections were performed by two collectors at an interval of 25–30 days over 12 months (August 2009–July 2010) on two consecutive days: from 12:00 to 18:00 h on the first day and from 6:00 to 12:00 h on the second day, for a total of 288 h of sampling. The bees were collected in entomological nets (while the insects were either flying or visiting flowers) using the methodology of Sakagami et al. (1967). To sample 45,000 m^2, a 450 m transect was walked at a slow pace by the two collectors simultaneously, and each bee that was observed feeding on a flower within a 50 m strip on each side of the observers was collected.

In addition, bowl traps (Moerike traps, 15 cm wide, 5 cm high, 300 ml of water and drops of dishwashing) were used simultaneously (Grundel et al., 2011). Bowls had different colours (yellow, blue, green, or white) and were deployed monthly for 48 h, for a total of 576 h of sampling (in 10 groups of four bowls each) in the same area where bees were netted. The bowls were placed on the ground (five groups) or on poles (1 m high, five groups) at 5 m intervals with interspersed colours. The collected insects were preserved and stored in 70% ethanol.

The bees were mounted on pins and deposited in the Bee Collection of the Laboratory of Bee Studies (LEACOL/Universidade Federal do Maranhão – UFMA). They were identified to the morphospecies level with the aid of taxonomic keys (Silveira et al., 2002), and to species level by comparison with the reference collection, and with the assistance of taxonomists. Moreover, were used Moure et al. (2012a,b) to confirm the distribution of species. To compare these data with those of previous studies, we considered corbiculate (Apini, Meliponini, and Euglossini) and non-corbiculate Apinae (as analysed by Gonçalves and Melo, 2005; Milet-Pinheiro and Schlindwein, 2008).

Temperature and air humidity data were obtained from the Geoenvironmental Centre of Maranhão State University, using the Urbano Santos station located approximately 85 km from the collection site. The Weather Forecasts and Climate Studies Centre in the Northeast Region (CPTEC, 2010) provided rainfall data.

Data analysis

The Shannon–Wiener index was applied to calculate the species diversity, and Pielou's index was used to calculate the area equitability. The calculations were performed using PAST (Paleontological Statistics 2.00) (Hammer et al., 2001).

For each species sampled by netting, the dominance (*D*) and constancy (*C*) were calculated according to Bodenheimer (1955). For dominance, $D = (\text{abundance of species } i/\text{total abundance}) \times 100$. If $D > 5\%$, then the species was considered dominant (*D*); if $2.5\% < D < 5\%$, then the species was considered accessory (*A*); and if $D < 2.4\%$, then the species was considered occasional (OC).

Constancy is the percentage of individuals present, calculated as $C = P \times 100/N$, where *P* is the number of samples containing the species, and *N* is the total number of samples. The bees collected in 12 h of netting per month were considered one sample. If $C > 50\%$, then the species was considered constant (*W*); if $25\% < C < 50\%$, then the species was considered accessory (*Y*); and if $C < 25\%$, then the species was considered accidental (*Z*) (Silveira-Neto et al., 1976).

The Morisita index was applied to analyse the similarity with bee communities equivalent to the restinga of PNLM, such as the restinga of Cabedelo, Paraíba (Madeira-da-Silva and Martins, 2003), Abaeté dunes and Salvador, Bahia (Viana and Kleinert, 2005; Silva et al., 2015), Panaquatira beach (São José de Ribamar), Maranhão (Oliveira et al., 2010), and São Marcos beach (São Luís), Maranhão (Albuquerque, 1998), using PAST. The Morisita index was only applied to the bee species collected with nets, the primary collecting method used in those studies.

To determine the representativeness of the community sampled with both methods, a species accumulation curve (collector curve) as well as richness estimators Chao 1 and Jackknife 1 were generated using BioDiversity Pro Version 2 (Mcaleece et al., 1997).

Results

Species richness and diversity

A total of 1211 individuals belonging to 59 species of the Apoidea were collected using entomological nets and bowl traps in the restinga of the PNLM (Tables 1 and 2). The descending order of richness per subfamily was as follows: non-corbiculate Apinae (24 spp.) > Megachilinae (14 spp.) > corbiculate Apinae (13 spp.) > Halictinae (6 spp.) > Andreninae (2 spp.). The abundance per subfamily was as follows: corbiculate Apinae (644 individuals) > non-corbiculate Apinae (384 ind.) > Andreninae (133 ind.) > Megachilinae (33 ind.) > Halictinae (17 ind.).

