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A N I N T E R N A T I O N A L J O U R N A L

Bee Community of a Beach Dune Ecosystem on Maranhão Island, Brazil

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ABSTRACT

The bee-plant community in a beach dune ecosystem in north-eastern of Brazil was studied concerning phenology and floral preference. The bees visited thirty-three species of 20 families of plants. The most visited species were Vernonia arenaria *(Asteraceae),* Chamaecrista hispidula *(Caesalpiniaceae),* Passiflora foetida *(Passifloraceae) and* Turnera melochioides *(Turneraceae). Fifty-five percent of plants presented an annual or long flowering period (from 5 to 7 months). The largest number of species blooming was observed from March to August (dry season), corresponding to the period of greatest abundance and diversity of bees. Based on the range of floral sources used by the dominant bees, three guilds of bees were noted: bees with a restricted range of floral sources:* Melitoma segmentaria, Centris tarsata, Centris flavifrons, Ceratinula *sp.; moderate generalists:* Megachile (Leptorachis) *sp.,* Euglossa cordata, Augochlorella *sp.,* Eulaema nigrita *and* Xylocopa frontalis*; and generalists:* Xylocopa cearensis, Apis mellifera, Exomalopsis analis *and* Pseudaugochloropsis pandora.

Key words: Apoidea, bee-plant interactions, beach dune, north-eastern Brazil

INTRODUCTION

Gottsberger et al. (1988) were the first to call attention to the predominance of melittophilous plants in neotropical beach dune systems investigating the floral biology and pollination ecology of some melittophilous plants in the beach dunes of Maranhão island. In spite of this, little attention has been paid so far to the pollinating agents of the dune ecosystem. Zanella et al. (1998) studied a bee-plant community in a secondary meadow, with forest elements and dune vegetation on the coast of Parana, southern Brazil. Alves-dos-Santos (1999a, 1999b) surveyed bees and plants in the north-eastern region of the state of Rio Grande do Sul, sampling an almost linear transect from the sea level up to ca. 800 m. Costa and Ramalho (2001) studied the pollination ecology of eight plant species in beach dunes, northeast of Salvador, Bahia, Brazil. Madeira-da-Silva and Martins (2003) and Viana and Kleinert (2005) using a standardized methodology collected bees and plants at the Abaeté sand dunes, Bahia and at a restinga area at Cabedelo, Paraiba, respectively.

The aim of the present study was to analyse the plant species used as pollen and nectar resources by the bees and their phenology more specifically, this study tried to answer the following questions:

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- What floral attributes govern the abundance or diversity of pollinators?
- Does the beach dune vegetation provide sufficient reward and alimentation for the bees all year round?

MATERIAL AND METHODS

Study site

The study was conducted in the secondary dunes (according to the zonation presented by Gottsberger et al.,1988), approximately 30 m high, of São Marcos beach, São Luis, Maranhão (2°29' S, 44°18' W), northeast of Brazil, in an area of 12,270 m^2. In this place, the climate is hot, semi-humid, with well-defined dry and rainy seasons, annual mean temperature of 26.7°C, rainfall 1,950 mm and relative humidity averages 81%.

The vegetation in the dunes is characterized by herbaceous and creeping species, such as *Canavalia rosea* and *Ipomoea spp.* The land area adjacent to the study site is characterized by shrubby vegetation and by scattered spots of secondary forest, where *Vismia*, *Cecropia* and babassu palm (*Orbignyia phalerata*) are the predominant elements.

Sampling

Sampling was done at 30-day intervals, from November 1993 to October 1994. The study area was divided into eight sections, of approximately equal size, in which bees were alternately collected by two people (P. Albuquerque and R. Ferreira). Each collector stayed 30 min. in each section, avoiding collecting for more than 3-5 min. in each plant specimen. All the surveyed area was searched once every two hours and six times in 12 h. Each survey had a 12 h duration (on the first day from 12 PM to 6 PM and on the second from 6 AM to 12 PM), totalling 288 h of survey, 144 h for each collector. All bee individuals visiting any plant species at any time were caught with entomological nets. Prolonged stays at any one flower patch were avoided. Bees and voucher specimens of plants have been deposited in the Entomological Collection of the Federal University of Maranhão – UFMA and duplicates of plants in the Paraense Emilio Goeldi Museum, Belém, Pará, Brazil. Data on opening and closing of flowers (every two hours), change in their colour, size, shape and resources offered (using visual observation to determine which was the principal flower reward), fall of flower or petals, number of flowers or inflorescences (approximately), and number of specimens of plants per section were collected by a third observer who also recorded climatic data.

The pattern of flowering phenology proposed by Newstrom et al. (1994) that considered four basic classes of flowering (continual, subannual, annual and supra-annual) was used in this study. The method of "occurrence probability" of Kato et al. (1952) was used to calculate the relative abundance of the predominant bee species and their confidence limits ($\alpha = 0.05$). The upper and lower confidence limits were obtained respectively, using the formula below:

Upper limit: $[(n_1.f_0)/(n_2 + n_1.f_0)] \cdot 100$, $n_1 = 2(K + 1)$; $n_2 = 2(N - K + 1)$

Lower limit: $[(1 - n_1.f_0) / (n_2 + n_1.f_0)] \cdot 100$, $n_1 = 2(N - K + 1)$; $n_2 = 2(K + 1)$,

where N was the total number of all specimens captured and K was the total number of specimens of each species, and f_0 was obtained from the F-distribution table at the degrees of freedom n_1 and n_2 ($p = 0.05$). The species whose lower confidence limit of relative abundance was higher than the upper limit when K = 0 (undiscovered species) were regarded as the predominant species.

