

Trophic niche breadth and niche overlap in a guild of flower-visiting bees in a Brazilian dry forest

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Received 3 May 2012 – Revised 21 August 2012 – Accepted 18 September 2012

Abstract – Trophic niche breadth and niche overlap of bees were studied in a region of Caatinga (a deciduous dry thorn scrub forest) in Brazil with the lowest mean annual rainfall of the country, highly seasonal environmental variation, and an unpredictable rainy season. A null model approach was used to determine if the observed niche overlap in the community differed from that expected by chance. In general, even bee species with wider trophic niches concentrated foraging efforts on flowers of only a few of the available plant species, with low trophic niche overlap between pairs of species and among all species in the community. A randomization test showed niche overlap among the 10 common species in the guild to be significantly less than expected by chance, suggesting the existence of functional complementarity. The structure of communities defined by high functional complementarity is likely to be more sensitive to variation in available resources (e.g., richness and abundance of floral resources for bees). Ecosystem services provided by such communities may be more greatly affected by environmental changes (anthropogenic activities and climate change) than are services provided by communities with greater functional redundancy.

stingless bees / Apoidea / solitary bees / Caatinga / semiarid / niche overlap

1. INTRODUCTION

Identification of the floral resources used by bees is an important tool to define conservation strategies, to understand the potential effects of the loss of populations of pollinators, and for the maintenance of ecosystem services associated with pollination. The geographical distributions of bee species are usually large, whereas the availability of data on their foraging requirements throughout their range often is limited. As a consequence, more locations and vegetation types

must be sampled to fully characterize the niche spaces and resource requirements of pollinators to better inform the conservation of these functionally important species.

Knowledge about bee–plant interactions in semiarid regions of Brazil has increased over the past two decades. Even though the Caatinga is considered one of the most important phytogeographic complexes in South America, information on its floral resources used by bees remains scant with available data limited to a few sites (Aguiar et al. 1995, 2003; Aguiar 2003; Lorenzon et al. 2003; Dórea et al. 2010a, b).

Quantitative studies that assess the trophic niches of bees within the context of the entire guilds of flower visitors in Brazilian semiarid

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Manuscript editor: Klaus Hartfelder

regions are scarce (e.g., Aguiar 2003; Aguiar and Santos 2007). In contrast, such studies have been conducted in rainforests (Wilms et al. 1996; Wilms and Wiechers 1997), in sandstone outcrop vegetation (Franco et al. 2009), and in the Brazilian savanna (= Cerrado; Martins 1995; Nogueira-Ferreira and Augusto 2007). The small sample sizes for bee populations collected from flowers, particularly for solitary bee species, is one of the primary constraints to ecological studies of this group. Overcoming this constraint has been a challenge for studies that endeavor to use rigorous quantitative approaches to elucidate aspects of niche ecology, such as diet breadth and niche overlap among species, which facilitate co-existence in highly diverse native bee communities.

Network analyses revealed that plant–pollinator interactions can display a relatively high degree of complementary specialization at the community scale (Blüthgen and Klein 2011). However, the empirical evidence for complementarity remains scarce. Comparative studies are needed on the effects of functional specialization and complementarity on ecosystems. For example, the way in which such community traits affect biodiversity or the functional relationships of plant–pollinator interactions is poorly understood. Moreover, the effects of habitat loss or fragmentation on niche breadth and overlap are important ecological and conservation issues that require more detailed autecological knowledge to inform conservation policy and management decisions (Bommarco et al. 2010). Generalist species may use several food resources and have a higher probability of meeting their resource needs in a larger number of habitat fragments than do specialists (Quinn et al. 1998; Swihart et al. 2003). In contrast, more specialized species are more reliant of the presence of a particular food resource and typically may satisfy their requirements in only a small subset of habitat fragments (Quinn et al. 1998).

In this work, we studied the trophic niche breadth and trophic niche overlap of bees that utilize floral resources in a semiarid region covered with hyperxerophilous Caatinga vegetation. This

is a highly seasonal environment in which the flowering of many plants is restricted to the wettest periods of the year, resulting in lower availability of floral resources for bees during the dry season (Aguiar et al. 1995). We expected a wider trophic niches and greater niche overlap among bee species with longer periods of activity including much of the dry season, such as social species and solitary species with several generations per year, compared to those with shorter seasons of activity. We used niche overlap measuring techniques and a null model approach to determine if observed levels of community-wide trophic niche overlap differed from those expected by chance.

