

Niche Overlap and Network Specialization of Flower-Visiting Bees in an Agricultural System

DM CARVALHO¹, SJ PRESLEY², GMM SANTOS¹

¹Lab de Entomologia, Univ Estadual de Feira de Santana, Feira de Santana, Bahia, Brasil

²Center for Environmental Sciences and Engineering and Dep of Ecology and Evolutionary Biology, Univ of Connecticut, Storrs, CT, USA

Keywords

Dietary complementarity, Guild structure, interactions, temporal redundancy, Specialization

Correspondence

GMM Santos, Laboratório de Entomologia, Univ Estadual de Feira de Santana, 44031-460 Feira de Santana, Bahia, Brazil; gmms.uefs@gmail.com

Edited by Fernando B Noll – UNESP

Received 1 April 2014 and accepted 24 August 2014
Published online: 11 September 2014

© Sociedade Entomológica do Brasil 2014

Abstract

Different resource use strategies manifest as differences in the realized niches of species. Niche segregation may involve several dimensions of the niche, such as diet, space, and time. We measured the level of redundancy and complementarity of a bee–plant interaction network in an agricultural system. Because flower resource diversity is high and resource abundance associated with flowering phenology varies throughout the year, we hypothesized that trophic overlap in the community would be low (i.e., high niche complementarity). In contrast, we expected a combination of physiological constraints and exploitation competition to create high temporal overlap, leading to high redundancy in the time of use of floral resources. Dietary overlap was low ($NO_{ih}=0.18$): niches of 88% of species pairs had less than 30% overlap. In contrast, temporal overlap was intermediate ($NO_{ih}=0.49$): niches of 65% of species pairs had 30% to 60% overlap. Network analysis showed that bees separated their dietary niches and had intermediate complementary specialization ($H_2'=0.46$). In terms of their temporal niches ($H_2'=0.12$), bees were generalists, with high temporal redundancy. Temperature was not a key factor in the determination of niche overlap, suggesting that environmental factors do not likely have a primary role in determining high redundancy in the temporal use of floral resources. Rather, temporal overlap is likely associated with the timing of nectar production by flowers. Our results suggest that bees partition a wide variety of available floral resources, resulting in low dietary overlap and intermediate temporal overlap.

Introduction

Niche theory predicts that structurally complex and species-rich natural habitats should contain a large number of resources to facilitate coexistence among species that partition resources into particular niche spaces (Chase & Leibold 2003, Chase 2011). Agricultural activities often simplify environments while increasing resource availability via planting of monocultures, irrigation, and fertilization (Santos *et al* 2009). Structurally complex environments tend to have high species richness and diversity (e.g., Humphrey *et al* 1999, Tews *et al* 2004, Clemente *et al* 2013, Dáttilo *et al* 2014b); because the number of microhabitats (i.e., niche spaces) in these environments is high. Complex habitats offer good

protection against predators, high availability and diversity of food, and a large number of nesting substrates, resulting in a large number of possible niches (Santos *et al* 2007).

Knowledge of floral resources is required for the successful conservation of bee communities (Aguiar *et al* 2012), especially in agricultural environments, where pollination deficit (Biesmeijer *et al* 2006) can lead to severe economic loss (Imperatriz-Fonseca *et al* 2012). Ecological attributes of the plant community (e.g., differences in flowering phenology) may determine the degree of dietary specialization, number of resource use strategies, and the diversity and abundance of the flower–visitor community (Heithaus 1979). Hence, variation in ecological attributes of the plant

community strongly affect the structure of the flower–visitor community, which may exhibit high complementarity (i.e., low niche overlap) or high redundancy (i.e., high niche overlap), depending on the way in which flower-visiting species partition niches (Blüthgen & Klein 2010).

Different resource use strategies (i.e., the type and amount of each resource used) manifest as differences in the realized niches of the species that comprise a guild (e.g., Chase & Leibold 2003, Chase 2011, Lange *et al* 2013). If niches of specialists are sufficiently different, they allow for coexistence via reduction of competition (Levine & HilleRisLambers 2009). Species may differ in diet (Aguiar 2003, Aguiar & Santos 2007), use of space (Hoehn *et al* 2008), activity time (Stone *et al* 1999, Castro-Arellano & Lacher 2009, Dáttilo *et al* 2014a), or multiple dimensions of their niche (Chase 2011). Evaluation of the amount of niche overlap among species in a guild can indicate the degree of specialization or generalization in resource use by each species, as well as the level of redundancy (i.e., multiple species performing the same function or occupying the same niche) or complementarity (i.e., the degree to which all species are required for all ecosystem functions to be conducted) in the community (Blüthgen & Klein 2010).

High complementarity in a flower-visiting community suggests that high plant diversity is important for the maintenance of pollinator diversity (Blüthgen & Klein 2010, Carvalho *et al* 2013), and that high pollinator diversity is required to maintain plant diversity. In general, faunal richness is expected to reflect the number of realized niches in a habitat or landscape and should be closely related to vegetational complexity (Díaz & Cabido 2001, Santos *et al* 2007, Jetz *et al* 2009). Moreover, pollinator richness is strongly related to plant richness (Weiner *et al* 2011); hence, identification of floral resources used by bees is important for the development of effective conservation strategies (Aguiar *et al* 2012). Abiotic factors may constrain times of activity for plant pollinators (Herrera 1995). This may be especially problematic for bees as they are endothermic during flight and heat production in wing muscles could lead to overheating when ambient temperatures exceed 33°C (Roberts & Harrison 1999). Consequently, time of day may be a limiting resource that is partitioned to reduce completion among bees. Nonetheless, nectar availability is often greatest at dawn (Saunders 1982, Goulson & Darvill 2004). As a result, nectar availability and abiotic constraints may combine to create high overlap of temporal activity patterns of bees.

We assessed the level of niche redundancy and complementarity of a bee community in an agricultural system. Because available flower resources in this agricultural system are highly diverse and highly seasonal, we hypothesized that dietary overlap among flower-visiting bees should be relatively low. In contrast, due to a combination of abiotic environmental constraints associated with temperature and

water use and the daily time of production of floral resources, we hypothesize that overlap should be high for the temporal niche axis.