The representation of the frequency distribution of the species classified according to the number of individuals was done by applying Preston's methodology (1948) adjusted to the truncated lognormal (Ludwig and Reynolds, 1988).

The Brillouin index was used to calculate the diversity of plants visited by each bee species, according to Pielou (1969, 1975), Krebs (1989) and Magurran (1988), using the formula as below:

$$H = (\ln N! - \sum \ln n_i!)/ N$$

where N was the total number of bee individuals and n_i was the number of bees in each plant species. The Evenness (E) for the Brillouin diversity index was obtained from the following formula:

$$E = H / H_{max} \quad , \quad H_{max} = 1/N \cdot \ln N! / \{[N/S]!\}^{s-r} .\{([N/S] + 1)!\}^{r}$$

where S = richness of plant species visited, r = N - S[N/S].

Flower preferences were calculated using the program PREFER as proposed by Krebs (1989), which calculates Manly's alpha index of preference. The variables required by the program are:

- The number of species of flowers present in the area.
- The number of flowers of each species in the area.
- The number of visits to each species of flowers by bees of a particular species.
- Whether the resource was renewable or not. It was decided to classify the resources as renewable, since few flowers secrete nectar at just one time. Pollen is not a renewable resource, but no single bee is likely to remove the entire quantity of pollen from a flower in just one visit.

RESULTS

The S.Marcos Dune Plant Community

Forty-two species of plants were found flowering in the study area (Tables 1 and 2). A total of 1581 specimens of bees were collected visiting 33 species of plants of 20 families, mainly Fabaceae (8 spp, 24%), Convolvulaceae (4 spp, 12 %), Asteraceae (3 spp, 9%), and Turneraceae (2 ssp, 6%). Each of the remaining plant families were represented by only one species (13 families, 65%) (Table 1).

Among the plant species found flowering, 85.8% were entomophilous (of which 81.0% were melittophilous, pollinated by bees, and 4.8% were generalist insect pollinated) and 7.1% anemophilous (7.1% of the plant species did not have a clearly definable floral syndrome determined). Purple (30.3%), white (27.3%) and yellow (24.2%) were the corolla colours most commonly found among flowers visited by bees.

Flowering Phenology

The number of plant species visited by bees in the rainy season was relatively small (Table 1) but increased during the dry season, from May to October, the principal blooming period (13 to 17 visited species). Most (79%) of the plants had annual or long flowering periods in which 58% had an extended flowering duration (> 5 mo). Among these, *Passiflora foetida*, *Ipomoea pes-caprae*, *I. littoralis*, *Heliotropium polyphyllum* were the plants most preferred by the bees; 35% had an intermediate flowering (1 – 5 mo) and *Zornia curvata* and *Mikania micrantha* had a brief flowering duration (< 1 mo). *Turnera melochioides*, *Crotalaria retusa*, *Solanum micranthum*, *Wulffia baccata*, *Vernonia arenaria*, *Chamaecrista hispidula* and *Centrosema brasilianum* had a continuous flowering pattern.

Chamaecrista hispidula, a species characteristic of dunes, occurred with great abundance in all sections of the dune, and presented peak flowering from April to June. *Canavalia rosea*, had its flowering peak in August and September. *Passiflora foetida* (flowering peak in Sep-Jan) and *Solanum* cf. *micranthum* (Jul-Sep) that are also characteristic dune species, were only observed in sections closest to the primary dune.

The number of flowering specimens per monthly sample of each plant species varied from 1 to 251. Eleven species (26.2%) were represented by small populations, with up to 10 specimens. The species with larger populations were: *Chamaecrista hispidula* (251 individuals), *Borreria verticcilata* (154), *Crotalaria retusa* (83), *Solanum* cf. *micranthum* (82), *Polygala monticola* (81), *Wulffia baccata* (78), *Ipomoea littoralis* (72).

Solanum cf. *micranthum*, *Wulffia baccata*, *Turnera melochioides*, *Chamaecrista hispidula*, *Passiflora foetida*, *Vernonia arenaria*, *Crotalaria retusa* and *Ipomoea pes-caprae* flowered and received visits for approximately 10 months. About 52% of the plant species had a flowering period of less than 6 months, and few bees visited them.

In most of the species, anthesis was between 5:00 a.m. and 6:00 a.m. and the flowers stayed open until 4:30 p.m., but some of the species closed in the morning. Flowers of *Ipomoea mauritiana*, *Centrosema* sp. and *Passiflora foetida* were available to the visitors for the shortest periods, anthesis occurring between 5:30 and 6:00 a.m. and by 11:00 a.m. they were completely closed. In *Passiflora foetida*, the flowers began to wither at about 8:30 a.m., but even so they still continued to receive some visits. Flowers of *Ipomoea pes-caprae*, *I. littoralis*, *Merremia aegyptia*, *Turnera ulmifolia* and *Centrosema brasilianum* closed at about 12:00 - 1:00 p.m. In *Chamaecrista hispidula* and *Macroptilium atropurpureum* (whose anthesis was between 5:30 - 6:00 a.m.), and *Turnera*

melochioides and *Crotalaria retusa* (anthesis at 7:00 a.m.), flowers closed at 4:00 - 4:30 p.m. Anthesis in *Solanum micranthum* and *Canavalia rosea* occurred at about 5:00 a.m., and flowers remained open even after 6:00 p.m.

