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# Overlap in trophic and temporal niches in the flower-visiting bee guild (Hymenoptera, Apoidea) of a tropical dry forest

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**Abstract** – In tropical dry and hot forests, flower-visiting bees are able to forage only during the few hours a day with mild temperatures, but they may chose more freely among the plant species to be visited. Therefore, we tested the hypothesis that the overlap in temporal niches should be higher than the overlap in trophic niches among these bees. Between pairs of species (Schoener index), the overlap in trophic niches varied from 0.007 to 0.745, whereas the temporal overlap varied from 0.062 to 0.865. In general, the trophic overlap was low, with 79 % of the species pairs scoring below 30 %, and the temporal overlap varied from moderate to high. At the community level, the observed overlap in trophic niches was higher than expected by chance, both for diet and foraging time. The network analysis confirmed at the community level that bees separate more strongly their trophic ( $E=0.82$ ) than their temporal niches ( $E=0.50$ ).

**trophic niche / temporal niche / niche overlap / bee guild / Apoidea**

## 1. INTRODUCTION

Many ecological studies aimed at understanding the processes that structure natural communities, and recently, several of them have stressed the importance of species interactions (Bascompte and Jordano 2007; Santos et al. 2010) as well as the role of scarcity of food resources (Vasconcelos et al. 2010) for community structure. Antagonistic and mutualistic interactions seem to be fundamental in this context; they may result in the formation of

subgroups of species with similar requirements that perform similar functions in the community: the guilds (Root 1967; Blondel 2003). Guilds can be structured in different ways, following two main possibilities: (1) the structure is mediated by competition and, in this case, guilds are expected in sites where resources are limited (Pianka 1980) or (2) the structuration of guilds happens due to convergent use of resources by species with similar ecological requirements (Hairston 1984).

When competition for food among species of the same guild is strong, a temporal segregation in resource use can attenuate competition and so facilitate coexistence (Hölldobler and Wilson 1990). Therefore, activity time is another

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important niche dimension (Pianka 1973). Studies on niche overlap help us understand better the guild structure of a community. There are several approaches to analyze niche overlap (Wilms et al. 1996; Thomson 2006; Behmer and Joern 2008; Presley et al. 2009). Currently, tools from network theory have been used for this task (Bascompte and Jordano 2007; Araújo et al. 2010). Those tools allow us to evaluate niche overlap not only between pairs of species but also in the community as a whole (see Presley et al. 2009; Santos et al. 2010).

In the present study, we assessed the overlap in trophic and temporal niches in the guild of flower-visiting bees in a Caatinga area (tropical dry forest). Since Caatinga areas are characterized by extreme abiotic conditions (e.g., semi-arid climate, with high temperature and low relative air humidity), with high temperature variations throughout the day and a dry season with food shortage for flower visitors, we tested the hypothesis that niche overlap among bee species should be determined by a balance between environmental restrictions and competition for food. We expected (1) that temporal niche overlap among species should be high since in tropical semi-arid environments, such as the Caatinga, there are hours a day when extremely high temperatures may limit bee foraging due to overheating (Willmer and Stone 1997) and (2) that trophic niche overlap should be low since competition should be intensified by the high overlap in temporal niches, leading to segregation of trophic niches, so that species may coexist.

## 2. MATERIALS AND METHODS

Data on bee–plant interactions were collected in Vale do Rio Paraguaçu, municipality of Castro Alves, state of Bahia, northeastern Brazil (12°45' S, 39°26' W). The study area is covered by open shrubby Caatinga vegetation with sparse trees, where part of the natural vegetation has been replaced by pastures. The regional climate is tropical semi-arid.

In each sampling session, two collectors captured bees visiting flowers with entomological nets along a

2-km trail. The collecting time per specimen of the flowering plant was standardized as 5 min (following Sakagami et al. 1967). The collection of bees and visited plants occurred every 2 weeks, from January 1994 to February 1995. Sampling was carried out from 0500 to 1800 hours, summing up 24 samples, each 13 h long, or 312 h of sampling per collector.

Abundance data for each species of flower-visiting bee were used in the niche overlap analysis. For this analysis, all species with total abundance below ten individuals were removed. Overlap degrees of trophic and temporal niches for each pair of bee species were calculated with the Schoener index (1986) using the formula  $NO_{ih} = 1 - 1/2 \sum_k |p_{ik} - p_{hk}|$ , where  $i$  and  $h$  represent the pair of species compared and  $p_{ik}$  and  $p_{hk}$  are the proportion of individuals of the bee species  $i$  and  $h$  collected in each plant species  $k$  in the trophic niche analysis, or in each sampling period  $k$  in the temporal niche analysis, respectively. The value of  $p_{ik}$  is calculated as the ratio between the number of individuals of the bee species  $i$  and the total number of individuals of this bee species collected in all plant species (trophic niche) or during the whole sampling period (temporal niche).

Additionally, we calculated the general overlap degree among all species in the community using the Pianka (1973) and Czechanowski indices (Feinsinger et al. 1981). To test whether the average overlap values found were higher or lower than expected by chance, we used a Monte Carlo approach (Presley et al. 2009). We used the software TimeOverlap and the algorithm Rosario with 10,000 iterations. This algorithm creates randomizations of the original matrix, calculates for each randomized matrix its degree of niche overlap, and then compares the value calculated for the original matrix with the distribution of randomized values. When the value of the real matrix was higher or lower than 95 % of the randomized values (two-tailed test), we considered the degree of niche overlap as significant ( $\alpha=0.05$ ).