Material and Methods

The study site, Chácara Bocaúva, covers an area of 23.4 ha and is located in the municipality of Feira de Santana, Bahia, northeastern Brazil (12°15'25"S, 38°57'54"W). Climate of the region is semi-arid with an average annual temperature of 23.5°C. A rainy period occurs from April to June, with an average annual rainfall of 867 mm and risk of drought (MMA 2009). Crops of fruits and vegetables dominate the landscape, including *Citrus sinensis* (orange), *Citrus limonum* (lime), *Mangifera indica* (mango), *Psidium guajava* (guava), *Passiflora edulis* (passion fruit), *Capsicum annuum* (papiakra), *Cucurbita* sp. (pumpkin), and *Cucumis anguria* (bur cucumber). All plants were cultivated with no chemical additives.

In each sampling session, two collectors captured flower-visiting bees with entomological nets along a 1,000-m long × 10-m wide transect. Each transect was sampled for 12 consecutive hours (0600 to 1800 hour). Sampling was carried out monthly from August 2011 to July 2012. Each plant was inspected for 5 min, following Sakagami *et al* (1967). Every hour, we recorded the temperature and relative humidity of the area. Insect specimens were deposited in the Entomological Collection Professor Johan Becker at the Zoological Museum of the State University of Feira de Santana (MZFS), and plants were deposited in the Herbarium of the State University of Feira de Santana (HUEFS). All plants visited by bees, cultivated plants or not, were recorded, collected, and identified.

To assess dietary and temporal overlap, we used data on bee abundance for each floral resource (i.e., flowering plant species) and time (i.e., 1-h time intervals of collection). To ensure that temporal and dietary niches were well characterized by the data, only species with at least 10 observations were included in analysis. We calculated the level of overlap of the dietary and temporal niches between pairs of bee species with the Schoener index (1982), $NO_{ih} = 1 - \frac{1}{2} \sum_k |p_{ik} - p_{hk}|$, where i and h are the total number of individuals collected in each plant species or time interval, and p_{ik} and p_{hk} are the relative abundances of each bee species.

We analyzed niche overlap among all species using the Pianka (1973) overlap index (Feinsinger *et al* 1981). To determine if community-wide niche overlap was different from that expected by chance, we used a null-model analysis based on 10,000 randomizations (Rosario algorithm) conducted in the TimeOverlap software (Castro-Arellano *et al* 2010). This algorithm creates randomized versions of the original matrix by shifting the distribution of each species to a random number of places (i.e., time intervals for

temporal activity and resource types of diet) between 1 and n (total number of timer intervals or resource types) and calculates niche overlap for each randomly generated matrix. The significance of observed values was determined by comparison of the empirical value to the resulting null distribution, using a two-tailed test and an α level of 0.05.

To determine if daily or seasonal variation in abiotic factors affected temporal niche overlap of flower-visiting bees, we used a generalized linear mixed-effects model (GLMM) with binomial error distribution. We used the amount of overlap and the number of visits as response variables with temperature as the independent variable and day, hour, and total bee abundance as model II random factors. Because microclimatic data are frequently correlated, we tested for a correlation between temperature and humidity to determine if they reflect independent sources of environmental variation.

In addition, we calculated the complementary specialization in interactions at the network level with the package bipartite for R (Dormann *et al* 2009). Data were organized as adjacency matrices and represented as bipartite graphs. We calculated the degree of specialization in diet and activity time using the index H_2' (see Blüthgen *et al* 2006), which varies from 0 (generalized interactions) to 1 (specialized interactions). This index (H_2') characterizes the degree of specialization or partitioning among two parties in the entire network and considers the number of interactions that occur for a given species within the network and how these interactions differ from those of other species. (Blüthgen *et al* 2006). We estimated the significance of H_2' with a Monte Carlo procedure in which 10,000 random matrices were generated using the null model Patefield (Blüthgen *et al* 2006).

Results

We collected 54 bee species visiting the flowers of 70 plant species (Table 1). The number of bee and plant species varied across months (Fig 1). The number of bee species collected each month varied from 7 to 29, and the number of plant species visited varied from 12 to 22. Among the bee species, 18 were represented by more than 10 individuals and were included in analyses.

We performed 153 pairwise comparisons for each niche axis (i.e., diet and time of activity) formed by 18 bee species (Table 1). The most abundant species were *Apis mellifera* Linnaeus ($n=833$), *Trigona spinipes* Fabricius ($n=722$), and *Tetragonisca angustula* Latreille ($n=116$). Among plants, *Citrus limonum* ($n=228$), *Portulaca oleracea* ($n=205$), and *Richardia grandiflora* ($n=194$) were the most frequently visited species, accounting for 27% of all visits.

Dietary overlap for species pairs (NO_{ih} index) varied from 0.0 (no dietary overlap) to 0.67, and was greatest between *Megachile (Dactylomegachile)* sp. and *Exomalopsis (Phamonalopsis)* sp. ($NO_{ih}=0.67$), *Pseudaugochlora* sp. and *Ceratina* sp1. ($NO_{ih}=0.67$), and *Augochlora* sp. 5 and *Augochlora* sp. 6 ($NO_{ih}=0.66$). Dietary overlap was low on average, with niches of 88% of species pairs exhibiting <30% overlap (Table 2). Temporal overlap varied from 0.0 to 0.79, and was greatest between *Apis mellifera* and *Tetragonisca angustula* ($NO_{ih}=0.79$), *Augochlora* sp. 6 and *Partamona* sp. 1 ($NO_{ih}=0.76$), and *Apis mellifera* and *Ceratina* sp. 1 ($NO_{ih}=0.71$). In general, temporal overlap was intermediate to high, with niche overlap of 65% of species pairs ranging from 30% to 60% (Table 3).

The time of day with the highest frequency of visits was in the morning from 0600 to 0800 hours, which encompassed 41% of all visits. Temperature and humidity data were highly correlated, resulting in the use of just temperature in the following analyses. Temperature was mild on average during these times: 22°C, 23°C, and 25°C, respectively. However, the activity of 15 of 18 species did not respond to temperature, with only *Augochlora* sp. 5 ($\chi^2=86.69$, $df=3$, $n=96$, $p=0.003$), *Exomalopsis (Phamonalopsis)* sp. ($\chi^2=81.74$, $df=3$, $n=48$, $p=0.004$), and *Xylocopa suspecta* ($\chi^2=91.90$, $df=3$, $n=48$, $p=0.002$) being negatively correlated with temperature. Considering that the activity of only 3 of 18 species was correlated with temperature, we can conclude that temperature is not a primary factor affecting patterns of temporal overlap in the community as a whole. Nonetheless, activity of particular bee populations may be affected by temperature.