Floral Preferences

Fig. 1 shows the flower preferences analysed by the PREFER program for the bees collected all year round in each plant species. Considering all the bees collected from each plant species without considering the month of collection, it was possible to observe a clear preference for one species of flower: *Vernonia arenaria* (α = 0.36) visited mainly *Apis mellifera* (64%) and *Xylocopa cearensis* (27%) for nectar foraging. For pollen foraging, *Chamaecrista hispidula* and *Solanum micranthum*, both having flowers with poricidal anthers were the second most preferred, visited mainly by *X. cearensis* (65%) (Fig. 1A).

In November, the bees showed a clear preference for *Wulffia baccata* (α = 0.68) and *Solanum micranthum* (α = 0.16) (Fig. 1B).

In December five species of flowers were foraged and *Solanum micranthum* (α = 0.51) was the most preferred (Fig. 1B). In January *Cassia hispidula* (α = 0.72) was preferred (Fig. 1B); and in February *Ipomoea mauritiana* (α = 0.31), *Passiflora foetida* (α = 0.26) and *Centrosema* sp. (α = 0.15).

In March, April, May, June, July and September the bees showed a clear preference for *Vernonia arenaria*, which were the most visited for nectar. In August, *Cassia hispidula* (α = 0.45) was the preferred flower pollen and *Vernonia arenaria* (α = 0.22) for nectar (Fig. 1B).

Table 1. - Number of bee visitors netted at flowering plants and principal reward (Pr) collected at S. Marcos beach dunes, S. Luís Island, MA, from November 1993 to October 1994. N = nectar; P = pollen; O = oil; * primary.

FAMILIES/SPECIES	Pr	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	TOTAL
Solanaceae														
Solanum cf. micranthum	P	7	4			1	5		2		5	11	14	49
Asteraceae														
Wulffia baccata	N	1		1	3		3	3	3	42	5			61
Vernonia arenaria	N	1				5	42	103	146	70	46	57	42	512
Mikania micrantha	N												1	1
Caesalpiniaceae														
Chamaecrista hispidula	P	12	4	1			7	79	41	6	118	15	18	301
Fabaceae														
Indigofera hirsuta	N							1						1
Canavalia rosea	N	6												6
Crotalaria retusa	N	1		2		1	13	5	1	6	6	1	1	37
Centrosema brasilianum	N				5	5	1	11	3			2	1	28
Centrosema sp.	N				3	5		2						10
Macroptilium atropurpureum	N				2		1		1	5	6			15
Galactia jussiaeana	N					1					1			2
Zornia curvata	N							2						2
Mimosaceae														
Mimosa diplotricha	P						1			2				3
Boraginaceae														
Heliotropium polyphyllum	N	4		20	39	1								64
Malvaceae														
Pavonia cancellata	N									1				1
Passifloraceae														
Passiflora foetida	N	25	46	3	27			1	5	2		10	7	126
Convolvulaceae														
Ipomoea pes-caprae	N	3	5			3	8	4	3	15	4	5	5	55

(Cont. ...)

(Cont. Table 1)

FAMILIES/SPECIES	Pr	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	TOTAL
Ipomoea mauritiana	N				3								6	9
Ipomoea littoralis	N						2	2	4	9	4	2	1	24
Merremia aegyptia	N									14	2	8		24
Portulacaceae *Talinum* sp.	P			1										1
Malpighiaceae *Tetrapterys* sp.	*O - P							3				2	2	7
Bignoniaceae *Arrabidaea brachypoda*	N									6	2			8
Turneraceae *Turnera melochioides*	N	12	23		2	2	2	3	7	23	19	6	22	121
Turnera ulmifolia	N					1			2	7	2		1	13
Rubiaceae *Borreria verticilata*	N								1	36	14			51
Lamiaceae *Marsypianthes hyptoides*	N									9	1			10
Lecythidaceae *Gustavia augusta*	P										1			1
Burseraceae *Protium heptaphyllum*	N	1												1
Polygalaceae *Polygala monticola*	N				4	14	12	2	1	2				35
Sapindaceae *Pseudima frutescens*	N							1						1
Commelinaceae *Commelina virginica*	P				1									1
Total of bee specimens		73	82	28	89	39	97	222	220	255	236	119	121	1581
Total of plant species visited		11	5	6	10	11	12	15	14	17	16	11	13	33
		Dry season				Rainy season					Dry season			

Table 2 - Plants visited in beach dunes of S. Marcos, S. Luís, MA, Brazil and number of specimens/bee species collected. (Hab) plant habit, (Tr) tree and shrub, (Hb) herbs, (SS) subshrub, (Cr) creeper, (A) *Apis mellifera*, (B) *Euglossa cordata*, (C) *Eulaema nigrita*, (D) *Eufriesea surinamensis*, (E) *Centris aenea*, (F) *C. leprieuri*, (G) *C. flavifrons*, (H) *Centris* sp., (I) *C. tarsata*, (J) *C. fuscata*, (K) *C.spilopoda*, (L) *Mesonychium asteria*, (M) *Ancyloscelis apiformis*, (N) *Melitoma segmentaria*, (O) *Diadasina* sp., (P) *Ptilothrix plumata*, (Q) *Exomalopsis analis*, (R) *Ceratina maculifrons*, (S) *Ceratinula* sp.2, (T) *Ceratinula* sp.n., (U) *Ceratinula* sp., (V) *Xylocopa frontalis*, (W) *X.cearensis*, (X) *X. muscaria*, (Y) *Pseudaugochloropsis Pandora*, (Z) *Augochlorella* sp., (A1) *Acamptopoeum prinii*, (B1) *Protomelliturga turnerae*, (C1) *Oxaea festiva*, (D1) *Megachile* (*Pseudocentron*) sp., (E1) *Megachile* (*Leptorachis*) sp., (F1) *Megachile* (*Leptorachis*) sp.2, (G1) *Megachile* (*Pseudocentron*) sp.3, (H1) *Megachile* (*Pseudocentron*) sp.2, (I1) *Dicranthidium arenarium*