2. MATERIALS AND METHODS

2.1. Study site

The study area is located at the São João do Cariri Experimental Station (EESJC), in São João do Cariri (7° 25'S, 36° 30'W), Paraíba State, Brazil. The local vegetation in the Cariris Velhos region is an open shrub Caatinga that is dominated by species of *Caesalpinia* and *Aspidosperma* (Andrade-Lima 1981). Climate is hot and semiarid, with summer rains (*Bsh*, Köppen climate classification). Mean annual rainfall is the lowest of the country (387 mm/year), the rainy season is highly unpredictable and the dry season may last up to 10 months (Núcleo de Meteorologia Aplicada 1987).

The year when sampling was conducted was drier than average for the region. During the first 6 months (July to December 1993) samples were collected under drought conditions. Rainfall was more abundant during the second half of the sampling (January to June 1994). Temperature and rainfall data were obtained at the EESJC climatological station.

2.2. Sampling

Flower-visiting bees were captured by two collectors who continuously walked a 3 km trail from 0800 to 1600 hours. The entire sampling trail occurred in typical open shrub Caatinga habitat; therefore, we assumed that all species of flower-visiting bees were

capable of locating and exploiting floral resources on which they typically forage along any portion of the sampling trail. Spatial variation in plant occurrence was not measured and was assumed to not affect patterns of trophic niche breadth or overlap. Samples were collected for 1 year (July 1993–June 1994), bimonthly, with a total of 24 samples collected during 384 h of sampling effort. All bees observed visiting flowers were captured using an entomological net (method by Sakagami et al. 1967). The plant species visited was recorded for each bee. Exsiccates of the visited plants were deposited at the Herbarium Lauro Pires Xavier, Universidade Federal da Paraíba. Voucher specimens of bees were deposited in the Entomological Collection at the Universidade Federal da Paraíba.

2.3. Data analysis

Niche breadth was calculated using the Shannon (1948) index ($H' = -\sum p_k \times \ln p_k$) and trophic niche overlap between pairs of species was calculated by the Schoener index ($NO_{ih} = 1 - \frac{1}{2} \sum k |p_{ik} - p_{hk}|$; Schoener 1968). The distribution of bee visits to plants was assessed for each pair of bee species using the Kolmogorov–Smirnov test for two independent samples (Siegel 1956). To minimize the effect of low abundance on the analyses, trophic niche breadth and niche overlap were calculated only for the 10 bee species represented by 10 or more individuals in the total sample. Amount of trophic overlap among the 10 common species of bees was estimated by the Pianka (1973) and Czechanowski (Feinsinger et al. 1981) indices.

We used a null model approach to compare observed niche overlap to a null distribution of overlap values calculated from randomly generated niche distributions. The null model utilized was the Rosario algorithm (Castro-Arellano et al. 2010), whose performance was previously tested by Presley et al. (2009) and Santos and Presley (2010). The Rosario algorithm preserves the structure of each species' distribution of resource use (e.g., temporal activity pattern, relative frequency of plants visited), thus limiting the randomly generated distributions to be biologically realistic (Presley et al. 2009). In each iteration, Rosario randomly shifts the entire distribution of occurrences (the visits) of each bee species and calculates the amount of overlap in the randomly generated data. The randomization

was repeated 10,000 times to create a null distribution of overlap values for each index (Pianka and Czechanowski); these were compared with the empirical values of the corresponding index to determine significance. As a consequence, the analysis was able to detect either coincidence of occurrences (visits) of bees on plants (i.e., if the observed overlap of the trophic niche was greater than that expected by chance) or segregation in occurrences of bee species on plants (i.e., a lower observed overlap than that expected by chance). This analysis was conducted using the program TimeOverlap (Castro-Arellano et al. 2010) available at <http://hydrodictyon.eeb.uconn.edu/people/willig/Research/activity%20pattern.html>.

3. RESULTS

Forty-one species of bees were recorded visiting the flowers of 51 plant species at the São João do Cariri Experimental Station. More than 10 individuals were recorded for 10 species of bee, which were used for the trophic niche analysis. The number of plants (S_{pi}) visited by each bee species ranged from 2 to 22, and niche breadth (H') varied between 0.15 and 2.25 (Table I). The species with the narrowest trophic niches were *Ceblurgus longipalpis* Urban & Moure, *Megachile (Pseudocentron)* sp. 5, and *Melitomella grisescens* (Ducke), whereas *Dialictus opacus* (Moure), *Trigona spinipes* (Fabricius), and *Frieseomelitta doederleini* (Friese) were the species with the widest trophic niches (Table I).