The tribe Megachilini contained 20% of the species, followed by Centridini (18%), Xylocopini (17%), Meliponini (12%), and Euglossini (8%). The most species rich genera were *Megachile* (12 spp.), *Centris* (10 spp.), *Ceratina*, *Xylocopa* (5 spp. each), and *Dialictus* (3 spp.) (Table 1). Eleven bee species were obtained only through bowl traps. The subfamily Andreninae, represented by *Callonychium (Callonychium) brasiliense* (Ducke, 1907) and *C. (Callonychium)* sp., were exclusively collected with this method and represented 60.5% of the individuals collected in the bowl traps. A total of 218 bees of 19 species were collected with bowl traps. In the blue bowls all 19 species and 56.4% of the individuals were captured (Table 1).

Table 1
Composition and number of bees (Hymenoptera, Apidae) of the restinga area of the PNLM captured by different methods. Sampling methods: nets (entomological nets) and bowl traps (Ye: yellow, Wh: white, Bl: blue, Gr: green) were used in this study; chemical baits, trap nests (number of emerging individuals) and *Byrsonima crassifolia* flower visitors (number of bee specimens collected at) were used in other surveys in the same study area.

Species	Net	Bowl traps				Chemical baits Silva et al. (2009)	Trap nest Ramos et al. (2006)	Murici visitors Rêgo et al. (2006)
		Ye	Wh	Bl	Gr			
Andreninae – Calliopsini								
Callonychium (Callonychium) brasiliense (Ducke, 1907)		27	26	52	1			
Callonychium (Callonychium) sp.			11	16				
Apinae – Apini								
Apis mellifera Linnaeus, 1758	170	1		1				1
Apinae – Euglossini								
Eufriesea nigrescens (Friese, 1923)						85		
Eufriesea ornata (Mocsáry, 1896)						56		
Eufriesea sp. 1	1							
Eufriesea sp. 2	1							
Eufriesea superba (Hoffmannesegg, 1817)						3		
Eufriesea surinamensis (Linnaeus, 1758)						16		
Euglossa (Euglossa) cordata Linnaeus, 1758	1					88	18	
Euglossa (Euglossa) fimbriata Moure, 1968						1		
Euglossa (Euglossa) gaianii Dressler, 1982						1	17	
Euglossa (Euglossa) liopoda Dressler, 1982						1		
Euglossa (Euglossa) melanotricha Moure, 1967						1		
Euglossa (Euglossa) modestior Dressler, 1982						19		
Euglossa (Glossura) chalybeata Friese, 1925						3		
Euglossa sp.	1							
Eulaema (Apeulaema) cingulata (Fabricius, 1804)						105		
Eulaema (Apeulaema) nigrita Lepeletier, 1841	1					49		
Eulaema (Eulaema) meriana (Olivier, 1789)						1		
Apinae – Meliponini								
Melipona (Melipona) subnitida Ducke, 1910	8							
Melipona (Michmelia) aff. *rufiventris* Lepeletier, 1836	8							
Partamona seridoensis Pedro and Camargo, 2003	21							
Plebeia minima (Gribodo, 1893)								8
Plebeia alvarengai Moure, 1994	61	1		2				
Tetragona sp.				1				
Trigona sp. gr. *fulviventris* Guérin, 1835	333			1				21
Trigonisca extrema Albuquerque and Camargo, 2007	22	1	2	4	2			11
Trigonisca pediculana (Fabricius, 1804)								4
Apinae – Anthophorini								
Anthophora sp.	4							
Apinae – Centridini								
Centris (Centris) aenea Lepeletier, 1841	78							
Centris (Centris) caxiensis Ducke, 1907	96							366
Centris (Centris) byrsonimae Mahlmann and Oliveira, 2012	20							
Centris (Centris) flavifrons (Fabricius, 1775)	3							22
Centris (Centris) decolorata Lepeletier, 1841								16
Centris (Centris) spilopoda Moure, 1969								3
Centris (Hemisiella) trigonoides Lepeletier, 1841	8							
Centris (Hemisiella) tarsata Smith, 1874							39	368
Centris (Melacentris) obsoleta Lepeletier, 1841	4							110
Centris (Ptilotopus) sponsa Smith, 1854	1							4
Centris (Trachina) longimana Fabricius, 1804								7
Centris (Xanthemisia) lutea Friese, 1899	1							
Centris (Xanthemisia) bicolor Lepeletier, 1841								1
Centris sp. 1	6							
Centris sp. 2								133
Epicharis (Epicharis) bicolor Smith, 1874								9
Epicharis (Epicharis) aff. *umbraculata* (Fabricius, 1804)	3							131
Apinae – Eucerini								
Florilegus (Florilegus) cf. *condignus* (Cresson, 1878)	1							
Exomalopsini								
Exomalopsis sp.								1
Apinae – Nomadini								
Odyneropsis sp.	4							
Apinae – Tapinotaspidini								
Paratetrapedia flavipennis (Smith, 1879)	2							
Xanthopedia globulosa (Friese, 1899)								67
Tropidopedia punctifrons (Smith, 1879)								72
Apinae – Xylocopini								
Ceratina (Ceratinula) sp.			3	9	1			
Ceratina (Ceratinula) sp. 1	2							
Ceratina (Ceratinula) sp. 2	6	1		1				
Ceratina (Crewella) maculifrons Smith, 1854	13							
Ceratina (Crewella) sp.	1		9	21				
Xylocopa (Neoxylocopa) carbonaria Smith, 1854	14							