The networks of bee visits to plants and of overlap in activity times were organized as adjacency matrices and represented as bipartite graphs using the package bipartite 1.17 for R (Dormann et al. 2009). The degree of dietary specialization was calculated

with the  $E$  index (Araújo et al. 2008), which varies from 0 (diets of all species are the same) to 1 (each species has a different diet). This index is based on the aggregation coefficient measured in unipartite networks (Costa et al. 2007). To calculate the aggregation coefficient, the original bipartite matrix (i.e., bees and plants) was transformed into a unipartite projection of the bee side, in which the connections are defined by niche overlap (i.e., bees that visit at least one common same plant or bees that forage at the same time), with weights calculated with the Schoener index (Araújo et al. 2008). The significance of  $E$  was estimated through a Monte Carlo procedure with 1,000 iterations ( $\alpha=0.05$ ) in the program Dieta (Araújo et al. 2008).

### 3. RESULTS

Eighty bee species were recorded visiting flowers of 83 native and exotic plant species (Table I). However, the number of bees and the plants visited varied widely from month to month. The number of bees collected monthly ranged from 2 to 38 species between months, while the number of plants visited varied from 4 to 24 species. (Figure 1). Among bees, 34 species were represented by more than ten individuals and, therefore, were included in the analysis. The bees *Apis mellifera* Linnaeus ( $n=1,374$ ), *Trigona spinipes* Fabricius ( $n=430$ ), and *Xylocopa grisescens* Lepeletier ( $n=140$ ) had higher abundance, representing 61 % of the sampled flower visitors. Among plant species, *Poincianella pyramidalis* (Tul.) L.P. Queiroz ( $n=486$ ), *Portulaca oleracea* L. ( $n=363$ ), and *Centratherum punctatum* Cass. ( $n=209$ ) were the most frequently visited and represented 60 % of all visits. The times of highest visit frequency to flowers were 1000–1100, 0900–1000, and 1400–1500 hours, when 557, 426, and 423 visits were recorded, respectively, summing up 41.15 % of all visits.

We analyzed 561 combinations of pairs of species formed with 34 bee species (Table II). Trophic niche overlap between pairs of bee species ( $NO_{ih}$ ), calculated from visit frequencies, varied from 0.007 to 0.745; the highest values

were found between *Diadasina riparia* Ducke and *Megachile paulistana* Schrottky ( $NO_{ih}=0.745$ ) and between *Xylocopa carbonaria* Smith and *Xylocopa cearensis* Ducke ( $NO_{ih}=0.745$ ), whereas the lowest values were recorded for the pairs *Gaesischia hyptidis* (Ducke) and *X. grisescens* ( $NO_{ih}=0.007$ ), and *G. hyptidis* and *Centris aenea* Lepeletier ( $NO_{ih}=0.007$ ; Table II).

The temporal overlap between pairs of bee species, inferred from the time of capture of each specimen during its visit to a flower, varied from 0.062 to 0.865, with higher average values than in the trophic niche overlap (Table III). The highest overlap values were observed between *Caenonomada unicalcarata* (Ducke) and *Melipona asilvai* Moure ( $NO_{ih}=0.860$ ) and between *Coelioxys simillima* Smith and *Trigonisca* sp. ( $NO_{ih}=0.820$ ). The lowest overlap values were observed between *Bombus morio* Swederus and *Diadasina paraensis* (Ducke) ( $NO_{ih}=0.062$ ) and between *Exomalopsis auropilosa* Spinola and *Plebeia* sp. 1 ( $NO_{ih}=0.062$ ; Table III). In general, trophic overlap was low, with 79 % of the pairs exhibiting values below 30 %, whereas temporal overlap varied from moderate to high, with 55 % of the pairs exhibiting values between 30 and 60 %.

Trophic niche overlap at the community level (i.e., among all 34 bee species analyzed) was higher than expected by chance, both for diet and foraging time. The average overlap values estimated with the indices of Pianka (diet axis=0.26; time axis=0.58) and Czechanowski (diet axis=0.18; time axis=0.49) were significant (both  $P<0.001$ ). The network analysis showed similar results as we observed that bees separate their niches more strongly in diet ( $E=0.82$ ,  $P<0.001$ ) than in foraging time ( $E=0.50$ ,  $P<0.001$ ; Figures 2 and 3).

### 4. DISCUSSION/CONCLUSION

In the present study, we observed that flower-visiting bees in our study area separate more strongly their trophic niches than

**Table 1.** Bee species and plants visited for floral resources in a Caatinga area in Castro Alves, northeastern Brazil.