Niche overlap (NO) between pairs of species varied between 0 and 52 %, and in most cases (40 of the 45 pairs analyzed) was less than or equal to 20 % (Table I). Trophic niche overlap was not significantly different in 1/3 of the cases, and was significantly different in 2/3 of the cases (Table II). No pairs of species exhibited significantly similar trophic niches. Three species (*M. grisescens*, *T. spinipes*, and *F. doederleini*) exhibited highly unique trophic niches that were significantly different from every other species of bee in the community (Table II). *D. opacus* had the highest trophic overlap with other bees, particularly with

Table I. Breadth of trophic niches (H'), richness of visited plants (S_{pl}), number of individuals in each bee species (N_{ind}), and niche overlap (NO) index values between pairs of native bee species in a restricted Caatinga area in Northeastern Brazil.

	H'	S_{pl}	N_{ind}	Niche overlap (NO)								
				At	Cl	Do	Me	Cu	Ea	Mg	Fd	Ts
<i>Sarocolletes</i> sp.	0.983	4	12	0.352	0.098	0.427	0	0	0	0	0.022	0.025
<i>Augochlora</i> cf. <i>thalia</i> Smith, 1879	1.851	11	41	–	0.395	0.522	0.122	0.122	0.122	0.140	0.157	0.099
<i>Ceblurgus longipalpis</i> Urban & Moure, 1993	0.150	3	139	–	0.050	0	0	0	0	0.014	0.022	0.025
<i>Dialictus opacus</i> (Moure, 1940)	2.248	20	96	–	0.083	0.125	0.094	0.143	0.137	0.067		
<i>Megachile</i> (<i>Pseudocentron</i>) sp. 5	0.393	2	15	–	0.133	0.133	0.042	0.457	0.054			
<i>Caenomada unicalcarata</i> (Ducke 1908)	1.446	6	20	–	0.200	0.078	0.043	0.022				
<i>Exomalopsis analis</i> Spinola, 1853	1.228	5	10	–	0.128	0.043	0.022					
<i>Melitoma. grisescens</i> (Ducke 1907)	0.794	5	71	–	0.042	0.042						
<i>Frieseomelitta doederleini</i> (Friese, 1900)	2.077	14	46	–	0.176							
<i>Trigona spinipes</i> (Fabricius, 1793)	2.225	22	317	–								

Augochlora cf. *thalia* Smith (NO=52 %) and *Sarocolletes* sp. (NO=43 %), despite having low overlap with other species (5–14 %). Overlap between the two species of stingless bees (*T. spinipes* and *F. doederleini*) was low (NO=18 %). The distributions of visits of *T.*

spinipes and *F. doederleini* on plant species were significantly different (Table II) indicating segregation of trophic niches. The frequencies of occurrence of these bees on the visited plants (Table III) suggest that the levels of importance of each plant was species-specific,

Table II. Significance of Kolmogorov–Smirnov tests for two independent samples to assess differences in the distribution of visits to plants between pairs of bee species.

	At	Cl	Do	Me	Cu	Ea	Mg	Fd	Ts
<i>Sarocolletes</i> sp.	NS	<0.01	NS	<0.01	NS	NS	<0.01	<0.01	<0.01
<i>Augochlora</i> cf. <i>thalia</i> Smith, 1879		<0.01	NS	<0.01	NS	NS	<0.01	<0.01	<0.01
<i>Ceblurgus longipalpis</i> Urban & Moure, 1993			NS	<0.01	NS	NS	<0.01	<0.01	<0.01
<i>Dialictus opacus</i> (Moure, 1940)				<0.01	NS	NS	<0.01	<0.01	<0.01
<i>Megachile</i> (<i>Pseudocentron</i>) sp. 5					NS	NS	<0.01	<0.01	<0.01
<i>Caenomada unicalcarata</i> (Ducke 1908)						NS	<0.01	<0.01	<0.01
<i>Exomalopsis analis</i> Spinola, 1853							<0.01	<0.01	<0.01
<i>M. grisescens</i> (Ducke 1907)								<0.01	<0.01
<i>Frieseomelitta doederleini</i> (Friese, 1900)									<0.01

Nonsignificant results ($P>0.05$) are represented by NS. Bee species code according to Table I

despite most of the 14 plants visited by *F. doederleini* also being visited by *T. spinipes*. Of the 11 plants shared, only *Poincianella pyramidalis* (Tul.) L.P. Queiroz was intensively visited by *F. doederleini*. Furthermore, the richness of plants visited by *T. spinipes* was much greater than for *F. doederleini* (22 and 14 plant species, respectively, 12 of which were visited by *T. spinipes* but not *F. doederleini*).