Table 1
(*Continued*)

Species	Net	Bowl traps				Chemical baits Silva et al. (2009)	Trap nest Ramos et al. (2006)	Murici visitors Rêgo et al. (2006)
		Ye	Wh	Bl	Gr			
Xylocopa (Neoxylocopa) cearensis Ducke, 1910	64			1				
Xylocopa (Neoxylocopa) frontalis (Olivier, 1789)	1							
Xylocopa (Neoxylocopa) suspecta Moure and Camargo, 1988	5							
Xylocopa (Schonnherria) muscaria (Fabricius, 1775)	1							
Halictinae – Augochlorini								
Augochlora sp.	1							
Augochlorella sp.				1				
Augochloropsis sp.								1
Augochloropsis sp. 1								1
Pseudaugochlora pandora (Smith, 1853)	1							
Halictinae – Halictini								
Dialictus sp. 1	3	1	1	6	1			
Dialictus sp. 2	1							
Dialictus sp. 3	1							
Megachilinae – Anthidiini								
Dicranthidium sp.							25	3
Epanthidium tigrinum (Schrottky, 1905)	3							
Saranthidium sp.	1							
Megachilinae – Megachilini								
Megachile (Pseudocentron) sp.	5							
Megachile (Pseudocentron) inscita Mitchell, 1930	3							
Megachile (Pseudocentron) cf. *terrestris* Schrottky, 1902	3							
Megachile sp. 1	1						30	
Megachile sp. 2	1							
Megachile sp. 3	1							
Megachile sp. 4				1				
Megachile sp. 5				2				
Megachile sp. 6			1	1				
Megachile sp. 7				2				
Megachile sp. 8			4	1				
Megachile sp. 9			1	2				
Total specimens	991	32	58	125	5	429	129	1360
Total species	48	6	9	19	4	14	5	23

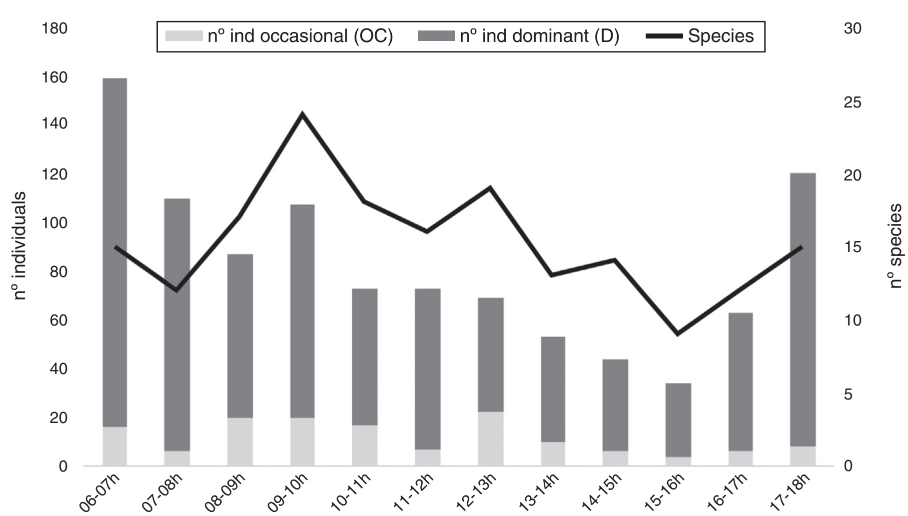

Fig. 1. Number of species netted and individuals recorded from August 2009 to 2010 of the restinga of the PNLM, Barreirinhas, MA, Brazil.