Dietary overlap for all abundant species as a group was not significantly different than expected by chance (Pianka's index=0.18, $p>0.05$). In contrast, temporal overlap was significantly greater than expected by chance (Pianka's index=0.49, $p<0.001$). Network analysis of diet indicated that bees were neither highly specialized nor highly generalized ($H_2'=0.46$, $p<0.001$), which is consistent with the results for dietary overlap (Fig 2). In terms of temporal overlap ($H_2'=0.12$, $p<0.001$), the bees were generalists (Fig 3), with most bees being active throughout the day.

Discussion

Results were consistent with our working hypotheses: (1) that flower-visiting bees in this agriculturally dominated system strongly partition the dietary niche axis exhibiting niche complementarity, and (2) that flower-visiting bees exhibit a great deal of overlap in the temporal niche dimension (time of day that flowers are visited). This difference in degree of partitioning between niche dimensions suggests that coexisting species may have similar environmental requirements, responding to a balance between resource availability

Table 1 Species of bees and visited plants in an agriculturally dominated landscape in the municipality of Feira de Santana, northeastern Brazil, from August 2011 to July 2012.

Bees	Code	<i>n</i>	Plants	Code
<i>Apis mellifera</i> Linnaeus	B1	833	<i>Citrus limonum</i>	Pc1
<i>Trigona spinipes</i> (Fabricius)	B2	722	<i>Portulaca oleracea</i>	Pi2
<i>Tetragonisca angustula</i> (Latreille)	B3	116	<i>Richardia grandiflora</i>	Pi3
<i>Exomalopsis (Phamonalopsis)</i>	B4	87	<i>Moringa oleifera</i>	Pc4
<i>Xylocopa frontalis</i> (Olivier)	B5	83	<i>Sechium edule</i>	Pc5
<i>Partamona</i> sp. 1	B6	66	<i>Bixa orellana</i>	Pc6
<i>Ceratina</i> sp. 1	B7	53	<i>Passiflora edulis</i>	Pc7
<i>Pseudaugochlora</i> sp.	B8	36	<i>Citrus sinensis</i>	Pc8
<i>Trigona</i> sp. 3	B9	34	<i>Stemodia foliosa</i>	Pi9
<i>Exomalopsis analis</i> Spinola	B10	19	<i>Commelina benghalensis.</i>	Pi10
<i>Melipona scutellaris</i> Latreille	B11	21	Rubiaceae (Species unidentified)	Pi11
<i>Augochlora</i> sp. 6	B12	16	<i>Cucurbita</i> sp.	Pc12
<i>Xylocopa suspecta</i> Moure & Camargo	B13	13	Unidentified Euphorbiaceae	Pc13
<i>Megachile (Dactylomegachile)</i>	B14	14	<i>Lippia alba</i>	Pc14
<i>Augochlora</i> sp. 5	B15	13	<i>Solanum stipulaceum</i>	Pi15
<i>Trigona</i> sp. 1	B16	14	<i>Borreria verticillata</i>	Pi16
<i>Centris aenea</i> Lepeletier	B17	10	<i>Anacardium occidentale</i>	Pc17
<i>Paratrigona subnuda</i> Moure	B18	10	<i>Merremia aegyptia</i>	Pi18
<i>Augochlora</i> sp. 3*	B19	9	<i>Persea americana</i>	Pc19
<i>Tetrapedia diversipes</i> Klug*	B20	8	<i>Zea mays</i>	Pc20
<i>Ceratina</i> sp. 6*	B21	7	<i>Citrus</i> sp.	Pc21
<i>Xylocopa nigrocincta</i> Smith*	B22	7	<i>Varonia</i> sp.	Pi22
<i>Paratetrapedia (Xanthopedia)*</i>	B23	5	<i>Scoparia dulcis</i>	Pi23
<i>Augochlora</i> sp. 2*	B24	5	<i>Schinus terebinthifolius</i>	Pc24
<i>Ceratina</i> sp5.*	B25	5	<i>Nicandra physaloides</i>	Pi25
<i>Xylocopa grisescens</i> Lepeletier*	B26	6	<i>Urochloa</i> sp.	Pi26
<i>Megachile (Sayapis)*</i>	B27	4	<i>Momordica charantia</i>	Pi27
<i>Ancylloscelis apiformis*</i>	B28	4	<i>Ocinum</i> sp.	Pc28
<i>Augochlora</i> sp. 4*	B29	4	<i>Cosmos sulphureus</i>	Pi29
<i>Augochloropsis</i> sp. 2*	B30	3	<i>Marsypianthes chamaedrys</i>	Pi30
<i>Xylocopa ordinaria</i> Smith*	B31	3	<i>Leucaena leucocephala</i>	Pi31
<i>Centris tarsata</i> Smith*	B32	3	<i>Melanthera latifolia</i>	Pi32
<i>Epicharis flava</i> Friese*	B33	3	<i>Rhaphanus raphanistrum</i>	Pi33
<i>Apidae (Emphorini)</i> Cf.*	B34	3	<i>Physalis angulata</i>	Pi34
<i>Trigona</i> sp. 2*	B35	3	<i>Solanum palinacanthum</i>	Pi35
<i>Centris fuscata</i> Lepeletier*	B36	2	(Unidentified)	Pi36
<i>Megachile (Tylomegachile)*</i>	B37	2	<i>Centratherum punctatum</i>	Pi37
<i>Megachile (Acentron)*</i>	B38	2	<i>Mimosa</i> sp.	Pi38
<i>Centris sponsa</i> Smith	B39	8	<i>Mangifera indica</i>	Pc39
<i>Frieseomelitta</i> sp.*	B40	3	<i>Psidium guajava</i>	Pc40
<i>Ceratina</i> sp. 2*	B41	2	<i>Byrsonima sericae</i>	Pi41
<i>Ceratina</i> sp. 3*	B42	3	<i>Ipomea</i> sp.	Pi42
<i>Ceratina</i> sp. 4*	B43	2	<i>Hyptis</i> sp. 1	Pi43
<i>Xylocopa</i> sp. 1*	B44	1	<i>Amaranthus</i> sp.	Pi44
<i>Bombus</i> sp.*	B45	2	<i>Alternanthera</i> sp.	Pi45
<i>Centris analis</i> Fabricius*	B46	1	<i>Malpighia glabra</i>	Pc46
<i>Oxaea</i> sp. 1*	B47	1	<i>Zygia latifolia</i>	Pi47
<i>Megachile (Pseudocentron)*</i>	B48	1	<i>Ipomea batata</i>	Pc48