The overlap between stingless bees and other bee species was low (NO=2–16 %), except for the pair *F. doederleini*/*Megachile* sp. 5. The high niche overlap index for these two species (NO=46 %) was due to the shared utilization of only two plant species with only *P. pyramidalis* being important for both. Nonetheless, a significant difference existed between the distributions of plant visits of these species (Table II). This finding combined with the analysis of frequency of the visits (Table III) reinforces that high trophic niche overlap between these two species is associated with shared use of *P. pyramidalis*.

C. longipalpis had a narrow trophic niche, with 97 % of its individuals captured on *Cordia leucocephala* Moric. flowers and few visits to two other plant species. The trophic niche of this species was highly distinct from those of other bees, with 0–9 % overlap with all species except *A. thalia*. Niche overlap between *C. longipalpis* and *A. thalia* (NO=39 %) was among the highest for any pair of species; nonetheless, a comparison of the distribution of the visits of *C. longipalpis* and *A. thalia* (Table II) revealed a significant difference between the species. These results in combination with analysis of frequency of the visits (Table III), reinforces the fact that niche overlap for this pair of species was strongly influenced by sharing the resources of one plant, *C. leucocephala*.

Sarocolletes sp. (Colletidae) had a low overlap (NO=0–2 %) with most bees, but higher niche overlap with *A. thalia* (NO=35 %) and *D. opacus* (NO=43 %). The distributions of the visits by *Sarocolletes* sp. and *A. thalia* or *Sarocolletes* sp. and *D. opacus* were not significantly different ($P > 0.05$; Table II). Nevertheless,

the frequency of visits (Table III) of these species to plants suggests that niche overlap was affected by the common use of *Sida galheirensis* Ulbr., the most visited plant by *Sarocolletes* sp. in the area. Trophic overlap among the 10 common species of bees was low (Pianka=0.038, Czechanowski=0.0034), and significantly less than expected by chance ($P < < 0.001$) for each index.

4. DISCUSSION

4.1. Breadth of trophic niches

The bee species with the widest trophic niches in the Caatinga of São João do Cariri were *D. opacus* and *T. spinipes*. Both, and particularly the latter, are known to be extreme generalists that use many plant species as pollen sources, with little relationship between plant phylogeny and resource use (Cortopassi-Laurino and Ramalho 1988; Aguiar 2003; Nogueira-Ferreira and Augusto 2007), and thus considered to be broadly polylectic (sensu Cane and Sipes 2006). Bees with wide trophic niches (*D. opacus*, *T. spinipes*, and *Augochlora* cf. *thalia*) visited >20 plant species, but concentrated their collection of floral resources on two to four of those plant species. The stingless *F. doederleini* also exhibited a wide trophic niche with 40 % of foragers on one plant species (*P. pyramidalis*) and the remaining individuals dispersed among 13 other plant species. It is expected that social species such as *T. spinipes*, *F. doederleini*, *Dialictus* spp., and *Augochlora* spp. (Brady et al. 2006; Michener 2007) should have wide trophic niches and be broadly polylectic because they require a high diversity of floral resources for long-term provision of their colonies (Michener 2007). In a study performed nearby (approximately 50 km), high trophic niche overlap based only on occurrence data was observed between congeneric stingless bees (Martins et al. 2003). That study also noted high use of *P. pyramidalis* (cited as *Caesalpinia pyramidalis* Tul.) by eusocial species.

The species with the narrowest niches were *C. longipalpis* ($H' = 0.15$), *Megachile* (*Pseudocentron*) sp. 5 ($H' = 0.39$), and *M.*

Table III. Plants visited by bee species to obtain floral resources in Caatinga area (São João do Cariri, Paraíba State, Brazil; modified from Aguiar et al. 1995).