Bees	Code	Plants	Code
<i>Acamptopoeum prinii</i> (Holmberg) <sup>a</sup>	B01	<i>Senegalia bahiensis</i> (Benth.)	P1
<i>Acamptopoeum vagans</i> (Cockerell) <sup>a</sup>	B02	<i>Senegalia langsdorffii</i> (Benth.)	P2
<i>Apis mellifera</i> Linnaeus	B03	Acanthaceae sp.1	P3
<i>Augochlora esox</i> (Vachal) <sup>a</sup>	B04	<i>Adenocalymma coriaceum</i> DC.	P4
<i>Augochlora</i> ( <i>Augochlora</i> ) sp. <sup>a</sup>	B05	<i>Aeschynomene mollicula</i> Kunth	P5
<i>Augochlora</i> ( <i>Oxystoglossella</i> ) sp. <sup>a</sup>	B06	<i>Ageratum conyzoides</i> L.	P6
<i>Augochlorella ephyra</i> (Schrottky) <sup>a</sup>	B07	<i>Albizia polycephala</i> (Kunth)	P7
<i>Augochlorella</i> sp. 1 <sup>a</sup>	B08	<i>Alternanthera tenella</i> Colla	P8
<i>Augochloropsis callichroa</i> (Cockerell)	B09	<i>Anadenanthera colubrina</i> (Vell.)	P9
<i>Augochloropsis cockerelli</i> Schrottky <sup>a</sup>	B10	<i>Astronium</i> cf. <i>macrocalyx</i> Engl.	P10
<i>Augochloropsis</i> sp. 1 <sup>a</sup>	B11	<i>Blanchetiodendron blanchetii</i> (Benth.)	P11
<i>Augochloropsis</i> sp. 2 <sup>a</sup>	B12	<i>Bowdichia virgilioides</i> Kunth	P12
<i>Augochloropsis terrestris</i> (Vachal) <sup>a</sup>	B13	<i>Sideroxylon obtusifolium</i> (Roemer & Schultes)	P13
<i>Bombus pauloensis</i> Friese <sup>a</sup>	B14	<i>Poincianella pyramidalis</i> (Tul.)	P14
<i>Bombus morio</i> (Swederus)	B15	<i>Capparis yco</i> Mart.	P15
<i>Caenonomada unicalcarata</i> (Ducke)	B16	<i>Cardiospermum corundum</i> L.	P16
<i>Centris</i> ( <i>Centris</i> ) sp. 1 <sup>a</sup>	B17	<i>Centratherum punctatum</i> Cass.	P17
<i>Centris</i> ( <i>Centris</i> ) sp. 2 <sup>a</sup>	B18	<i>Centrosema virginianum</i> L.	P18
<i>Centris trigonoides</i> Lepeletier <sup>a</sup>	B19	<i>Cereus jamacaru</i> DC.	P19
<i>Centris</i> ( <i>Melacentris</i> ) sp. 1 <sup>a</sup>	B20	<i>Cissus simsiana</i> Roem. & Schult.	P20
<i>Centris</i> ( <i>Melacentris</i> ) sp. 2 <sup>a</sup>	B21	<i>Commelina</i> cf. <i>benghalensis</i> L.	P21
<i>Centris aenea</i> Lepeletier	B22	<i>Copaifera langsdorffii</i> Desf.	P22
<i>Centris flavifrons</i> (Fabricius) <sup>a</sup>	B23	<i>Cordia superba</i> Cham.	P23
<i>Centris fuscata</i> Lepeletier	B24	<i>Crataeva tapia</i> L.	P24
<i>Centris hyptidis</i> Ducke <sup>a</sup>	B25	<i>Crotalaria incana</i> L.	P25
<i>Centris decolorata</i> Lepeletier <sup>a</sup>	B26	<i>Croton campestris</i> A. St.-Hil.	P26
<i>Centris spilopoda</i> Moure <sup>a</sup>	B27	<i>Croton moritibensis</i> Baill.	P27
<i>Centris tarsata</i> Smith	B28	<i>Cuphea</i> aff. <i>ramosa</i> Schott ex Koehne	P28
<i>Chilicola</i> sp. <sup>a</sup>	B29	<i>Desmodium triflorum</i> (L.) DC.	P29
<i>Coelioxys simillima</i> Smith	B30	<i>Dioclea grandiflora</i> Mart. ex. Benth.	P30
<i>Coelioxys tolteca</i> Cresson <sup>a</sup>	B31	<i>Erythrina velutina</i> Willd.	P31
<i>Diadasina paraensis</i> (Ducke)	B32	<i>Evolvulus</i> sp.1	P32
<i>Diadasina riparia</i> (Ducke)	B33	<i>Harrisia adscendens</i> (Gurke)	P33
<i>Dialictus opacus</i> (Moure) <sup>a</sup>	B34	<i>Heliotropium angiospermum</i> Murray	P34
<i>Dialictus</i> sp. <sup>a</sup>	B35	<i>Herissantia crispa</i> (L.) Briz.	P35
<i>Dichranthidium luciae</i> Urban <sup>a</sup>	B36	<i>Hyptis fruticosa</i> Salzm.	P36
<i>Epanthidium tigrinum</i> (Schrottky) <sup>a</sup>	B37	<i>Inga vera</i> Willd.	P37
<i>Euglossa cordata</i> (Linnaeus) <sup>a</sup>	B38	<i>Ipomoea bahiensis</i> Willd.	P38
<i>Euglossa securigera</i> Dressler <sup>a</sup>	B39	<i>Jatropha mollissima</i> Baill.	P39
<i>Eulaema nigrata</i> Lepeletier	B40	<i>Lippia</i> cf. <i>alba</i> (Mill.) N.E.Br.	P40
<i>Exomalopsis analis</i> Spinola	B41	Lythraceae sp.1	P41
<i>Exomalopsis auropilosa</i> Spinola	B42	<i>Lonchocarpus cultratus</i> (Vell.)	P42
<i>Florilegus festivus</i> (Smith) <sup>a</sup>	B43	<i>Machonia spinosa</i>	P43