Table 1 (continued)

Bees	Code	<i>n</i>	Plants	Code
<i>Epicharis nigrita</i> Friese *	B49	1	<i>Ipomea bahiensis</i>	Pi49
<i>Melipona</i> sp.*	B50	1	<i>Phaseolus</i> sp.	Pc50
<i>Partamona</i> sp. 2*	B51	1	<i>Capsicum annuum</i>	Pc51
<i>Augochlora</i> sp. 1*	B52	1	<i>Cucumis anguria</i>	Pc52
<i>Augochloropsis</i> sp. 1*	B53	1	<i>Merremia cissoides</i>	Pi53**
<i>Ceratina</i> sp. 7*	B54	1	<i>Abelmoschus</i> sp.	Pc54
			<i>Spondias purpurea</i>	Pc55
			<i>Passiflora</i> sp.	Pc56
			<i>Cordia curassavica</i>	Pi57
			<i>Waltheria indica</i>	Pi58
			<i>Luffa</i> sp.	Pc59
			<i>Ipomea</i> sp.	Pi60
			<i>Talinum triangulare</i>	Pi61
			<i>Duranta vestita</i>	Pi62
			<i>Heliotropium</i> sp.	Pi63
			<i>Corchorus hirtus</i>	Pi64
			<i>Foeniculum vulgare</i>	Pi65
			<i>Hyptis</i> sp2.	Pi66
			<i>Callistemon citrinus</i>	Pi67
			<i>Piriqueta racemosa</i>	Pi68
			<i>Solanum</i> sp.	Pi69
			<i>Senna</i> sp.	Pi70

Plants are classified as cultivated plants (Pc) or weeds (Pi)

*Bees represented by less than 10 individuals were excluded from the analysis.

**Plant visited by only by bee species with less than 10 individuals that was excluded from the analysis.

and environmental parameters (Leibold 1998). More specifically, abiotic filtering may determine which species can occur in the system, rather than the time at which species are active. Because nectar is most abundant at sunrise and

decreases in abundance throughout the day as it is consumed, intra-specific competition may favor individuals (or colonies) that forage earlier in the day. In contrast, interspecific competition appears to be greatly reduced via

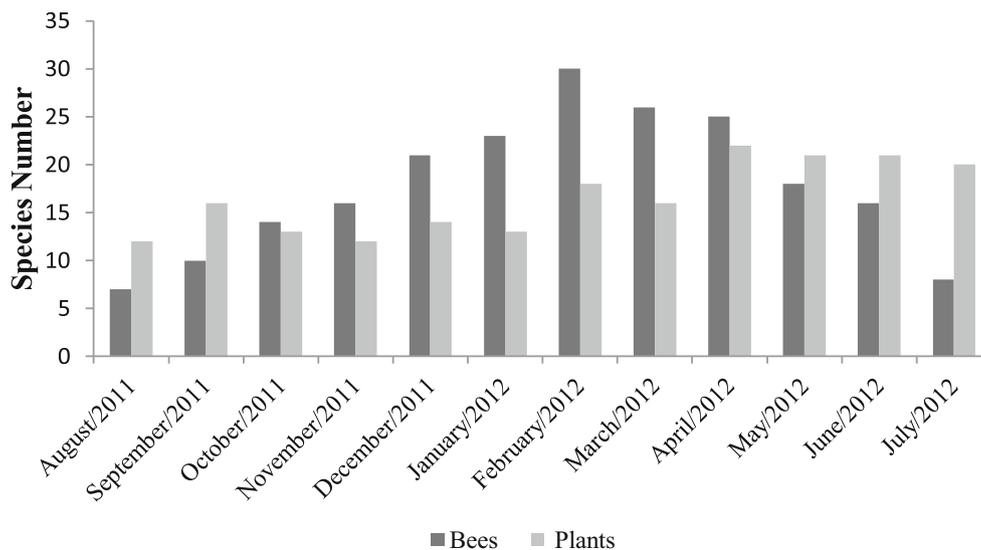


Fig 1 Number of bee species and visited plant species in an agricultural system in the municipality of Feira de Santana, northeastern Brazil.

Table 2 Dietary overlap (NO_{ih}) among flower-visiting bees in an agriculturally dominated landscape in Feira de Santana, northeastern Brazil, from August 2011 to July 2012.

	B1	B2	B3	B4	B5	B7	B6	B8	B9	B11	B10	B12	B14	B16	B13	B15	B17
B2	0.24																
B3	0.27	0.24															
B4	0.13	0.17	0.18														
B5	0.08	0.17	0.07	0.07													
B7	0.44	0.08	0.19	0.12	0.04												
B6	0.24	0.40	0.18	0.15	0.33	0.10											
B8	0.32	0.01	0.03	0.01	0.01	0.67	0.02										
B9	0.33	0.15	0.08	0.03	0.07	0.22	0.19	0.15									
B11	0.08	0.12	0.10	0.06	0.34	0.03	0.36	0.00	0.06								
B10	0.22	0.31	0.20	0.58	0.17	0.18	0.21	0.11	0.14	0.16							
B12	0.33	0.08	0.03	0.03	0.08	0.28	0.10	0.25	0.27	0.06	0.22						
B14	0.06	0.01	0.15	0.67	0.00	0.11	0.02	0.00	0.00	0.00	0.32	0.06					
B16	0.35	0.17	0.18	0.34	0.08	0.25	0.20	0.14	0.27	0.07	0.34	0.21	0.07				
B13	0.07	0.10	0.01	0.01	0.62	0.03	0.30	0.00	0.06	0.33	0.11	0.06	0.00	0.07			
B15	0.28	0.04	0.05	0.10	0.05	0.18	0.02	0.15	0.21	0.00	0.18	0.66	0.15	0.14	0.08		
B17	0.00	0.03	0.06	0.10	0.00	0.00	0.00	0.00	0.00	0.00	0.10	0.00	0.00	0.10	0.00	0.00	
B18	0.12	0.29	0.07	0.07	0.28	0.05	0.36	0.00	0.06	0.30	0.26	0.06	0.00	0.14	0.30	0.00	0.00

partitioning of the dietary axis. For a species-rich system, this combination of dietary specialization and generalized time use is logical because there are many more viable niche spaces (i.e., niche partitions that are sufficiently large to support viable population sizes) along the dietary axis than along the temporal axis. Great floral resource abundance and diversity creates many options along the dietary axis. In

contrast, bees require a certain amount of time to gather the necessary energy to sustain their populations, which greatly reduces the ability to partition the temporal niche and maintain viable populations.