Plant species	Bee species									
	Sa	At	Cl	Do	Me	Cu	Ea	MgMG	Fd	Ts
<i>Cereus jamacaru</i>										13
<i>Opuntia palmadora</i>										4
<i>Nicotiana glauca</i>									6	11
<i>Cleome spinosa</i>									2	6
<i>Mimosa ophthalmocentra</i>									1	2
<i>Ipomoea cf. martii</i>		1		1		1	1	51		6
<i>Croton sonderianus</i>		2		3					2	1
<i>Poincianella pyramidalis</i>		2			13			1	19	16
<i>Pilosocereus sp. 1</i>									1	25
<i>Encholirium spectabile</i>										86
<i>Pseudobombax sp. 1</i>										3
<i>Opuntia inamoena</i>				1						80
<i>Gomphrena vaga</i>									2	1
<i>Astronium urundeuva</i>									1	3
<i>Aspidosperma pyriformium</i>									2	1
<i>Caesalpinia ferrea</i>										37
<i>Cordia leucocephala</i>	1	15	135	2					1	8
<i>Croton cf. argyrophyloides</i>				1						
<i>Manihot glaziovii</i>								1		2
<i>Diodia apiculata</i>		3		8	2	3	6	2	2	1
<i>Froelichia humboldtiana</i>							1			
<i>Combretum leprosum</i>				4					4	
<i>Dioclea grandiflora</i>										3
<i>Sida galheirensis</i>	8	11	2	39						
<i>Ipomoea nil</i>		1					1			
<i>Merremia aegyptia</i>		1								
<i>Ipomoea bahiensis</i>		3	2	10				16		
<i>Evolvulus glomeratus</i>				6						
<i>Oxalis sp.1</i>		1		2		10				
<i>Portulaca cf. pilosa</i>				1						
<i>Centrosema cf. brasilianum</i>				1						
<i>Commelina sp. 1</i>				2						
<i>Aniseia martinicensis</i>				5						6
<i>Cassia sericea</i>				1		2				
<i>Evolvulus ovatus</i>				2						
<i>Jacquemontia agrestis</i>		1		3						
<i>Chamaecrista nictitans</i>						3				
<i>Turnera ulmifolia</i>				1						
<i>Gaya gaudichaudiana</i>	2									

Table III (continued)

Plant species	Bee species									
	Sa	At	Cl	Do	Me	Cu	Ea	MgMG	Fd	Ts
<i>Blainvillea lanceolata</i>							1			
Boraginaceae sp. 1										2
<i>Cuphea campestris</i>						1				
<i>Waltheria americana</i>	1									
<i>Spondias tuberosa</i>										2
Unidentified species 1										1
Unidentified species 2				3						

Bee species code according to Table 1

griseascens ($H'=0.79$). The food specialization of *C. longipalpis* on floral resources of *C. leucocephala* (Boraginaceae) had been previously reported by Aguiar and Martins (1994). A recent study (Milet-Pinheiro and Schlindwein 2010) revealed one-to-one reproductive interdependence for members of this bee–plant interaction. *C. longipalpis* evolved prolonged mouthparts that are rare for short-tongued bees and that enable them to access pollen from *C. leucocephala* flowers with short-level anthers as well as the nectar at the base of the flower tube (Milet-Pinheiro and Schlindwein 2010).

Our data suggests that *M. griseascens* was highly food specific (Table III). A preferred association between *Melitomella* spp. and species of Convolvulaceae, mainly *Ipomoea* spp., has been reported previously (Linsley et al. 1980; Schlindwein 2004). Visits of *M. griseascens* to the flowers of plants belonging to three other botanical families in our study may be due to foraging specifically for nectar, at least in *P. pyramidalis* (Leite and Machado 2009) and *Diodia apiculata* K.Schum. (unpublished data).

Almost all individuals of *Megachile* sp. 5 were collected from *P. pyramidalis*; however, this observed narrow trophic niche likely does not represent food specialization. The sample size for this bee was relatively small ($n=15$) and most of the individuals were collected from a single nectar-producing plant (*P. pyramidalis*; Leite and Machado 2009), which can be highly attractive to a large number of bee species in the

community (Aguiar et al. 1995). The niche breadth ($H'=0.98$) of *Sarocolletes* sp. is not among the most narrow, but the distribution of individuals among four plant species shows a narrow relationship between this bee and species of Malvaceae (especially *S. galheirensis*), a common pattern for bees of this genus (Schlindwein 1998, 2004; Aguiar 2003; Zanella and Martins 2003).

4.2. Trophic niche overlap between pairs of species

Approximately 90 % of the pairs of species exhibited low niche overlap (≤ 20 %), similar to observations from the Atlantic Forest (Wilms et al. 1996) and in a different area of Caatinga (Aguiar 2003). Low niche overlap is expected between pairs of species where at least one species has a more specialized diet, such as *C. longipalpis* and *M. griseascens*. The only overlap value above 20 % for *C. longipalpis* occurred with a generalist (*A. thalia*), and was related to common use of *C. leucocephala*, the preferred resource for *C. longipalpis*. The very low niche overlap between *Sarocolletes* sp. and other bees reflects its food specialization, with the only exceptions being the overlap values between it and two generalists (*A. thalia*, $NO=0.35$; *D. opacus*, $NO=0.43$) that use the resource on which *Sarocolletes* sp. specializes (*S. galheirensis*). Nonetheless, small sample size for *Sarocolletes* sp. (12 individuals distributed in four plant species) may have poorly characterized its trophic niche, leading to unreliable overlap

estimates with the more common generalist species *A. thalia* and *D. opacus*.