Activity pattern

The highest number of individuals was collected in the morning, between 6:00 and 10:00 h. This number gradually decreased throughout the day reaching a new peak of capture at 17:00 h, when the highest relative humidity and the lowest temperatures were recorded (Fig. 1). There was a positive correlation ($p > 0.05$) between temperature, relative humidity and abundance of individuals per hour of the day.

Bees were captured in all months of the year, with a decline in abundance between August 2009 and March 2010 (Table 2), which is the period that corresponds to the lowest precipitation amount (the entire dry season and the beginning of the rainy season). Between April and July, there was a peak in abundance coinciding with the rainy season. The months of August and September had the greatest species richness, coinciding with the beginning of the dry season (Table 2). According to the annual distribution, the following species were considered constant (W): *Trigona* sp. gr. *fulviventris*

Table 2
The most frequent species of Apidae captured with net and bowl traps in the restinga of the PNLM in Maranhão, Brazil, from August 2009 to July 2010.

Species	A	S	O	N	D	J	F	M	A	M	J	J	Total	Class	
														Constancy[a]	Dominance[b]
Trigona sp. gr. *fulviventris* Guérin, 1835	32	6	3	11	18	35	29	16	39	42	31	72	334	100.0 W	36.53 D
Apis mellifera Linnaeus, 1758	2	8	37	6	2	7	8	9	22	16	55		172	91.66 W	17.11 D
Callonychium (Callonychium) brasiliense (Ducke, 1907)	15	1					1	1	28	11	2	52	111	66.4 W	9.16 D
Centris (Centris) caxiensis Ducke, 1907	5	4	1	2	4	4	22	9	6	10	14	15	96	100.00 W	9.69 D
Centris (Centris) aenea Lepeletier, 1841	30	20	10	15	2		1						78	50.00 W	7.87 D
Xylocopa (Neoxylocopa) cearensis Ducke, 1910	3	2	1	4	3		15	5	11	6	6	9	65	91.66 W	6.44 D
Plebeia alvarengai Moure, 1994		1	2	2	12	3	4	1	17	14	4	4	64	91.66 W	6.14 D
Trigonisca extrema Albuquerque and Camargo, 2007		2	2	15			1			4	7		31	41.66 Y	2.21 OC
Ceratina (Crewella) sp.	1	4	3	5	5			3	1			8	30	66.4 W	2.47 OC
Callonychium (Callonychium) sp.	4	1				15			7				27	33.32 Y	2.22 OC
Partamona seridoensis Pedro and Camargo, 2003			3	14	1	1			2				21	41.66 Y	2.11 OC
Centris (Centris) byrsonimae Mahlmann and Oliveira, 2012	3	14		1	1		1						20	41.66 Y	2.0 OC
Xylocopa (Neoxylocopa) carbonaria Smith, 1854					2	2			10				14	25.00 Z	1.4 OC
Ceratina (Ceratinula) sp.		1	1	2		2		1	1	1	2	3	14	74.97 W	1.15 OC
Ceratina (Crewella) maculifrons Smith, 1854		1				2		2	3	1	3	1	13	50.00 Y	1.3 OC
Dialictus sp. 1	3	3										6	12	24.9 Z	0.9 OC
Others species	17	13	13	1	8	4	1	5	11	6	12	18	109		
Total of specimens	115	81	76	78	58	75	83	52	158	111	136	188	1211		
Total of species	20	20	16	12	14	12	10	15	15	16	16	18	59		

[a] Constancy (*C*): *W* = constant: *C* > 50%; *Y* = accessory: *C* > 25% and <50%; *Z* = accidental: *C* < 25%.
[b] Dominance (*D*): *D* = dominant: *D* > 5%; *A* = accessory: *D* > 2.5% and <5%; OC = occasional: (*D*) < 2.4%.

and *C. caxiensis* (captured in all sampling months), *Apis mellifera*, *X. cearensis*, and *Plebeia alvarengai* (captured in 11 months), *Callonychium brasiliense* (8 months) and *C. aenea* (6 months) (Table 2). Of the other species 65.3% were classified as accidental and 20.4% as accessory.

Only five species were classified as Dominant, and they represented 74.7% of the individuals collected by netting, all of which belonged to the Apinae (*A. mellifera*, *P. alvarengai, T.* sp. gr. *fulviventris, C. caxiensis*, *C. aenea*, *C. brasiliense*, and *X. cearensis*) (Table 3).

The species rarefaction curve showed a tendency to asymptote; however, it continued to increase throughout the months of collection (Fig. 2). Because of the non-stabilization of the accumulation curve, we used non-parametric total richness estimators, which ranged from 89 (Jackknife 1) to 163 species (Chao 1) for the 12 collection months for both methods (entomological nets and bowl traps). These indices suggest that between 67.41% and 36.8% of the bee fauna at the site were sampled using these two collection methods.