Apis mellifera and *Trigona spinipes* were the most abundant bee species and interacted with several plant species; however, most bee species were highly specialized with

Table 3 Temporal overlap (NO_{ih}) among flower-visiting bees in an agriculturally dominated landscape in Feira de Santana, northeastern Brazil, from August 2011 to July 2012.

	B1	B2	B3	B4	B5	B7	B6	B8	B9	B11	B10	B12	B14	B16	B13	B15	B17
B2	0.72																
B3	0.79	0.62															
B4	0.61	0.67	0.61														
B5	0.57	0.56	0.59	0.51													
B7	0.71	0.68	0.65	0.65	0.56												
B6	0.49	0.53	0.41	0.43	0.36	0.38											
B8	0.35	0.29	0.34	0.27	0.14	0.50	0.16										
B9	0.61	0.56	0.44	0.39	0.31	0.66	0.31	0.61									
B11	0.63	0.60	0.44	0.36	0.35	0.49	0.60	0.32	0.60								
B10	0.58	0.56	0.55	0.60	0.46	0.65	0.30	0.42	0.50	0.32							
B12	0.39	0.46	0.42	0.35	0.23	0.39	0.76	0.24	0.32	0.58	0.31						
B14	0.51	0.58	0.45	0.57	0.42	0.63	0.33	0.34	0.43	0.37	0.55	0.31					
B15	0.53	0.50	0.41	0.30	0.33	0.43	0.64	0.34	0.46	0.70	0.36	0.54	0.37				
B13	0.58	0.60	0.54	0.44	0.56	0.48	0.45	0.11	0.29	0.46	0.37	0.34	0.29	0.43			
B16	0.50	0.56	0.31	0.36	0.34	0.38	0.51	0.20	0.51	0.63	0.30	0.27	0.38	0.59	0.45		
B17	0.33	0.26	0.40	0.16	0.29	0.13	0.51	0.06	0.21	0.42	0.21	0.46	0.00	0.48	0.46	0.37	
B18	0.32	0.25	0.33	0.40	0.34	0.32	0.13	0.44	0.29	0.16	0.11	0.06	0.21	0.23	0.24	0.18	0.10

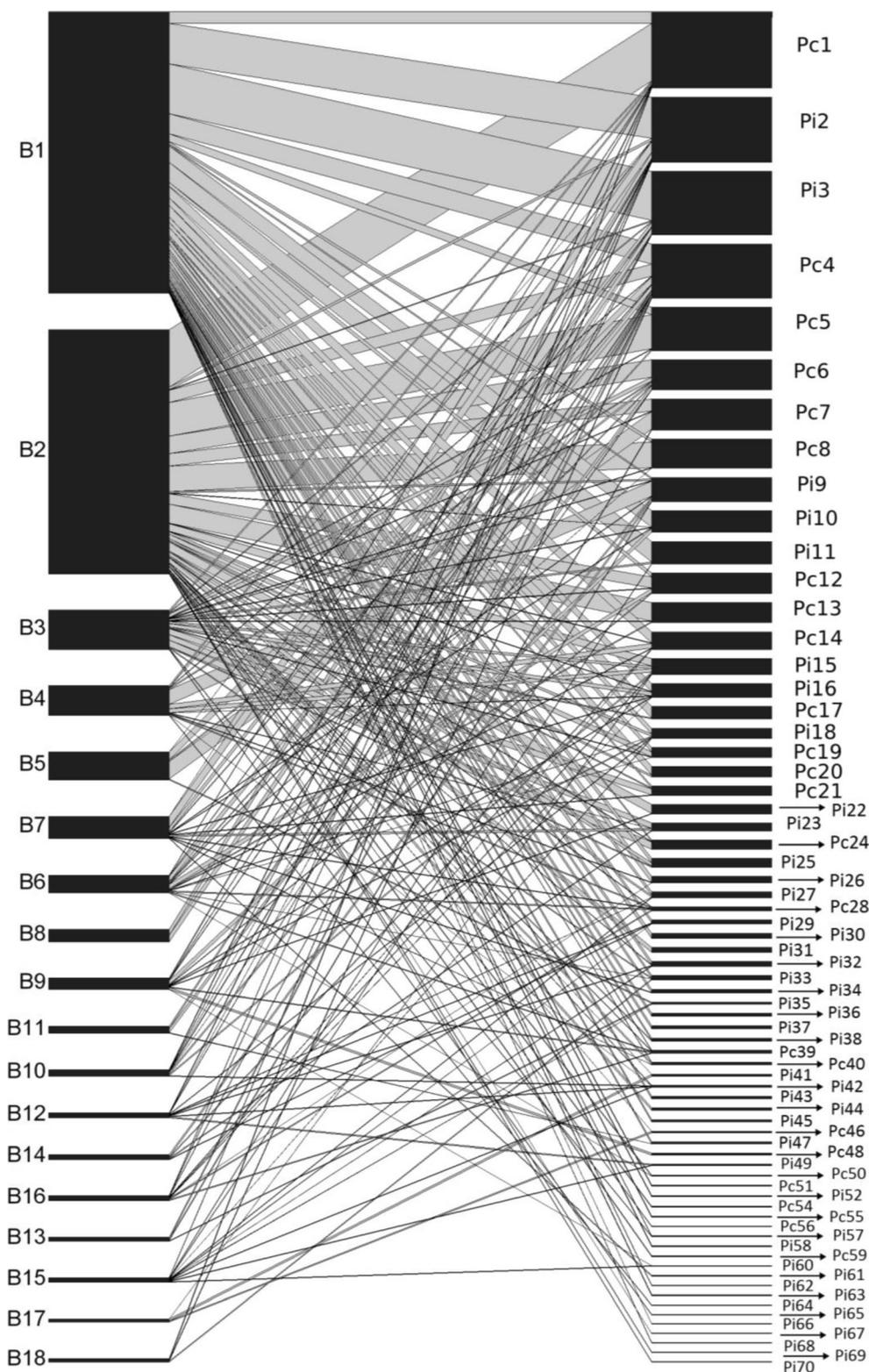


Fig 2 Network of flowers visited by bees in an agriculturally dominated landscape in Feira de Santana, northeastern Brazil. Bees are represented as rectangles on the left-hand side and plants are represented as rectangles on the right-hand side. The size of each rectangle is proportional to the number of visits recorded for each bee or plant species. Line thickness (interaction) is proportional to the number of bees observed visiting each species of plant. Species codes are listed in Table 1.