In our study, we observed that the structure of the bee guild utilizing floral resources in the Caatinga can be affected by the level of flower-feeding specialization of bees as well as by fluctuations in flower abundance of food resources used by bees (e.g., *P. pyramidalis* is highly abundant in the area and is exploited by different bee species throughout the year). These two aspects affect both the trophic niche breadth and the niche overlap between species of generalists, and between generalists and specialists.

4.3. Trophic niche overlap among the 10 common species of bees

Analyses that simultaneously evaluated trophic niche overlap of 10 common species in the guild provided additional evidence that overlap among bee species generally is low and significantly less than expected by chance. A similar low overlap among the most common bee species in a flower-visiting guild was found in a different area of Caatinga (Aguiar and Santos 2007). By using the Petraits (1979) index, they found only 28 % of niche overlap among 10 bee species, as opposed to that observed among the seven most common species of social wasps occurring in the same area, whose overlap was much higher (58 %). Low trophic niche overlap for flower-visiting species in Caatinga suggests that functional complementarity may be common in this biome.

4.4. Specialization and functional complementarity

If species differ in their contribution to ecosystem function or services provided (functional complementarity), several species are required to maintain a high level of functional performance in the ecosystem (Blüthgen and Klein 2011). From the viewpoint of bee requirements, several species of plants are required to supply a bee population because different plant species may provide different kinds of food resources

(pollen, nectar, and oils) that are important for adult and larva survival; thus, plant species are engaged in “resource complementarity” (Blüthgen and Klein 2011). In addition, such resources may be available at different times of year with the plants that provide resources for bee populations with longer activity seasons (such as *T. spinipes*, *F. doederleini*, and *D. opacus*) being engaged in “phenological complementarity” (Blüthgen and Klein 2011). For a more precise characterization of resource complementarity of different plant species, more complete observations are needed to determine the kinds of floral resources made available by each plant for flower-visiting bees. Nevertheless, the roles of *P. pyramidalis* and *D. apiculata* (nectar sources), and of pollen providers are well established as examples of resource complementarity for several species of flower-visiting bees in this community. Food source specialization and functional complementarity of the floral visitors are related, considering that complementarity requires a certain degree of specialization of each bee species. Complementarity means that species are functionally different, which requires relatively narrow niches. Alternatively, a high degree of generalization is associated with high niche overlap and functional redundancy (Blüthgen and Klein 2011). In our study, we observed low niche overlap, differential use of resources, and specialization on certain plant species by some floral visitors. These results suggest that functional complementarity, a consequence of niche differentiation by flower-visiting bees, is common and pervasive in bee–plant interactions in the Caatinga, playing a key role in species coexistence and in maintaining taxonomic and functional diversity among bees. It is not clear if the observations on niche breadth and complementarity of bees in the Caatinga are applicable to more mesic adjacent biomes where the bee faunas are characterized by several eusocial species with high abundance (e.g., Menezes-Pedro and Camargo 1991; Wilms et al. 1996; Wilms and Wiechers 1997), which may partition niche space differently.

The low trophic niche overlap and the variations in frequency of visits by different

bee species on several plant species reveal distinct diets of populations and complementarity in the use of the available floral resources in the environment. Such segregation in trophic niches may have resulted from a combination of factors such as the existence of several levels of preference/fidelity of the bee species for specific plants, temporal and spatial fluctuations in resource abundance, duration of the blooming period, length of the adult bee activity period, and differences in the communication capacity about food resources among different bee species.

ACKNOWLEDGEMENTS

G.M.M. Santos thanks to the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) of Brazil for a grant (N° 309711/2009-6). S. Presley was supported by the Center for Environmental Sciences and Engineering at the University of Connecticut and by a grant (DEB-0620910) from the National Science Foundation (NSF) to the Institute of Tropical Ecosystem Studies, University of Puerto Rico, and the International Institute of Tropical Forestry as part of the Long-Term Ecological Research Program in the Luquillo Experimental Forest.

Etendue et chevauchement des niches trophiques chez une guilda d'abeilles butinant les fleurs dans une forêt sèche brésilienne

Abeille sans aiguillon / Apoidea / abeille solitaire / Caatinga / Brésil / chevauchement de niche / zone semi-aride

Breite und Überlappungen der Nahrungsnischen einer Gilde blütenbesuchender Bienen in einem brasilianischen Trockenwald

Stachellose Bienen / Apoidea / solitäre Bienen / Caatinga / Halbtrockenzzone / Nischenüberlappung

REFERENCES

Aguiar, C.M.L. (2003) Utilização de recursos florais por abelhas (Hymenoptera: Apoidea) em uma área de