**Table 1.** (continued)

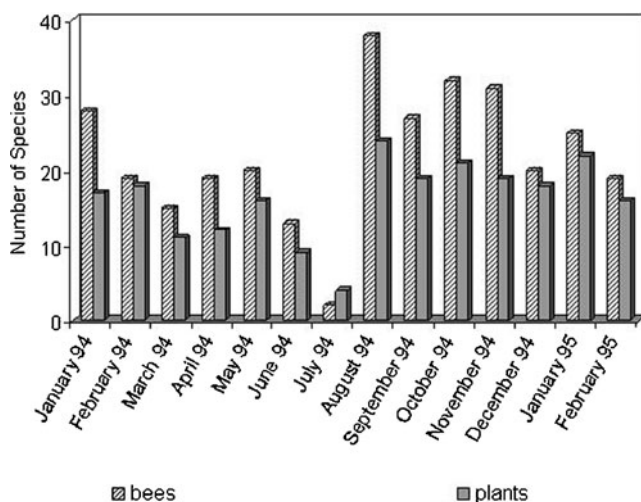
Bees	Code	Plants	Code
<i>Frieosemelitta</i> sp.	B44	<i>Malpighia emarginata</i> DC.	P44
<i>Gaesischia glabrata</i> Urban <sup>a</sup>	B45	Malpighiaceae sp.1	P45
<i>Gaesischia hyptidis</i> (Ducke)	B46	<i>Malvastrum tomentosum</i> (L.) S.R. Hill	P46
<i>Megachile (Acentron)</i> sp.	B47	<i>Mascagnia rigida</i> Griseb.	P47
<i>Megachile (Austromegachile)</i> sp.	B48	<i>Melochia tomentosa</i> L.	P48
<i>Megachile paulistana</i> Schrottky	B49	<i>Microtea maypurensis</i> G. Don	P49
<i>Megachile (Pseudocentron)</i> sp.1	B50	<i>Mimosa arenosa</i> Poir.	P50
<i>Megachile (Pseudocentron)</i> sp.2	B51	<i>Mimosa invisa</i> Mart.	P51
<i>Megachile (Pseudocentron)</i> sp. 3 <sup>a</sup>	B52	<i>Momordica charantia</i> L.	P52
<i>Megachile cylindrica</i> Friese	B53	<i>Ocimum americanum</i> L.	P53
<i>Melipona asilvai</i> Moure	B54	<i>Ocimum canum</i> Sims	P54
<i>Melipona quadrifasciata</i> Lepeletier <sup>a</sup>	B55	<i>Oxalis psoraleoides</i> Mart.	P55
<i>Melissodes nigroaenea</i> Smith	B56	<i>Passiflora aff. violacea</i> Vell.	P56
<i>Melissoptila pubescens</i> Smith	B57	<i>Peltogyne pauciflora</i> Benth.	P57
<i>Melitoma segmentaria</i> (Fabricius) <sup>a</sup>	B58	<i>Petiveria alliacea</i> L.	P58
<i>Mesoplia</i> sp. <sup>a</sup>	B59	<i>Piptocarpha</i> sp.1	P59
<i>Nomiocolletes cearensis</i> (Ducke) <sup>a</sup>	B60	<i>Piriqueta racemosa</i> Sweet.	P60
<i>Paratetrapedia</i> sp.	B61	<i>Platymiscium floribundum</i> Vogel	P61
<i>Parepeolus aterrimus</i> Friese <sup>a</sup>	B62	<i>Polygala violacea</i> Albl.	P62
<i>Parepeolus</i> sp. <sup>a</sup>	B63	<i>Portulaca oleracea</i> L.	P63
<i>Plebeia</i> sp. 1	B64	<i>Priva bahiensis</i> DC.	P64
<i>Plebeia</i> sp. 2 <sup>a</sup>	B65	<i>Prosopis juliflora</i> (Sw.) DC.	P65
<i>Psaenythia variabilis</i> Ducke <sup>a</sup>	B66	<i>Ptilochaeta bahiensis</i> Turcz.	P66
<i>Centris sponsa</i> Smith <sup>a</sup>	B67	<i>Rhynchosia minima</i> (L.) DC.	P67
<i>Tapinotaspoides serraticornis</i> (Friese)	B68	<i>Ruellia paniculata</i> L.	P68
<i>Tetragonisca angustula</i> (Latreille)	B69	<i>Ruprechtia laxiflora</i> Meisn.	P69
<i>Triepeolus</i> sp. <sup>a</sup>	B70	<i>Senna macranthera</i> (Collad.)	P70
<i>Trigona spinipes</i> (Fabricius)	B71	<i>Senna spectabilis</i> DC.	P71
<i>Trigonisca</i> sp.	B72	<i>Sida paniculata</i> L.	P72
<i>Xylocopa carbonaria</i> Smith	B73	<i>Solanum paniculatum</i> L.	P73
<i>Xylocopa cearensis</i> Ducke	B74	<i>Spondias tuberosa</i> Arruda	P74
<i>Xylocopa cf. suspecta</i> Moure & Camargo <sup>a</sup>	B75	<i>Stigmaphyllon auriculatum</i> A. Juss.	P75
<i>Xylocopa frontalis</i> (Olivier)	B76	<i>Tabebuia aurea</i> Benth. & Hook.f.	P76
<i>Xylocopa grisescens</i> Lepeletier	B77	<i>Handroanthus impetiginosus</i> (Mart. ex DC.)	P77
<i>Xylocopa muscaria</i> (Fabricius) <sup>a</sup>	B78	<i>Talinum patens</i> Juss.	P78
<i>Xylocopa ordinaria</i> Smith <sup>a</sup>	B79	<i>Trichilia hirta</i> L.	P79
<i>Xylocopa</i> sp. 1 <sup>a</sup>	B80	<i>Turnera chamaedrifolie</i> Cambess.	P80
		<i>Turnera</i> sp. 1	P81
		<i>Waltheria indica</i> L.	P82
		<i>Ziziphus joazeiro</i> Mart.	P83