respect to diet (Fig 2). *Apis mellifera* and *Trigona spinipes* are generalists (Kleinert & Giannini 2012); each was common and

visited 40 or more plant species at the study site. Despite being invasive, *A. mellifera* plays an important role in

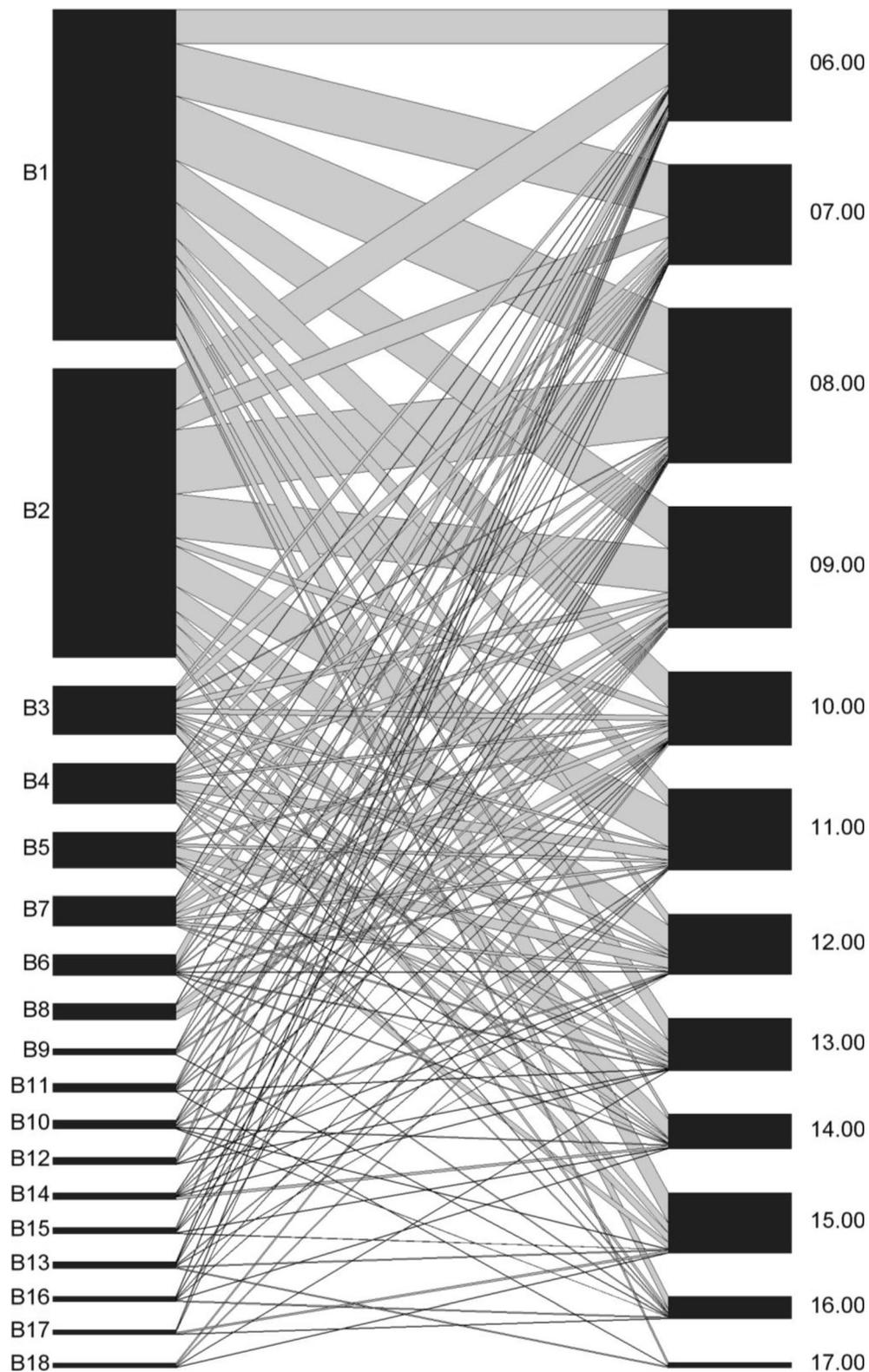


Fig 3 Network of foraging time of bees in an agriculturally dominated landscape in Feira de Santana, northeastern Brazil. Bees are represented as *rectangles* on the *left-hand side* and visit times are represented as *rectangles* on the *right-hand side*. The *size* of each rectangle is proportional to the number of visits observed for each bee species or visit time. *Line thickness* (interaction) is proportional to the number of bees observed visiting plants at a given time. Species codes are listed in Table 1.

interaction networks (Santos *et al* 2012); however, many studies suggest that it is harder for invasive species to become established in species-rich systems than in species-poor systems (Pimm 1991, Rosenzweig 1995). Although *Trigona spinipes* is considered harmful to some crops (Silva *et al* 1997), we observed this species visiting and transporting pollen of several plant species, suggesting that it may be a legitimate pollinator in urban settings.

The species that showed the highest values of dietary overlap were those of the genera *Megachile* (*Dactylomegachile*) and *Exomalopsis* (*Phamonalopsis*). These bees have similar morphology, are very hairy, and the females have a hairy scopa. The families of these species, Megachilidae and Apidae, respectively, are characterized by long tongues (Silveira *et al* 2002, Michener 2007). The pairs of species with the second highest dietary overlap values were those of the genera *Pseudaugochlora* and *Ceratina*, which are small and slender bees that have low pilosity. High overlap between particular species may result from morphological similarities that determine which species can effectively forage from particular species of flowers. For example, tongue length is an important factor that may determine which resources are available to each species (Michener 2000, Silveira *et al* 2002). However, it is important to note that variation in tongue size exists within each family (Michener 2007).