			Bee rate																						
	Hab	**Plant rate**	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	
Solanaceae	Tr	*Solanum cf. micranthum*			7			1	3															6	
Asteraceae	Tr	*Wulffia baccata*	1													1			38	1					
	SS	*Vernonia arenaria*	327	1			4	15		2			1		1				10	2					
	Cr	*Mikania micrantha*	1																						
Caesalpiniaceae	SS	*Chamaecrista hispidula*			25	3	15	12	15		7	2			1				1					2	
Fabaceae	Hb	*Indigofera hirsuta*																							
	Cr	*Canavalia rosea*			1																			5	
	SS	*Crotalaria retusa*																						32	
	Cr	*Centrosema brasilianum*		6	3	2														1					
	Cr	*Centrosema* sp.	1		1																				
	Cr	*Macroptilium atropurpureum*					2	2		1															
	Cr	*Galactia jussiaeana*																							
	Hb	*Zornia curvata*																							
Mimosaceae	SS	*Mimosa diplotricha*	1																2						
Boraginaceae	Hb	*Heliotropium polyphyllum*	40					2													1	1			
Malvaceae	Hb	*Pavonia cancellata*																1							
Passifloraceae	Cr	*Passiflora foetida*	52																	1				1	
Convolvulaceae	Cr	*Ipomoea pes-caprae*		1											11	36	3	1		2					
	Cr	*Ipomoea mauritiana*		1											1	4				1					
	Cr	*Ipomoea littoralis*													14	5	2		2						
	Cr	*Merremia aegyptia*	2												9				11						
Portulacaceae	Hb	*Talinum* sp.																		1					
Malpighiaceae	Tr	*Tetrapterys* sp.					3	1			2	1													
Bignoniaceae	Tr	*Arrabidaea brachypoda*																							
Turneraceae	Hb	*Turnera melochioides*	18				2						1	2					16	1	16	15	3		
	Hb	*Turnera ulmifolia*																	5	1					
Rubiaceae	Hb	*Borreria verticilata*	12																35						
Lamiaceae	Hb	*Marsypianthes hyptoides*								2									1						
Lecythidaceae	Tr	*Gustavia augusta*																							
Burseraceae	Tr	*Protium heptaphyllum*																							
Polygalaceae	Hb	*Polygala monticola*	1																						
Sapindaceae	Tr	*Pseudima frutescens*																							
Commelinaceae	Hb	*Commelina virginica*																		1					
Total Bee Sample			**456**	**9**	**37**	**5**	**26**	**33**	**18**	**5**	**9**	**3**	**2**	**2**	**37**	**46**	**5**	**2**	**121**	**12**	**17**	**16**	**3**	**46**	
																								Total	

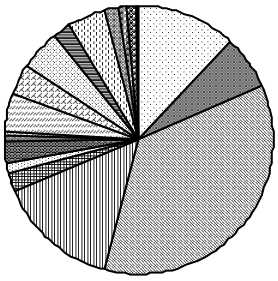
	Hab	**Plant rate**	W	X	Y	Z	A1	B1	C1	D1	E1	F1	G1	H1	I1	**Spp.**	**Sp.**
Solanaceae	Tr	*Solanum cf. micranthum*	32													**49**	**6**
Asteraceae	Tr	*Wulffia baccata*	17							2		1				**61**	**7**
	SS	*Vernonia arenaria*	139		1	1	1			1	4	1		1		**512**	**18**
	Cr	*Mikania micrantha*														**1**	**1**
Caesalpiniaceae	SS	*Chamaecrista hispidula*	198	1	19											**301**	**14**
Fabaceae	Hb	*Indigofera hirsuta*													1	**1**	**1**
	Cr	*Canavalia rosea*														**6**	**2**

(Cont. ...)

(Cont. Table 2)

	SS	*Crotalaria retusa*	5													**37**	**2**
	Cr	*Centrosema brasilianum*	15						1							**28**	**6**
	Cr	*Centrosema* sp.	7						1							**10**	**4**
	Cr	*Macroptilium atropurpureum*	10													**15**	**4**
	Cr	*Galactia jussiaeana*	2													**2**	**1**
	Hb	*Zornia curvata*									2					**2**	**1**
Mimosaceae	SS	*Mimosa diplotricha*														**3**	**2**
Boraginaceae	Hb	*Heliotropium polyphyllum*	20													**64**	**5**
Malvaceae	Hb	*Pavonia cancellata*														**1**	**1**
Passifloraceae	Cr	*Passiflora foetida*	61		11											**126**	**5**
Convolvulaceae	Cr	*Ipomoea pes-caprae*			1											**55**	**7**
	Cr	*Ipomoea mauritiana*	1		1											**9**	**6**
	Cr	*Ipomoea littoralis*			1											**24**	**5**
	Cr	*Merremia aegyptia*			2											**24**	**4**
Portulacaceae	Hb	*Talinum* sp.														**1**	**1**
Malpighiaceae	Tr	*Tetrapterys* sp.														**7**	**4**
Bignoniaceae	Tr	*Arrabidaea brachypoda*	8													**8**	**1**
Turneraceae	Hb	*Turnera melochioides*	35		3	6					3					**121**	**13**
	Hb	*Turnera ulmifolia*				4		3								**13**	**4**
Rubiaceae	Hb	*Borreria verticilata*	1		1								1	1		**51**	**6**
Lamiaceae	Hb	*Marsypianthes hyptoides*	6												1	**10**	**4**
Lecythidaceae	Tr	*Gustavia augusta*	1													**1**	**1**
Burseraceae	Tr	*Protium heptaphyllum*	1													**1**	**1**
Polygalaceae	Hb	*Polygala monticola*	31			2				1						**35**	**4**
Sapindaceae	Tr	*Pseudima frutescens*	1													**1**	**1**
Commelinaceae	Hb	*Commelina virginica*														**1**	**1**
Total Bee Sample			**591**	**1**	**40**	**13**	**1**	**3**	**2**	**4**	**9**	**2**	**1**	**2**	**2**	**1581**	**36**