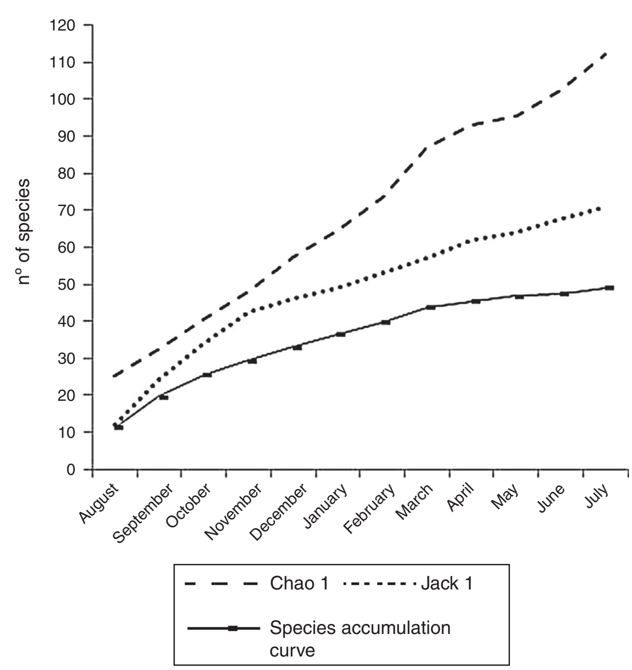

Fig. 2. Species accumulation curve (collector curve) and curves of species richness estimators Chao 1 and Jackknife 1 for the bees collected by netting and bowl traps in the restinga of PNLM, Barreirinhas, MA, Brazil, from August 2009 to July 2010.

Bees in restinga areas in northeastern Brazil

Based on other studies conducted in the same area using other collection methods, the total restinga bee fauna of the PNLM comprises 86 species in 30 genera. From that total, 43% of the species would not have been collected if only nets had been used. Overall, 32 species were collected only with nets, 11 species were exclusive to the bowl traps, 11 Euglossini species were captured only with aromatic baits, 12 species were collected only on murici flower (Table 3).

According to other bees of research conducted in restinga areas of northeastern Brazil, network collection obtained representatives of 50 genera for several restingas (Table 3). Of these genera more than 50% were recorded in Salvador and PNLM, 40% were present in Abaeté, São Marcos and Cabedelo, and only 27% were recorded in Panaquatira. The total bee diversity is very similar among these areas, with only Panaquatira having slightly lower diversity (Table 3). However, differences exist among the subfamilies. For Apinae, the number of species is the same between Salvador

Table 3
Number of species per genus of bees collected in the restinga in northeastern Brazil: Abaete (Viana and Kleinert, 2005), Salvador (Silva et al., 2015), Cabedelo (Madeira-da-Silva and Martins, 2003), S. Marcos beach (Albuquerque, 1998), Panaquatira beach (Oliveira et al., 2010) and PNLM (present study). Sub-totals in the first column indicate the number of genera; sub-totals for each site indicate the number of species and, in brackets, of genera.