Dietary overlap was low at the community level as well as for pairs of species with 88% of species pairs having less than 30% overlap. This suggests that morphological differences between bee species, such as a variation in the length of their mouthparts (Michener 2000, Silveira *et al* 2002), as well as behavioral differences such as the synchronization with flowering events and temporal memory, allow bees to select different floral resources (Aguiar & Santos 2007). Low dietary overlap for a highly diverse bee assemblage that exploited floral resources from 26 species of cultivated plants in an urban ecosystem (Table 1) suggests a high degree of niche partitioning along the dietary axis. In addition, this pattern suggests that competition may reduce niche overlap for abundant cultivated resources via exploitative or interference mechanisms, possibly resulting in exclusion of competitors from local areas.

Temporal overlap varied from intermediate to high, with 65% of the pairs ranging between 30% and 60% and temporal overlap of 0.49 for the community. The times with highest frequency of visits were all in early morning, including 0800, 0600, and 0700 hours. At these times, the temperature was milder. However, there was no correlation between temperature and foraging time, indicating that temperature was not a key structuring factor of temporal overlap in the community. Other factors may affect

community structuring such as variation in the amount of resources (pollen and nectar) available throughout the day, time of resource production (Stone *et al* 1999), variation in the availability of resources in space and time, and flowering phenology (Heithaus 1979, Gottlieb *et al* 2005).

Network analysis on specialization corroborated results of the niche overlap analysis. The bee community presented some degree of dietary specialization ($H_2' = 0.46$), with the vast majority of niches being highly segregated and complementary. This high complementarity may occur because a high diversity of plants may support a high diversity of flower visitors (Blüthgen and Klein, 2010). Nonetheless, some degree of competition likely is required to maintain these segregated niches or to exclude species with coincident dietary niches that occur in the region but not in the study area. In general, foraging times were redundant ($H_2' = 0.12$), which is likely associated with the time of nectar and pollen production by flowers, making some times more valuable for foraging than others (Stone *et al* 1999). More specifically, nectar availability is often greatest at dawn (Saunders 1982, Goulson & Darvill 2004), and declines during the day as nectar is consumed. Consequently, foraging earlier in the day is more effective and efficient than foraging later during the day, and would explain the consistent pattern among species, as most species foraged throughout daylight hours but foraged most intensively during the first half of the day. Foragers later in the day may be performing reconnaissance to better inform future foraging bouts as patterns of flower production change in space and time.

Our results suggest that a low dietary overlap and an intermediate temporal overlap may result from a high variety of flowers that can be selected by different bee species, which use a broad spectrum of resources (Aguiar *et al* 2007). Indeed, segregation along the dietary axis may allow coexistence and obviate the need for segregation of other niche dimensions (e.g., time, space). This may be a strategy developed by bees to minimize the competition for food, and to enhance foraging efficiency while facilitating coexistence. Future studies should evaluate bee and flower morphology to determine the mechanisms that contribute to dietary segregation in these species-rich and complex plant–animal networks.

Acknowledgments We thank the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) and the Fundação de Amparo à Pesquisa do Estado da Bahia (FAPESB) for financial support. G.M.M. Santos received a productivity fellowship from CNPq. D.M. Carvalho received a scholarship from FAPESB. S. Presley was supported by the Center for Environmental Sciences and Engineering at the University of Connecticut and by a grant (DEB-0620910) from 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.