A. Cumulative data from Nov/1993 to Oct/1994 (n= 1581)



Solanum micranthum
Vernonia arenaria
Indigofera hirsuta
Crotalaria retusa
Centrosema sp
Zornia curvata
Pavonia cancellata
Ipomoea pes-caprae
Ipomoea littoralis
Talinum sp
Tetrapterys sp
Turnera ulmifolia
Marsypianthes hyptoides
P. monticola
(index less than 0.005)
Wulffia baccata
Chamaecrista hispidula
Canavalia rosea
Centrosema brasilianum
Macroptilum atropurpureum
Heliotropium polyphyllum
Passiflora foetida
Ipomoea mauritiana
Merremia aegyptia
Commelina virginica
Turnera melochioides
Borreria verticcilata
Gustavia augusta
P. frutescens

B.

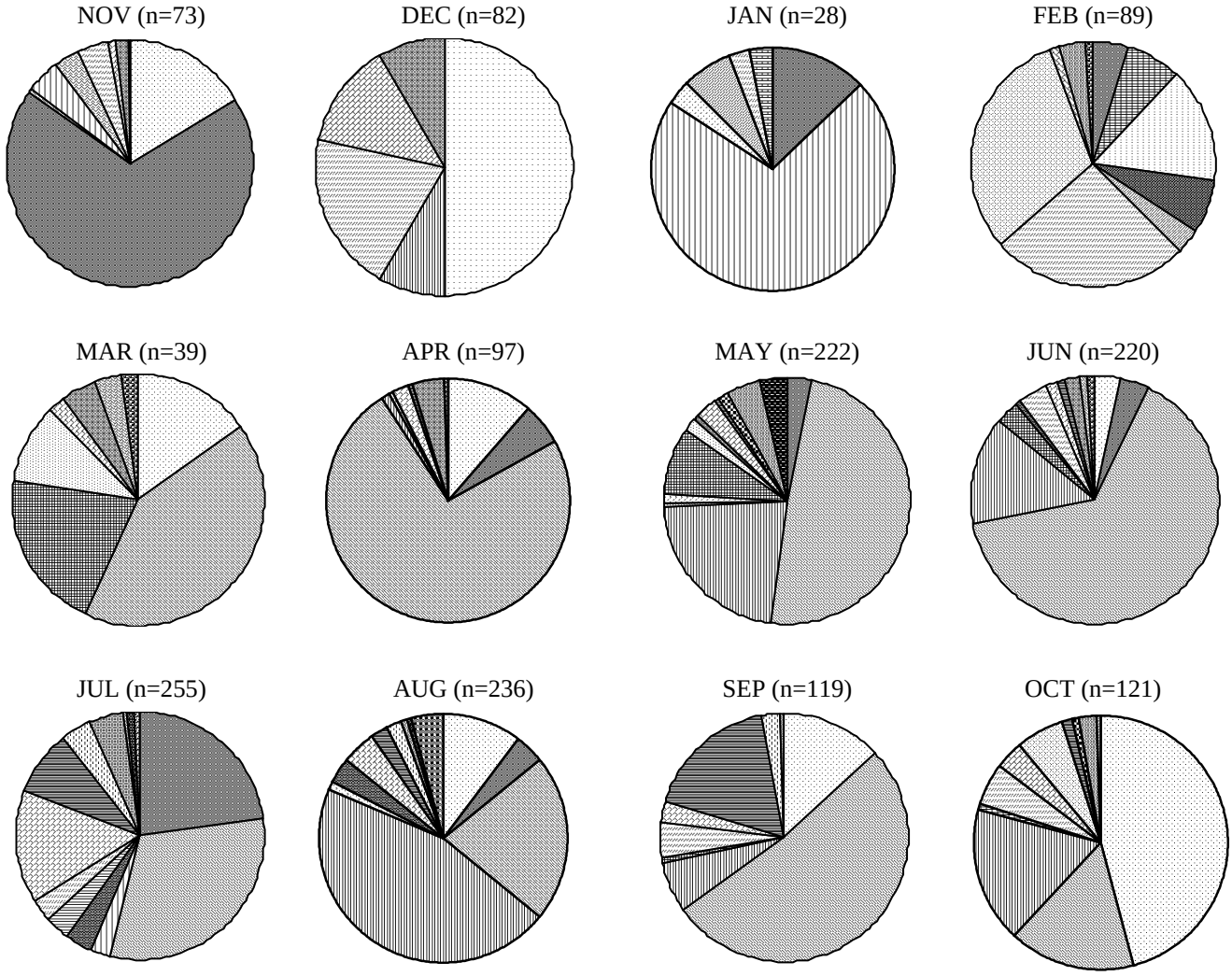


Figure 1 - Flower preferences as assessed by bees at S. Marcos beach dunes, S. Luis, MA, from November 1993 to October 1994. (n = number of bees collected), using Manly's alpha index of preference (Krebs, 1989). A. Cumulative data, B. Preference per month

Bee Diversity on Plants

Among the species of bees collected, 18 were considered predominant, according to the methodology of Kato et al. (1952) (Fig. 2). The frequency distribution of the species in relation to their classes of abundance was a truncate curve (Fig. 3). Variation in plant species visited was observed for these bees (Table 3). *Ceratinula* sp. 2, *Ceratinula* sp.nov., *Centris flavifrons*, *C. tarsata* and *Melitoma segmentaria* were species that used few floral resources, hence, these were considered as bees with a restricted range of floral sources. The 16 and 17 individuals, respectively of *Ceratinula* sp.nov. and *Ceratinula* sp.2. used or exploited two plant species for nectar foraging only, of which flowers of *Turnera melochioides* (Turneraceae) received about 94% of visits. About 98% of specimens of *Melitoma segmentaria* were collected from flowers of Convolvulaceae, among which *Ipomoea pes-caprae* received 80% of the visits.