Taxon	Abaete/BA	Salvador/BA	Cabedelo/PB	S. Marcos/MA	Panaquatira/MA	PNLM/MA nets	PNLM/MA Total[a]
ANDRENINAE							
Acamptopoeum				1			
Oxaea		2		1	1		
Protomeliturga			1	1			
Callonychium							2
***Sub-total* (4)(3[b])**	**0 (0)**	**2 (1)**	**1 (1)**	**3 (3)**	**1 (1)**	**0 (0)**	**2 (1)**
COLLETINAE							
Chilicola	1						
Colletes	1						
Hylaeus		2	1				
***Sub-total* (3)**	**2 (2)**	**2 (1)**	**1 (1)**	**0 (0)**	**0 (0)**	**0 (0)**	**0 (0)**
HALICTINAE							
Augochlora	2	2	2			1	1
Augochlorella				1			1
Augochloropsis	2	1	1				2
Dialictus	1	2	1			3	3
Pseudaugochlora	1	1		1	1	1	1
***Sub-total* (5)**	**6 (4)**	**6 (4)**	**4 (3)**	**2 (2)**	**1 (1)**	**5 (3)**	**8 (5)**
MEGACHILINAE							
Dicranthidium	2	1		1			1
Epanthidium			1			1	1
Hypanthidium			1				
Larocanthidium			1				
Megachile	3	5	2	5	2	6	12
Saranthidium						1	1
***Sub-total* (6)**	**5 (2)**	**6 (2)**	**5 (4)**	**6 (2)**	**2 (1)**	**8 (3)**	**15 (4)**
APINAE							
Acanthopus		1			1		
Ancyloscelis				1	2		
Anthophora						1	1
Apis	1	1	1	1	1	1	1
Bombus	1	1					
Centris	12	13	10	7	14	10	15
Ceratina	2	1	4	4		4	5
Diadasina				1			
Epicharis	2	4	1		1	1	2
Eufriesea		1		1	1	2	6
Euglossa	1	6	1	1	1	2	8
Eulaema	3	4	1	1	1	1	3
Exomalopsis		4		1			1
Florilegus	1	1	2			1	1
Frieseomellita	2	1					
Melipona						2	2
Melitoma				1			
Mesocheira		1					
Mesonychium	1	1	1	1	1		
Mesoplia	2	2	1	2	1		
Nanotrigona		1	1				
Odyneropsis					1	1	1
Oxytrigona		1					
Partamona		1				1	1
Paratrigona		1					
Paratetrapedia		1				1	1
Plebeia		1				1	2
Ptilothrix				1			
Scaptotrigona		3					
Tetragona							1
Tetragonisca		1					
Thygater		1					
Trigona	1	3	1			1	1
Trigonisca	1	1				1	2
Tropidopedia							1
Xanthopedia							1
Xylocopa	6	7	5	4	2	5	5
***Sub-total* (37)(35[b])**	**36 (14)**	**64 (27)**	**29 (12)**	**27 (14)**	**27 (12)**	**35 (15)**	**61 (20)**
Total (55)(50[b])	49 (22)	80 (35)	40 (21)	38 (21)	31 (15)	48 (21)	86 (30)

[a] Include other methods of sampling: pan traps, chemical baits (Silva et al., 2009), trap nest (Ramos et al., 2006) and murici visitors (Rêgo et al., 2006).
[b] Include genus only collected with entomological nets.

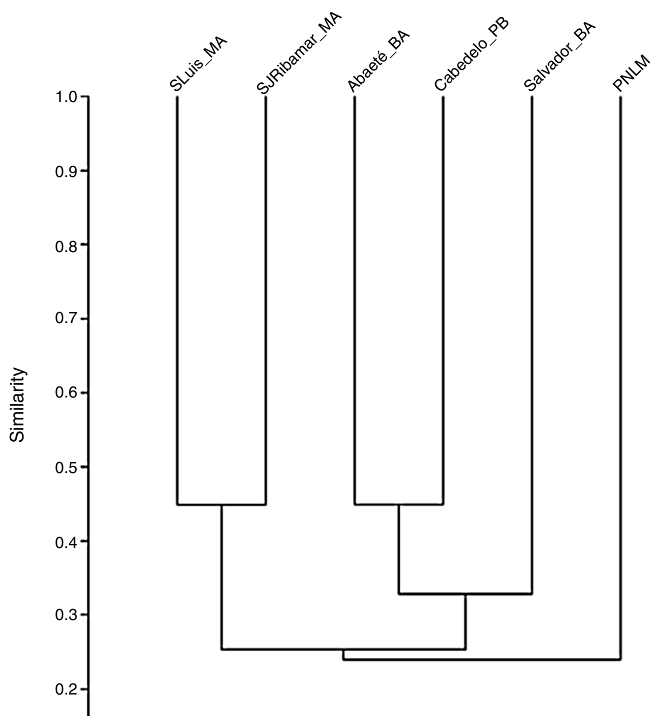

Fig. 3. Dendrogram of Morisita similarity of the bee species collected between PNLM (Barreirinhas, MA) and other restinga and dune areas of northeastern Brazil: Paraíba (Madeira-da-Silva and Martins, 2003), Bahia (Viana and Kleinert, 2005), Salvador (Silva et al., 2015), Panaquatira (Oliveira et al., 2010), and São Luís (Albuquerque et al., 2007).

and PNLM and is slightly less but very similar among Abaeté, São Marcos, Panaquatira, and Cabedelo (Table 3). The Apinae generic diversity of Salvador and PNLM are greater than in other areas. PNLM also had more Megachilinae and Halictinae species and a higher general diversity than the others restinga areas. São Marcos had the highest specific and generic species richness of Andreninae, however, two species of this subfamily were collected in PNLM by bowl traps. Colletinae was also very poorly represented in the restinga habitats of northeastern Brazil.