<sup>a</sup> Bees represented by less than ten individuals and, hence, were excluded from the analysis

their temporal niches, with most bee species of the day. This means that, in extreme concentrating their activities at specific hours environments, such as the Caatinga, abiotic



**Figure 1.** Number of bees species and plant species visited in the Caatinga of Castro Alves, northeastern Brazil.



conditions might play an important role in structuring the community of flower-visiting bees. On the other hand, the foraging activity of some bee species may be more strongly influenced by fluctuations in the availability of food resources throughout the day (Stone et al. 1999; Gottlieb et al. 2005).

In a harsh environment such as the Caatinga, where temperature is too high and humidity is too low for bees at some hours of the day, bee species are probably hindered from segregating their foraging times since they have to concentrate their activity at milder hours. Several studies conducted in the Brazilian tropical dry forests have shown that during the dry season, the availability of food resources is very low for insects (Vasconcelos et al. 2010; Santos et al. 2010). Although 80 bees species were recorded visiting flowers of 83 plant species, on average, only 16 plant species were visited each month. In the peak of the dry season, from June to July, the number of flowering plants visited by bees was very small (ranging from four to nine plant species visited each month). The overlap between pairs of species was lower for the trophic niche (79 % of the pairs exhibiting values below 30 %) than for the temporal niche (45 % of the pairs exhibiting

values above 50 %). Our results indicate that bees have developed strategies to attenuate the competition for food, thus allowing their coexistence.

Similar results have been obtained in other studies, with low trophic niche overlap (Schoener's index) among most pairs of bee species in forests (Wilms et al. 1996) and caatingas (Aguiar and Santos 2007). Therefore, species that coexist in a given locality should be more similar in some features than in others, responding to a balance between food and environmental requirements, as proposed by Liebold (1997). Our results are also consistent with Gause's (1934) principle of competitive exclusion which states that ecologically similar species that coexist in a given area must differ strongly in at least one dimension of their niches, so they do not exclude each other.

It is interesting that the results of the conventional niche analysis and of the network analysis were very similar, reinforcing our interpretations. Future studies could investigate the biological mechanisms that determine niche overlap among particular pairs of species in order to understand why some species are able to overlap their niches more strongly than others.

**Table II.** Trophic niche overlap ( $NO_{it}$ ) between flower-visiting bees in the Caatinga of Castro Alves, northeastern Brazil.