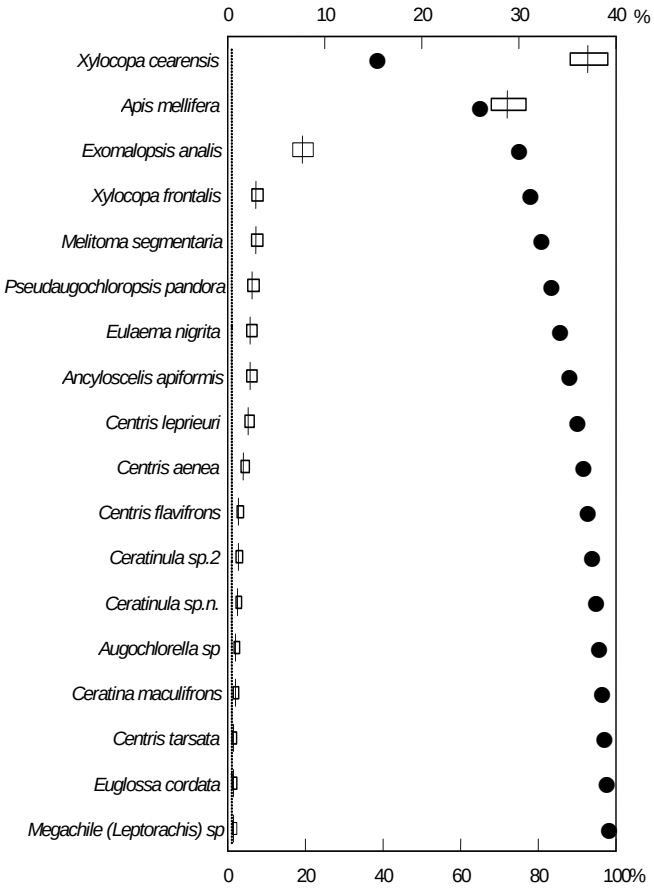


Figure 2 - The relative abundance of the predominant bee species visiting flowers in beach dunes of S. Marcos, S. Luís, MA, Brazil from November 1993 to October 1994 as calculated by Kato et al. (1952). Ends of each bar show upper and lower limits of confidence (p = 0.05) and vertical broken line is the upper limit when K = 0 (undiscovered species); the black dots are the cumulative percentage (lower scale) according to each individual

About 83% of the individuals of *Centris flavifrons* and 77.8% of *C. tarsata* were captured on flowers of *Chamaecrista hispidula* (Caesalpiniaceae) for pollen foraging. *Megachile (Leptorachis)* sp., *Euglossa cordata*, *Augochlorella* sp and *Xylocopa frontalis* visited three to five species of plants showing some preference while nectar foraging: *Vernonia arenaria* (Asteraceae), *Centrosema brasilianum* (Fabaceae), *Turnera melochioides* (Turneraceae) and *Crotalaria retusa* (Fabaceae) respectively. *Eulaema nigrita* visited five species of plants most of them for pollen collection. These five bee species could be considered moderate generalists. *Xylocopa cearensis*, *Apis mellifera*, *Exomalopsis analis* and *Pseudaugochloropsis Pandora*, visited 20, 11, 10 and 9 plant species respectively (Table 2), being considered generalist.

DISCUSSION

The prevalence of melittophilous plants in a coastal ecosystem of dunes was noted by Gottsberger et al. (1988) in Sao Luis and in five apifauna surveys were carried out including the coastal dunes of Brazil (Viana and Alves-dos-Santos 2002). On S. Marcos beach dunes, almost 49% (774) of individuals and 36% (13) of species were large bees (bees of medium-large body length ≥ 1.2 cm) that visited mainly Caesalpiniaceae (*Cassia hispidula*), Asteraceae (*Vernonia arenaria*), Fabaceae (*Crotalaria retusa*), Passifloraceae and Solanaceae. Viana and Alves-

dos-Santos (2002), analysing four different dune surveys in Brazil, have mentioned the predominance of large solitary bees in this ecosystem, due to their foraging ability despite the adverse dry conditions of the dunes. Costa and Ramalho (2001) suggested that the dominance of bee pollination in those places could be a local response to bee species resident in adjacent communities in the coastal landscape, since there were few species of bees resident in the dunes.