The similarity in the composition of the species sampled in the restinga of PNLM and other areas of dunes and restingas of northeastern Brazil (Panaquatira, São Marcos, Cabedelo, Salvador and Abaeté) was relatively low, as it was ≤44% (Fig. 3). The species diversity (H) for the bee community of PNLM was 2.41, and the equitability index (J) was 0.97.

Discussion

Bee species richness at PNLM

Similar to previous studies (Krug and Alves-dos-Santos, 2008; Kamke et al., 2011; Topic et al., 2013; Moreira et al., 2016), the present study indicates that using complementary methods of collection, such as bowl traps, should be considered when the goal is to determine the specific diversity within an area. If only entomological nets had been used, the most commonly used method in bee surveys in Brazil (Pinheiro-Machado et al., 2002, 2006), then 43% of the bee species present in PNLM would remain unidentified.

The number of bee species known to occur at PNLM was more than doubled. This is certainly due to the combination of different methods of collecting bees as well as the increasing of sampling hours. While netting yielded more species than the other methods together, it failed for some bee taxa like orchid bees. *Callonychium* species are captured in bowl traps, due that the flowers visited by those bees were not known or not sampled by us. Williams et al. (2001) called attention to the fact that "rare species are rare because they are not readily detected", for example due to the dependence of *Melissodes sexcincta* (Lepeletier) by pollen of *Triumfetta*, this common and widespread bee species in Brazil, had never been collected until 1993 (Silveira and Godínez, 1996).

Some Meliponini, as *Trigonisca* for example, which are attracted by sweat, are so small that they are hardly collected with entomological nets, always being very poorly represented in the various inventories. In addition to these limitations in the methodologies of data collection, there are also species that are oligolectic with a low spectrum of flowers visited. *Florilegus (Florilegus)* cf. *condignus* (Cresson, 1878) is oligolectic, restricting the nectar collection of *Pontederia* (Pontederiaceae) flowers (Schlindwein, 1998, 2004).

The species rarefaction curve did not completely stabilize using only the net and bowl traps methods, suggesting the existence of non-sampled species, which was demonstrated when we compared the species collected in the same study area using other sampling techniques (Ramos et al., 2006; Rêgo et al., 2006; Silva et al., 2009). Although the PNLM bee inventory was much improved, diversity indices suggest that our sampling is not complete, so many more species are to be expected. It is of course difficult to predict which species are present but not yet recorded, but it is plausible to assume that species in genera like *Mesoplia*, *Mesonychium*, *Acamptopoeum*, *Oxaea*, *Protomeliturga*, and others, already collected in other restinga in northeastern Brazil (Albuquerque, 1998; Madeira-da-Silva and Martins, 2003; Viana and Kleinert, 2005; Oliveira et al., 2010; Silva et al., 2015) might be present as well.

Diurnal and annual activity pattern

The diurnal activity total pattern of bees is bimodal with peaks in the early morning and late afternoon. In environments such as the restinga, high temperatures and low humidity are limiting factors for bee activity. The bees most likely use primarily the first and last hours of the day with lower temperatures to avoid heat-induced stress (Hilário et al., 2001; Ferreira-Júnior et al., 2010). When we exclude the dominant bee species (D), the diurnal activity pattern is altered, being similar to that observed in coastal environments where there is a decrease in activity throughout the day (Albuquerque, 1998; Viana and Kleinert, 2005; Oliveira et al., 2010). Nevertheless, bee activity at in PNLM is continuous, indicating that flowers of several plant species remain open throughout the day. For example, flowers of *B. crassifolia* remain open for approximately two days (Rêgo and Albuquerque, 2006). It is well documented that many bees species synchronized their activity to periods when floral resources are available (Viana and Kleinert, 2005; Oliveira et al., 2010) and probably there is greater availability in the hours that showed greater activity.

There was a higher abundance of bees throughout the year in PNLM during the rainy period (April–August) and a greater number of species per month from June to October. A similar pattern occurred in the others two restinga areas at Maranhão (Panaquatira and São Marcos), with a greater abundance during the rainy season (Oliveira et al., 2010; Albuquerque, 1998). The opposite pattern occurred in Abaeté and Cabedelo, where a higher abundance during the dry season was observed (Viana and Kleinert, 2005; Madeira-da-Silva and Martins, 2003). Flowering phenology strongly influences the temporal pattern of the abundance of flower visitors (Newstrom et al., 1994), and this explains the pattern observed in Maranhão (Panaquatira, São Marcos and PNLM), where flowering was dependent on the rainy season.