	B03	B09	B14	B15	B16	B22	B24	B28	B30	B32	B33	B40	B41	B42	B44	B46	B47	B48	B49	B50	B51	B54	B56	B57	B61	B64	B68	B69	B71	B72	B73	B74	B76
B09	0.39																																
B14	0.07	0.05																															
B15	0.02	0.00	0.00																														
B16	0.36	0.32	0.07	0.01																													
B22	0.29	0.27	0.12	0.04	0.15																												
B24	0.12	0.16	0.17	0.03	0.06	0.57																											
B28	0.14	0.22	0.16	0.25	0.05	0.47	0.60																										
B30	0.40	0.18	0.06	0.00	0.33	0.16	0.05	0.01																									
B32	0.09	0.13	0.11	0.00	0.38	0.06	0.08	0.06	0.29																								
B33	0.11	0.12	0.05	0.00	0.43	0.03	0.02	0.01	0.29	0.60																							
B40	0.08	0.04	0.47	0.21	0.07	0.23	0.08	0.27	0.06	0.00	0.00																						
B41	0.23	0.06	0.13	0.00	0.16	0.11	0.09	0.07	0.33	0.09	0.09	0.09																					
B42	0.08	0.00	0.21	0.00	0.13	0.22	0.09	0.09	0.06	0.13	0.18	0.19	0.09																				
B44	0.11	0.20	0.00	0.00	0.00	0.51	0.50	0.33	0.08	0.00	0.00	0.00	0.00	0.00																			
B46	0.09	0.00	0.00	0.00	0.28	0.01	0.00	0.01	0.17	0.60	0.40	0.00	0.03	0.10	0.00																		
B47	0.36	0.21	0.07	0.00	0.33	0.40	0.28	0.29	0.23	0.17	0.17	0.07	0.09	0.10	0.22	0.20																	
B48	0.35	0.29	0.19	0.05	0.57	0.16	0.14	0.17	0.20	0.27	0.26	0.05	0.16	0.18	0.00	0.09	0.23																
B49	0.11	0.08	0.00	0.00	0.40	0.03	0.02	0.01	0.29	0.54	0.75	0.00	0.09	0.13	0.00	0.48	0.17	0.20															
B50	0.42	0.29	0.03	0.05	0.66	0.21	0.11	0.12	0.22	0.24	0.26	0.03	0.12	0.06	0.05	0.24	0.43	0.63	0.26														
B51	0.38	0.23	0.10	0.05	0.60	0.19	0.06	0.09	0.16	0.13	0.22	0.10	0.13	0.20	0.03	0.22	0.39	0.65	0.28	0.69													
B54	0.46	0.46	0.05	0.05	0.40	0.39	0.27	0.25	0.33	0.25	0.28	0.05	0.17	0.04	0.22	0.13	0.50	0.31	0.25	0.38	0.35												
B56	0.32	0.18	0.14	0.00	0.42	0.27	0.03	0.05	0.24	0.24	0.29	0.25	0.09	0.31	0.00	0.11	0.26	0.37	0.18	0.37	0.39	0.20											
B57	0.21	0.13	0.00	0.00	0.47	0.07	0.03	0.04	0.23	0.49	0.48	0.00	0.09	0.13	0.02	0.45	0.30	0.24	0.58	0.39	0.35	0.33	0.19										
B61	0.10	0.13	0.10	0.00	0.25	0.12	0.05	0.02	0.12	0.13	0.18	0.10	0.09	0.23	0.17	0.10	0.10	0.16	0.25	0.09	0.20	0.20	0.10	0.25									
B64	0.22	0.22	0.05	0.00	0.00	0.06	0.00	0.00	0.29	0.06	0.06	0.00	0.09	0.06	0.06	0.00	0.02	0.05	0.00	0.02	0.00	0.09	0.06	0.00	0.00								
B68	0.23	0.24	0.00	0.00	0.52	0.07	0.02	0.05	0.28	0.49	0.54	0.00	0.06	0.11	0.00	0.41	0.29	0.34	0.56	0.39	0.38	0.36	0.33	0.54	0.31	0.00							
B69	0.22	0.25	0.06	0.00	0.07	0.23	0.22	0.27	0.19	0.00	0.00	0.06	0.14	0.02	0.17	0.00	0.31	0.06	0.00	0.14	0.09	0.33	0.06	0.08	0.03	0.39	0.05						
B71	0.38	0.34	0.06	0.00	0.13	0.44	0.42	0.41	0.19	0.03	0.06	0.06	0.13	0.04	0.31	0.03	0.38	0.15	0.06	0.21	0.11	0.37	0.06	0.13	0.08	0.13	0.10	0.36					
B72	0.27	0.19	0.02	0.00	0.08	0.22	0.11	0.10	0.31	0.05	0.05	0.02	0.16	0.02	0.14	0.00	0.13	0.08	0.05	0.14	0.07	0.26	0.03	0.08	0.08	0.57	0.06	0.61	0.23				
B73	0.24	0.22	0.10	0.11	0.15	0.66	0.45	0.38	0.13	0.03	0.03	0.17	0.12	0.17	0.40	0.00	0.46	0.12	0.03	0.19	0.19	0.37	0.19	0.06	0.13	0.04	0.04	0.20	0.39	0.18			
B74	0.21	0.22	0.10	0.08	0.17	0.65	0.48	0.41	0.06	0.00	0.00	0.13	0.09	0.13	0.42	0.00	0.49	0.15	0.00	0.22	0.23	0.35	0.21	0.07	0.10	0.00	0.08	0.22	0.36	0.11	0.72		
B76	0.15	0.30	0.10	0.07	0.10	0.51	0.61	0.57	0.03	0.10	0.03	0.00	0.06	0.06	0.38	0.00	0.29	0.22	0.03	0.16	0.09	0.32	0.07	0.10	0.03	0.00	0.10	0.22	0.39	0.14	0.47	0.52	
B77	0.24	0.21	0.14	0.07	0.14	0.66	0.64	0.46	0.08	0.04	0.02	0.14	0.11	0.09	0.64	0.01	0.38	0.14	0.01	0.17	0.15	0.30	0.13	0.06	0.07	0.01	0.06	0.23	0.40	0.13	0.53	0.57	0.53