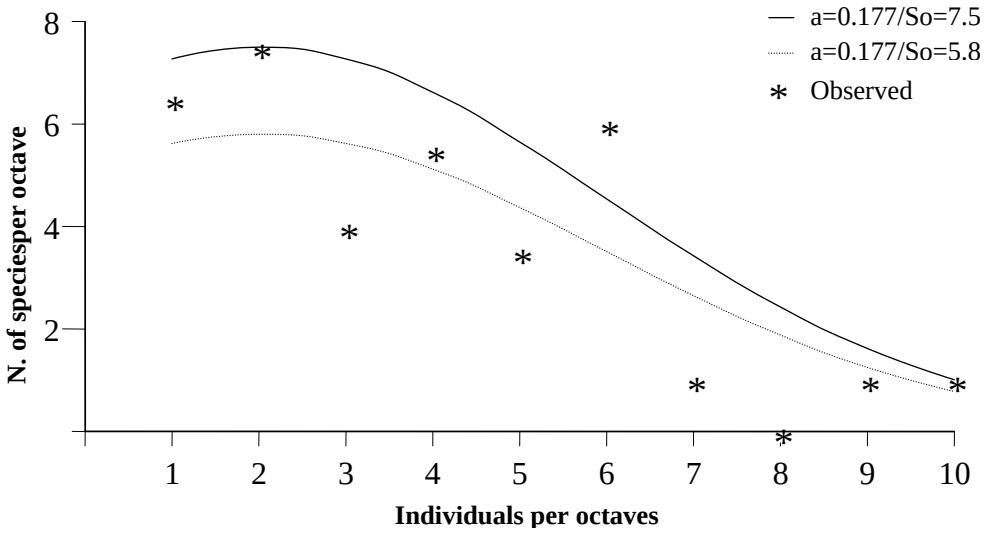


Figure 3 - Distribution of the frequencies of bee species in classes of abundance (Preston, 1948) in S. Marcos beach dunes, S.Luis, MA. So modal = 7.5; Estimated So = 5.8

Table 3 - Diversity of plants visited by predominant native bees collected in the sand dunes of S. Marcos beach, Maranhão, Brazil from November 1993 to October 1994. **n** = richness of plant species visited; **N** = number of bee specimens collected; **H** = Brillouin diversity index; $\mathbf{E_2}$ = Brillouin evenness index.

BEE SPECIES	***n***	***N***	***H***	E_2
Ceratinula sp.2	2	17	0.17	0.29
Ceratinula sp.n.	2	16	0.17	0.29
Centris (*Centris*) *flavifrons*	2	18	0.37	0.62
Centris (*Hemisiella*) *tarsata*	2	9	0.40	0.74
Melitoma segmentaria	4	46	0.64	0.51
Megachile (*Leptorachis*) sp.	3	9	0.79	0.96
Euglossa (*Euglossa*) *cf. cordata*	4	9	0.69	0.70
Augochlorella sp.	4	13	0.93	0.86
Eulaema (*Apeulaema*) *nigrita*	5	37	0.84	0.59
Xylocopa (*Megaxylocopa*) *frontalis*	5	46	0.85	0.59
Ceratina (*Crewella*) *maculifrons*	10	12	1.55	1.00
Centris (*Centris*) *aenea*	5	26	1.04	0.76
Centris (*Centris*) *leprieuri*	6	33	1.08	0.70
Ancyloscelis apiformis	6	37	1.18	0.76
Pseudaugochloropsis pandora	9	40	1.27	0.68
Exomalopsis analis	10	121	1.64	0.76
Apis mellifera	11	456	0.98	0.42
Xylocopa (*Neoxylocopa*) *cearensis*	20	587	2.01	0.69

In spite of many existing typical plant species of dunes and sandbanks, the bee visitors were almost all non-coastal in terms of nesting habitats. In São Luís, only *Centris leprieuri* and *C. aenea* nested in beach dunes, but they were not restricted to this habitat as they were also found in inland, continental areas (nesting in sandbanks – see Gottsberger et al., 1988). *Xylocopa cearensis*, the most common visitor to plants on the dunes of S. Marcos beach was also the main pollinator along beach dunes in Salvador, Bahia (Costa and Ramalho 2001; Viana and Kleinert. 2005).

The pattern of abundance of bee's species in the dunes of S. Luis was a left truncated curve. The truncation point is called the veil line and the left-hand portion of the curve representing the rare and harder to sample species (Magurran, 2004). Among the species of bees collected at S.Marcos beach dunes, 50% were represented by the three first classes, including less than eight individuals (Table 2).

Comparing the Brillouin diversity index of S. Luis with similar ecosystems in the Northeast of Brazil, S. Luis (2.01) is placed between those ecosystems in Bahia (1.97) and Paraíba (2.38) (Viana and Kleinert, 2005; Madeira-da-Silva and Martins, 2003). The Brillouin evenness index (E_2) varied from a minimum of 0.51 in Bahia, to a maximum of 0.65 in Paraíba. Accordingly to Kevan et al. (1997) although the most acceptable means of measuring ecosystem stress are the diversity indexes, environmental problems cannot be detected by diversity analyses *in vacuo*. Hence the lognormal model of species diversity and abundance has been used to assess the ecosystem integrity (Minshall et al., 1985; Laroca et al., 1989; Kevan et al., 1997). Thus, according to the above hypothesis, the S. Luís beach dunes ecosystems are under a disequilibrium caused by anthropogenic activity. Pedroso Júnior (2003) has mentioned the critical situation of the ridges of restinga for being located on the coastal plins that coincidentally shelter or are under direct influence of the biggest urban gathering in the country. Accordingly to Viana and Alves-dos-Santos (2002) the dunes were the most fragile environment among all ecosystems on the coast.

Our results based on the Brillouin index showed that there was a significant positive correlation between the abundance of bees of each species and their preference score (r = 0.53). This could suggest that bees abundant if they could use more host plants. This result was in accordance with the theory of the nested structure of flower/flower-visitor interaction webs (Bascompte et al., 2003) in which "the most generalist plant and animal species interacted among them generating a dense core of interactions to which the rest of the community was attached".