The high number of bees collected during the rainy season was also caused by the increased activity of the eusocial species *Apis mellifera*, *Trigona fulviventris*, and *Plebeia alvarengai* during peak flowering, which caused these species to become dominant in the community. The species *Centtris caxiensis* and *Xylocopa cearensis* were also dominant and constant probably due to the availability of floral resources in the area. *Centris caxiensis* was among the most frequent visitors of *B. crassifolia*, as seen by Rêgo et al. (2006). The constancy of species such as *C. caxiensis*, *C. aenea* and also *X. cearensis* were also observed in other restinga areas in northeastern Brazil (Albuquerque, 1998; Viana and Kleinert, 2005; Oliveira et al., 2010).

As judged by netting Euglossini were classified as occasional and accidental, but this is a methodological flaw as the host plants visited by these bees are mostly unknown and therefore not sampled. The use of scent baiting, however, revealed large populations of several species of orchid bees (Silva et al., 2009). In fact, *Euglossa cordata* and species of *Eulaema* are known to reproduce in communal or primitively social multifemale nests so that large numbers of offspring are produced. Megachilinae were also occasional and accidental, but again this is a methodological bias, as a different method (trap nesting) may yield many individuals.

Species richness in northeastern restinga areas

The PNLM bee diversity ($H' = 2.41$) was similar to that found in Cabedelo (2.45) and greater than those at Panaquatira beach (2.28), São Marcos beach (2.05), and the Abaeté dunes (2.04). The Pielou equitability index indicated that the individuals were evenly distributed among the sampled species (Ludwig and Reynolds, 1988), as observed in the restinga environments.

In coastal environment the Apinae typically exhibit the highest species richness (Viana and Kleinert, 2005; Albuquerque et al., 2007; Oliveira et al., 2010; Silva et al., 2015). However, the small number of corbiculate Apinae in this environment appears to relate rather to the habitat condition than to latitudinal gradients, as reported by Gonçalves and Melo (2005) and Biesmeijer and Slaa (2006). In contrast, the non-corbiculate Apinae exhibited the highest richness in coastal areas, ranging from 49% to 74% of the sampled species (Madeira-da-Silva and Martins, 2003; Viana and Kleinert, 2005; Oliveira et al., 2010) and corroborating the results found in the present study. The most striking feature of this inventory was the genus *Anthophora*, which was only collected with bowl traps and had never been previously collected on the 15 Maranhão bee surveys (Rebêlo et al., 2003). This is the first record of this species in a restinga area. Only two species from this genus occur in Brazil, found in the highlands of São Paulo, Minas Gerais, Paraná and Brasília (Urban and Melo, 2005; Moure et al., 2012a,b). The genera *Melipona* and *Plebeia alvarengai* and *P. minima* were also reported for the first time in a restinga ecosystem. The abundance of these species at PNLM shows that the area has some trees with large cavities for nest building and sufficient floral resources available. The absence of stingless bees was also observed by Kamke et al. (2011) in a restinga at Santa Catarina, most likely due to the lack or scarcity of food plants in a region of young forest that was distant from areas with greater availability of nesting substrate.

Few species of Megachilinae, Halictinae, and Andreninae were recorded with the procedure described by Sakagami et al. (1967) at PNLM, which is similar to the estimates for these subfamilies reported for other restinga and dune areas in northeastern Brazil (Madeira-da-Silva and Martins, 2003; Viana and Kleinert, 2005; Albuquerque et al., 2007) using the same methodology. Probably the true richness of these subfamilies could be much higher than estimated if there was continuity of temporal sampling and diversification of methods. Andreninae are practically absent in the restingas of northeastern Brazil. Although the richness of Halictinae and Megachilinae is somewhat greater than that of Andreninae, it is much lower than in restingas from southern Brazil (Laroca, 1974; Zanella, 1991; Schwartz-Filho and Laroca, 1999; Alves-dos-Santos, 1999; Steiner et al., 2010; Kamke et al., 2011). A gradient of increasing species richness along the north-south axis becomes evident, which was postulated by Michener (2000) and discussed by Gonçalves and Melo (2005) in a study of diversity in Paraná.

All these methods of collecting are associated with several types of bias; for example, some species are often not captured with nets because they are fast, small and inconspicuous, being less flashy than other slow-moving, large and colourful insects (Nielsen et al., 2011) or due to a low spectrum of flowers visited (oligolects) and those flowers are not at collection areas. Bowl traps have been shown to be an efficient and unbiased method, but they capture many insects, not just bees. Therefore, if we are interested in bee diversity, chemical baits, trap nests and even bowl traps should all be used as a complement to net collections.

Conflicts of interest

The authors declare no conflicts of interest.

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