References

- Aguiar CML (2003) Utilização de recursos florais por abelhas (Hymenoptera, Apoidea) em uma área de caatinga (Itatim, Bahia, Brasil). *Rev Bras Zool* 20:457–467
- Aguiar CML, Santos GMM (2007) Compartilhamento de Recursos Florais por Vespas Sociais (Hymenoptera: Vespidae) e Abelhas (Hymenoptera: Apoidea) em uma Área de Caatinga. *Neotrop Entomol* 36:836–842
- Aguiar CML, Santos GMM, Martins CF, Presley SJ (2012) Trophic niche breadth and niche overlap in a guild of flower-visiting bees in a Brazilian dry forest. *Apidologie* 43, doi: 10.1007/s13592-012-0167-4
- Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, Schaffers AP, Potts SG, Kleukers R, Thomas CD, Settele J, Kunin WE (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science* 313:351–354
- Blüthgen N, Klein AM (2010) Functional complementarity and specialisation: the role of biodiversity in plant–pollinator interactions. *Basic Applied Ecol* 12(4):282–291. doi:10.1016/j.baae.2010.11.001
- Blüthgen N, Menzel F, Blüthgen N (2006) Measuring specialization in species interaction networks. *BMC Ecol* 6:1–12
- Carvalho DM, Aguiar CML, Santos GMM (2013) Food niche overlap among neotropical carpenter bees (Hymenoptera: Apidae: Xylocopini) in an agricultural system. *Sociobiology* 60(3):283–288. doi:10.13102/sociobiology.v60i3.283-288
- Castro-Arellano I, TE Lacher JR (2009) Temporal niche segregation in two rodent assemblages of subtropical Mexico. *J Trop Ecol* 25:593–603
- Castro-Arellano I, TE Lacher JR, Willig MR, Rangel TFLVB (2010) Assessment of assemblage-wide temporal niche segregation using null models. *Methods Ecol Evol* 1:311–318
- Chase JM (2011) Ecological niche theory. In: Scheiner SM, Willig MR (eds) *The Theory of Ecology*. University of Chicago Press, Chicago, pp 93–107
- Chase JM, Leibold MA (2003) *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago
- Clemente MA, Lange D, Dáttilo W, Del-Claro K, Prezoto F (2013) Social wasp-flower visiting guild in less structurally complex habitats are more susceptible to local extinction. *Sociobiology* 60:337–344
- Dáttilo W, Fagundes R, Gurka CAQ, Silva MSA, Vieira MCL, Izzo TJ, Diaz-Castelazo C, Del-Claro K, Rico-Gray V (2014a) Individual-based ant–plant networks: diurnal-nocturnal structure and species-area relationship. *PLoS ONE* 9(6):e99838. doi:10.1371/journal.pone.0099838
- Dáttilo W, Marquitti FMD, Guimarães PR, Izzo TJ (2014b) The structure of ant plant ecological networks: is abundance enough? *Ecology* (Brooklyn, New York, NY) 95:475–485
- Diaz S, Cabido M (2001) Vive la difference: plant functional diversity matters to ecosystem processes. *Trends Ecol Evol* 16:646–655
- Dormann CF, Fründ J, Blüthgen N, Gruber B (2009) Indices, graphs and null models: analyzing bipartite ecological networks. *Open Ecol J* 2:7–24
- Feinsinger P, Spears EE, Poole RW (1981) A simple measure of niche breadth. *Ecology* 62:27–32
- Gottlieb D, Keasar T, Shmida A, Motro U (2005) Possible foraging benefits of bimodal daily activity in *Proxyclopa olivieri* (Lepeletier) (Hymenoptera: Anthophoridae). *Environ Entomol* 34:417–424
- Goulson D, Darvill B (2004) Niche overlap and diet breadth in bumblebees; are rare species more specialized in their choice of flowers? *Apidologie* 35:55–63
- Heithaus ER (1979) Flower-feeding specialization in wild bee and wasp communities in seasonal neotropical habitats. *Oecologia* 42: 179–194
- Herrera CM (1995) Floral biology, microclimate, and pollination by ectothermic bees in an early-blooming herb. *Ecology* 76:218–228
- Hoehn P, Tschantke T, Tylianakis JM, Steffan-Dewenter I (2008) Functional group diversity of bee pollinators increases crop yield. *Proc R Soc Ser B* 275:2283–2291
- Humphrey JW, Hawes C, Pearce AJ, Ferris-Khan R, Jukes MR (1999) Relationships between insect diversity and habitat complexity in plantation forests. *For Ecol Manag* 113:11–21
- Imperatriz-Fonseca VL, Canhos DAL, Alves D de A, Saraiva NA (2012) Polinizadores e Polinização – Um tema global. In: Imperatriz-Fonseca VL, Canhos DAL, Alves D de A, Saraiva AN (Orgs.) *Polinizadores no Brasil*. Edusp, São Paulo, 25–45.
- Jetz W, Krefl H, Ceballos G, Mutke J (2009) Global associations between terrestrial producer and vertebrate consumer diversity. *Proc Royal Soc B* 276:269–278
- Kleinert A. de M P, Giannini TC (2012) Generalist bee species on Brazilian bee–plant interaction networks. Hindawi Publishing Corporation. *Psyche*. Article ID 291519, 7 pages. doi:10.1155/2012/291519
- Lange D, Dáttilo W, Del-Claro K (2013) Influence of extrafloral nectary phenology on ant–plant mutualistic networks in a neotropical savanna. *Ecol Entomol* 38:463–469
- Levine JM, HilleRisLambers J (2009) The importance of niches for the maintenance of species diversity. *Nature* 461:254–257
- Liebold MA (1998) Similarity and local co-existence of species in regional biotas. *Evol Ecol* 12:95–110
- Michener, CD (2000) *The Bees of the World*. The Johns Hopkins University, Baltimore, USA. 913p
- Michener CD (2007) *The bees of the world* 2nd ed. The Johns Hopkins University Press North Charles Street Baltimore, Maryland, 972p
- Ministério do Meio Ambiente – MMA (2009) Secretaria Estadual de Meio Ambiente Programa Nacional de capacitação de gestores ambientais – PNC. Gestão Ambiental Compartilhada – GAC. Plano Municipal de Meio Ambiente de Feira de Santana, Brasil
- Pianka ER (1973) The structure of lizard communities. *Ann Rev Ecol Syst* 4:53–74
- Pimm SL (1991) *The balance of nature? Ecological issues in the conservation of species and communities*. The University of Chicago Press, Chicago
- Roberts SP, Harrison JF (1999) Mechanisms of thermal stability during flight in the honeybee *Apis mellifera*. *J Exp Biol* 202:1523–1533
- Rosenzweig ML (1995) *Species diversity in space and time*. Cambridge University Press, Cambridge
- Sakagami SF, Laroza SF, Moure JSM (1967) Wild bee biocenotics in São José dos Pinhais (PR), South Brasil. Preliminary report. *J Fac Sci Hokkaido Univ Ser VI, Zool* 16:253–291
- Santos GMM, Bichara Filho CC, Resende JJ, Cruz JD, Maques OM (2007) Diversity and community structure of social wasps (Hymenoptera: Vespidae) in three ecosystems in Itaparica Island, Bahia State. *Brazil Neotrop Entomol* 36:180–185
- Santos GMM, da Cruz JD, Maques OM, Gobbi N (2009) Diversidade de Vespas Sociais (Hymenoptera: Vespidae) em Áreas de Cerrado na Bahia. *Neotrop Entomol* 38:317–320
- Santos GMM, Aguiar CML, Genini J, Martins CF, Zanella FCV, Mello MAR (2012) Invasive Africanized honeybees change the structure of native pollination networks in Brazil. *Biol Invasions* 14:2369–2378
- Saunders DS (1982) *Insect Clocks*, 2nd edn. Pergamon Press, Oxford, p 409
- Schoener TW (1982) The controversy over interspecific competition. *Amer Sci* 70:586–595

- Silva MM, Buckner CH, Picanço M, Cruz CD (1997) Influência de *Trigona spinipes* Fabr. (Hymenoptera: Apidae) na polinização do maracujazeiro amarelo. *An Soc Entomol Brasil* 26:217–221
- Silveira FA, Melo GAR, Almeida EAB (2002) *Abelhas brasileiras. Sistemática e Identificação*. Fundação Araucária, Belo Horizonte, 253 pp
- Stone GN, Gilbert F, Willmer P, Potts S, Semida F, Zalot S (1999) Windows of opportunity and the temporal structuring of foraging activity in a desert solitary bee. *Ecol Entomol* 24:208–221
- Tews J, Brose U, Grimm V, Tielbörger K, Wichmann MC, Schwager M, Jeltsch F (2004) Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. *J Biogeogr* 31: 79–92
- Weiner CN, Werner M, Linsenmair KE, Blüthgen N (2011) Land use intensity in grasslands: changes in biodiversity, species composition and specialisation in flower–visitor networks. *Bas App Ecol* 12:292–299