Caatinga (Itatim, Bahia, Brasil). *Rev. Bras. Zool.* **20**, 457–467

Aguiar, C.M.L., Martins, C.F. (1994) Fenologia e preferência alimentar de *Ceblurgus longipalpis* Urban & Moure, 1993 (Hymenoptera, Halictidae, Dufoureaeinae). *Rev. Nordest. Biol.* **9**, 125–131

Aguiar, C.M.L., Martins, C.F., Moura, A.C.A. (1995) Recursos florais utilizados por abelhas (Hymenoptera, Apoidea) em área de Caatinga (São João do Cariri, Paraíba). *Rev. Nordest. Biol.* **10**, 101–117

Aguiar, C.M.L., Zanella, F.C.V., Martins, C.F., Carvalho, C.A.L. (2003) Plantas visitadas por *Centris* spp. (Hymenoptera, Apidae, Centridini) para obtenção de recursos florais na caatinga. *Neotrop. Entomol.* **32**, 247–259

Aguiar, C.M.L., Santos, G.M.M. (2007) Compartilhamento de recursos florais por vespas sociais (Hymenoptera: Vespidae) e abelhas (Hymenoptera: Apoidea) em uma área de Caatinga. *Neotrop. Entomol.* **36**, 836–842

Andrade-Lima, D. (1981) The Caatingas dominium. *Rev. Bras. Bot.* **4**, 149–163

Bommarco, R., Biesmeijer, J.C., Meyer, B., Potts, S.G., Pöyry, J., Roberts, S.P.M., Steffan-Dewenter, I., Öckinger, E. (2010) Dispersal capacity and diet breadth modify the response of wild bees to habitat loss. *Proc. R. Soc. B* **277**, 2075–2082

Blüthgen, N., Klein, A.M. (2011) Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic Appl. Ecol.* **12**, 282–291

Brady, S.G., Sipes, S., Pearson, A., Danforth, B.N. (2006) Recent and simultaneous origins of eusociality in halictid bees. *Proc. R. Soc. B* **273**, 1643–1649

Cane, J.H., Sipes, S. (2006) Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty. In: Waser, N.M., Ollerton, J. (eds.) *Plant–pollinator interactions: from specialization to generalization*, pp. 99–122. The University of Chicago Press, Chicago

Castro-Arellano, I., Lacher Jr., T.E., Willi, M.R., Rangel, T.F. (2010) Assessment of assemblage-wide temporal niche segregation using null models. *Method. Ecol. Evol.* **1**, 311–318

Cortopassi-Laurino, M., Ramalho, M. (1988) Pollen harvest by africanized *Apis mellifera* and *Trigona spinipes* in São Paulo: botanical and ecological views. *Apidologie* **19**, 1–24

Dórea, M.C., Aguiar, C.M.L., Figueroa, L.E.R., Lima, L.E.R., Santos, F.A.R. (2010a) Pollen residues in nests of *Centris tarsata* Smith (Hymenoptera, Apidae, Centridini) in a tropical semiarid area in NE Brazil. *Apidologie* **41**, 557–567

Dórea, M.C., Aguiar, C.M.L., Figueroa, L.E.R., Lima, L.E.R., Santos, F.A.R. (2010b) Residual pollen in nests of *Centris analis* (Hymenoptera, Apidae, Centridini) in an area of Caatinga vegetation from Brazil. *Oecol. Aust.* **14**, 232–237