The codes used for bees are listed in Table I

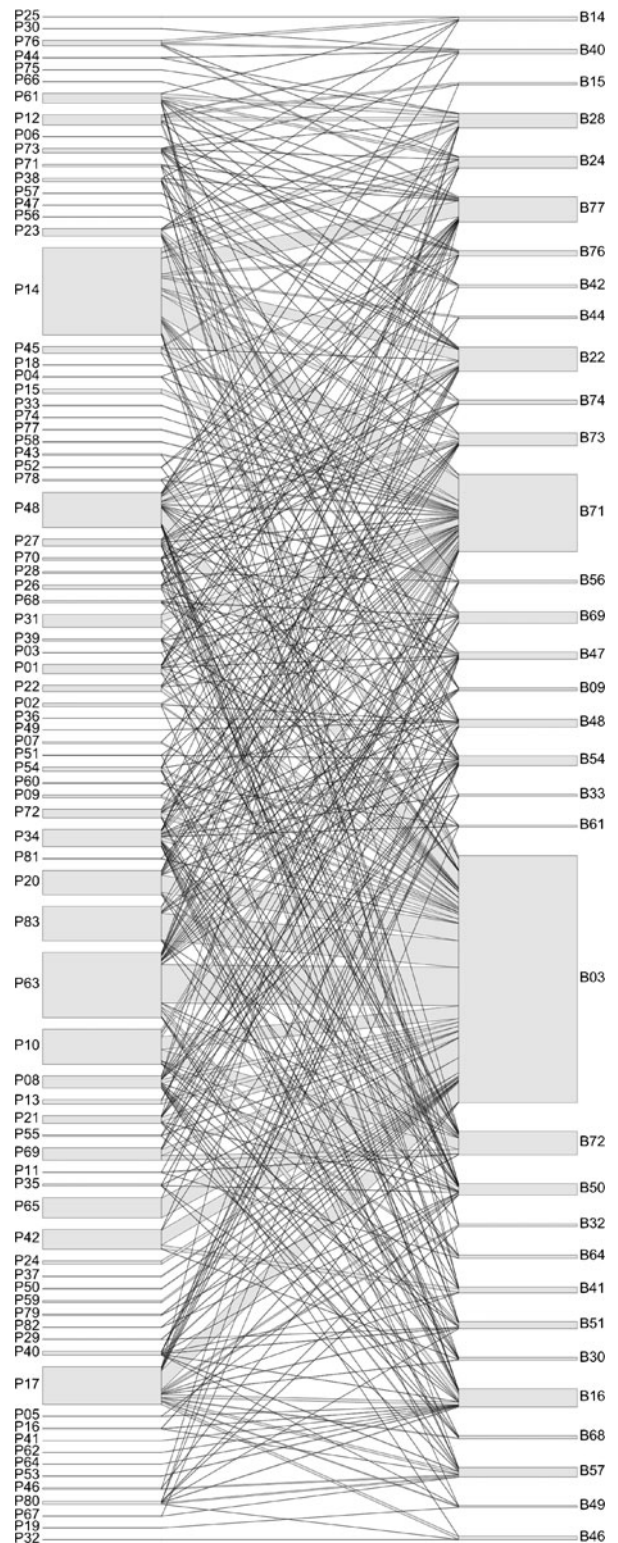


**Table III.** Temporal niche overlap ( $NO_{it}$ ) between flower-visiting bees in the Caatinga of Castro Alves, northeastern Brazil.