The most frequent habits of plants in the dunes of S. Luis (herbs and creepers) were different from those found by Costa and Ramalho (2001) and Viana (1999, cited by Costa and Ramalho, 2001) in Bahia, where shrubs (37%) were the most common. The same was observed with regard to corolla colours. The pattern presented by Viana (1999, cited by Costa and Ramalho, 2001) (white – 48%, purple – 32% and yellow – 16%) and Costa and Ramalho, 2001 (white – 42%, yellow – 24% and purple – 18%) was different from that found in S. Luis dunes (purple – 30.3%, white – 27.3%, yellow – 16%). These results suggested a spatial heterogeneity and perhaps variation in ecological interactions (flower-visitor) in these ecosystems, as proposed by Costa and Ramalho (2001).

The flowering pattern observed at S. Marcos beach dunes – many species with long and synchronous flowering period (1 –2 flowers per individual) and few species having a long bloom – was typical of ecosystems with adverse climatic conditions. In beach dunes, where strong winds restrict pollinator activity, long blooming periods can represent an adaptive advantage.

It has been observed that convergent selection in the flowering period of sympatric species may be present in some cases (Bawa, 1983). *Ipomoea pes-caprae*, *I. littoral*is and *I. mauritiana* share the same pollinators (*M. segmentaria*, *Ancyloscelis apiformis*) and have the same flowering period. The proximity of individuals with the same flower shape and colour could be a long-distance-attraction-mechanism.

Gottsberger et al. (1988) registered temporal differentiation in anthesis of *Passiflora foetida* and *Turnera melochioides*. With the data obtained from the S. Marcos beach dunes, it was observed that *Ipomoea mauritiana* and *Centrosema* sp. had the same diurnal flowering schedule as *P. foetida*, and *Crotalaria retusa* the same flowering period

of *T. melochioides*. Temporal differentiation of the blooming period among species that share the same pollinators seems to be a common pattern in tropical forests or ecosystems in climax (Vogel and Westerkamp, 1991).

Without doubt, the principal floral reward explored by bees in the S. Marcos beach dunes was nectar and for the majority of bee species collected a certain relation was noted between the proboscis length of the bees and many of the flower forms found, as well as an association between the proboscis length and the body aspect that had also been observed in other communities (Inoye, 1978, 1980; Frankie and Haber, 1983, Armbruster and Guinn, 1989). *Ceratinula*, Augochlorini and *Protomelliturga turnerae*, short proboscis bees, visited mainly short-tubed and radially symmetrical flowers such as Turneraceae (where 55.6% of short proboscis bees were collected) and Passifloraceae (16.6%). While the large proboscis bees (Centridini, Xylocopini and *Melitoma*) were more frequent in tubular corolla flowers that were not so long and narrow, mainly Asteraceae. Euglossini and *X. frontalis* (a very large proboscis bee) showed a close relation with papilionate corolla flowers. Among the large bees (Euglossini, Centridini, Ericrocidini, Xylocopini, Megachilini and *Oxaea*), there was also a great frequency of colourful and zygomorphic flowers: mainly species of Fabaceae, Caesalpiniaceae, Lamiaceae, Asteraceae and Passifloraceae. Short bees (*Exomalopsis*, *Ceratinula*, *Augochlorella* and *Dicranthidium*) were more frequent (66.3%) in Turneraceae, Boraginaceae, Rubiaceae with short and pale (white or yellow) flowers, but in many cases, they were only occasional pollinators.

Pollen was the principal or sole reward in six species (Table 1) and two of these were continuous flowering species. Of the four remaining species, two, *Mimosa diplotricha* and *Commelina virginica*, although not categorised as continuous flowering plants, did produce pollen for about seven months. It was common to collect pollen by touching the surfaces of anthers (Roubik, 1989). This strategy was used mainly by short bees (Ceratinini, Anthidiini, Emphorini) in flowers of *Ipomoea*, *Vernonia*, *Mimosa*, *Passiflora* and others. On the other hand, buzz collecting was dominant in the studied area among species of Euglossini, Centridini, *Xylocopa*, *Exomalopsis*, *Augochlorella* and *Pseudaugochloropsis.*

At S. Marcos beach dunes, bees can be considered one of the principal components in the plant-pollinator communities – the great majority of plants in this ecosystem are melittophilous. Considering plant phenology, the relative constancy in the number of species and individuals flowering in the dry and wet season, offers rewards all the the year round for the visiting bees.

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RESUMO

A comunidade de abelhas silvestres de um ecossistema de dunas de praia do nordeste do Brasil foi estudada quanto a fenologia e preferência por recursos florais. As abelhas visitaram trinta e três espécies de 20 familias de plantas. As espécies mais visitadas foram *Vernonia arenaria* (Asteraceae), *Chamaecrista hispidula* (Caesalpiniaceae), *Passiflora foetida* (Passifloraceae) e *Turnera melochioides* (Turneraceae). Cinquenta e cinco porcento das plantas apresentaram um padrão de florescimento anual ou longo (de 5 a 7 meses). O maior número de espécies floridas foi observada de março a agosto (estação seca), que é o período de maior abundância e diversidade de abelhas. Com base na utilização dos recursos florais pelas abelhas predominantes, três guildas foram observadas:

abelhas com uma utilização restrita de recursos polínicos: *Melitoma segmentaria*, *Centris tarsata*, *Centris flavifrons*, *Ceratinula* sp.; moderadamente generalistas: *Megachile (Leptorachis)* sp., *Euglossa cordata*, *Augochlorella* sp., *Eulaema nigrita* e *Xylocopa frontalis*; e generalistas: *Xylocopa cearensis*, *Apis mellifera*, *Exomalopsis analis* e *Pseudaugochloropsis pandora*.

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