- Feinsinger, P., Spears, E.E., Poole, R.W. (1981) A simple measure of niche breadth. *Ecology* **62**, 27–32
- Franco, E.L., Aguiar, C.M.L., Ferreira, V.S., Rebouças, P.L.O. (2009) Plant use and niche overlap between the introduced honey bee (*Apis mellifera*) and the native bumblebee (*Bombus atratus*). *Sociobiology* **53**, 141–150
- Leite, A.V., Machado, I.C. (2009) Biologia reprodutiva da "catingueira" (*Caesalpinia pyramidalis* Tul. Leguminosae-Caesalpinioideae), uma espécie endêmica da caatinga. *Rev. Bras. Bot.* **32**, 79–88
- Linsley, E.G., MacSwain, J.W., Michener, C.D. (1980) Nesting biology and associates of *Melitoma* (Hymenoptera, Anthophoridae). *Univ. Calif. Publ. Entomol.* **90**, 1–39
- Lorenzon, M.C., Matrangolo, C.A.R., Schoederer, J.H. (2003) Flora visitada pelas abelhas eussociais (Hymenoptera, Apidae) na Serra da Capivara, em Caatinga do Sul do Piauí. *Neotrop. Entomol.* **32**, 27–36
- Martins, C.F. (1995) Flora apícola e nichos tróficos de abelhas (Hym, Apoidea) na Chapada Diamantina (Lençóis-BA, Brasil). *Rev. Nordest. Biol.* **10**, 119–140
- Martins, C.F., Moura, A.C.A., Barbosa, M.R.V. (2003) Bee plants and relative abundance of corbiculate Apidae species in a Brazilian caatinga area. *Rev. Nordest. Biol.* **17**, 63–74
- Menezes-Pedro, S.R., Camargo, J.M.F. (1991) Interactions on floral resources between the Africanized honey bee *Apis mellifera* L. and the native bee community (Hymenoptera: Apoidea) in a natural "cerrado" ecosystem in southeast Brazil. *Apidologie* **22**, 397–415
- Michener, C.D. (2007) The bees of the world, 2nd edn, p. 953. The Johns Hopkins University Press, Baltimore
- Milet-Pinheiro, P., Schlindwein, C. (2010) Mutual reproductive dependence of distylic *Cordia leucocephala* (Cordiaceae) and oligolectic *Ceblurgus longipalpis* (Halictidae, Rophitinae) in the Caatinga. *Ann. Bot.* **106**, 17–27
- Nogueira-Ferreira, F.H., Augusto, S.C. (2007) Amplitude de nicho e similaridade no uso de recursos florais por abelhas eussociais em uma área de cerrado. *Biosci. J.* **23**, 45–51
- Núcleo Meteorologia de Aplicada (1987) Atlas Climatológico do Estado da Paraíba. Universidade Federal da Paraíba, Campina Grande
- Petratis, P.S. (1979) Likelihood measures of niche breadth and overlap. *Ecology* **60**, 703–710
- Pianka, E.R. (1973) The structure of lizard communities. *Annu. Rev. Ecol. Syst.* **4**, 53–74
- Presley, S.J., Willig, M.R., Castro-Arellano, I., Weaver, S.C. (2009) Effects on habitat conversion on temporal activity patterns of phyllostomid bats in lowland Amazonian rainforest. *J. Mammal.* **90**, 210–221
- Quinn, R.M., Caston, K.J., Roy, D.B. (1998) Coincidence in the distributions of butterflies and their foodplants. *Ecography* **21**, 279–288
- Sakagami, S.F., Laroca, S., Moure, J.S. (1967) Wild bee biocenotics in São José dos Pinhais (PR) South Brazil—preliminary report. *J. Fac. Sci. Hokkaido U Ser. Zool.* **16**, 253–291
- Santos, G.M.M., Presley, S. (2010) Niche overlap and temporal activity patterns of social wasps in a Brazilian cashew orchard. *Sociobiology* **56**, 121–131
- Schlindwein, C. (1998) Frequent oligolecty characterizing a diverse bee–plant community in a xerophytic bushland of subtropical Brazil. *Stud. Neotrop. Fauna E.* **33**, 46–59
- Schlindwein, C. (2004) Are oligolectic bees always the most effective pollinators? In: Freitas, B.M., Pereira, J.O.P. (eds.) Solitary bees—conservation, rearing and management for pollination, pp. 231–240. Universidade Federal do Ceará, Fortaleza
- Schoener, T.W. (1968) The *Anolis* lizard of Bimini: resource partitioning in a complex fauna. *Ecology* **49**, 704–726
- Shannon, C.E. (1948) The mathematical theory of communication. In: Shannon, C.E., Weaver, W. (eds.) The mathematical theory of communication, pp. 3–91. University Illinois Press, Urbana
- Siegel, S. (1956) Nonparametric statistics for behavioral sciences. McGraw-Hill, New York
- Swihart, R.K., Gehring, T.M., Kolozsvary, M.B., Nupp, T.E. (2003) Responses of 'resistant' vertebrates to habitat loss and fragmentation: the importance of niche breadth and range boundaries. *Div. Dist.* **9**, 1–18
- Wilms, W., Imperatriz-Fonseca, V.L., Wolf, E. (1996) Resource partitioning between highly eusocial bees and possible impact of the introduced Africanized honey bee on native stingless bees in the Brazilian rain forest. *Stud. Neotrop. Fauna E.* **31**, 37–151
- Wilms, W., Wiechers, B. (1997) Floral resource partitioning between native *Melipona* bees and the introduced Africanized honey bees in the Brazilian Atlantic rain forest. *Apidologie* **28**, 339–355
- Zanella, F.C.V., Martins, C.F. (2003) Abelhas da caatinga: biogeografia, ecologia e conservação. In: Leal, I.R., Tabarelli, M., Silva, J.M.C. (eds.) Ecologia e Conservação da Caatinga, pp. 75–134. Editora Universitária, UFPE, Recife