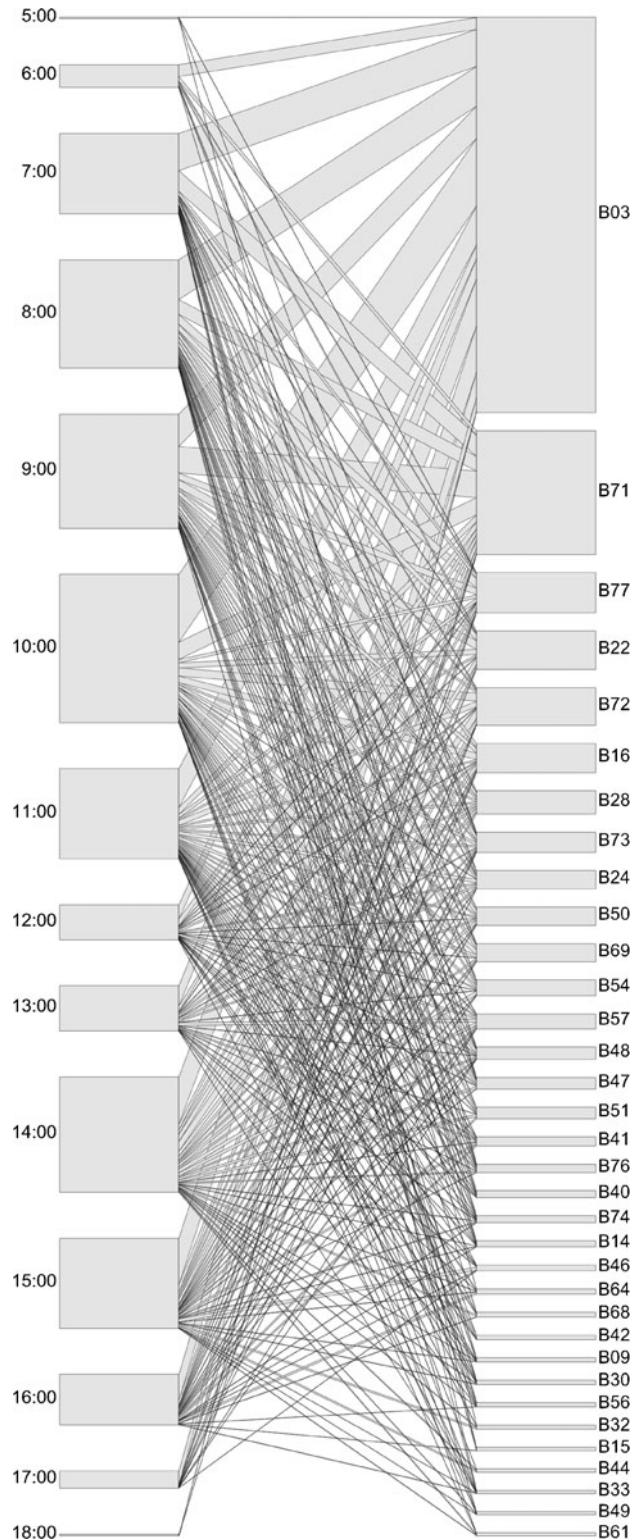
	B3	B9	B14	B15	B16	B22	B24	B28	B30	B32	B33	B40	B41	B42	B44	B46	B47	B48	B49	B50	B51	B54	B56	B57	B61	B64	B68	B69	B71	B72	B73	B74	B76	
B9	0.52																																	
B14		0.60	0.58																															
B15		0.26	0.20	0.57																														
B16		0.75	0.60	0.58	0.22																													
B22		0.69	0.62	0.63	0.24	0.80																												
B24		0.62	0.52	0.60	0.28	0.55	0.50																											
B28		0.75	0.69	0.67	0.27	0.73	0.70	0.67																										
B30		0.72	0.44	0.45	0.12	0.68	0.64	0.51	0.64																									
B32		0.48	0.39	0.38	0.06	0.42	0.47	0.50	0.52	0.54																								
B33		0.64	0.44	0.54	0.38	0.66	0.51	0.46	0.61	0.59	0.29																							
B40		0.54	0.35	0.67	0.58	0.54	0.45	0.51	0.53	0.44	0.23	0.67																						
B41		0.55	0.42	0.38	0.08	0.45	0.39	0.48	0.52	0.57	0.53	0.51	0.26																					
B42		0.33	0.19	0.21	0.00	0.38	0.27	0.22	0.30	0.42	0.13	0.36	0.35	0.22																				
B44		0.40	0.20	0.19	0.00	0.38	0.40	0.14	0.35	0.52	0.56	0.23	0.17	0.34	0.17																			
B46		0.40	0.31	0.29	0.08	0.29	0.24	0.28	0.39	0.37	0.42	0.37	0.14	0.58	0.19	0.55																		
B47		0.68	0.48	0.48	0.15	0.78	0.71	0.58	0.65	0.71	0.50	0.60	0.56	0.39	0.47	0.39	0.17																	
B48		0.78	0.41	0.47	0.16	0.68	0.57	0.55	0.64	0.68	0.46	0.66	0.54	0.50	0.48	0.38	0.30	0.74																
B49		0.55	0.55	0.37	0.00	0.62	0.66	0.48	0.52	0.65	0.63	0.40	0.33	0.46	0.29	0.42	0.18	0.63	0.55															
B50		0.67	0.65	0.52	0.21	0.82	0.79	0.57	0.70	0.60	0.41	0.53	0.41	0.49	0.26	0.32	0.31	0.66	0.56	0.68														
B51		0.59	0.52	0.44	0.21	0.73	0.74	0.41	0.52	0.58	0.34	0.47	0.37	0.41	0.26	0.37	0.19	0.64	0.48	0.63	0.81													
B54		0.69	0.55	0.54	0.22	0.87	0.81	0.54	0.69	0.69	0.44	0.56	0.51	0.39	0.33	0.44	0.20	0.77	0.62	0.62	0.80	0.77												
B56		0.58	0.36	0.37	0.12	0.65	0.46	0.43	0.46	0.53	0.29	0.53	0.43	0.42	0.65	0.23	0.21	0.65	0.70	0.46	0.57	0.52	0.58											
B57		0.61	0.45	0.39	0.08	0.56	0.49	0.49	0.64	0.69	0.46	0.41	0.23	0.67	0.30	0.38	0.57	0.47	0.51	0.45	0.58	0.45	0.51	0.38										
B61		0.51	0.27	0.24	0.00	0.49	0.45	0.33	0.43	0.71	0.59	0.44	0.33	0.51	0.26	0.70	0.30	0.57	0.55	0.62	0.41	0.40	0.55	0.38	0.47									
B64		0.49	0.30	0.29	0.14	0.34	0.31	0.42	0.42	0.46	0.53	0.46	0.18	0.64	0.06	0.22	0.31	0.31	0.47	0.44	0.36	0.34	0.31	0.29	0.46	0.42								
B68		0.54	0.29	0.35	0.19	0.57	0.54	0.44	0.48	0.69	0.49	0.49	0.38	0.47	0.22	0.44	0.19	0.60	0.50	0.57	0.60	0.59	0.64	0.45	0.49	0.67	0.48							
B69		0.66	0.51	0.49	0.11	0.71	0.71	0.58	0.58	0.68	0.52	0.59	0.48	0.47	0.44	0.35	0.20	0.80	0.80	0.74	0.66	0.61	0.69	0.67	0.42	0.56	0.41	0.52						
B71		0.74	0.60	0.73	0.33	0.70	0.75	0.68	0.66	0.52	0.35	0.58	0.57	0.41	0.32	0.25	0.31	0.60	0.59	0.52	0.69	0.62	0.67	0.51	0.43	0.30	0.31	0.41	0.64					
B72		0.74	0.43	0.43	0.10	0.69	0.62	0.50	0.63	0.82	0.58	0.57	0.49	0.54	0.37	0.57	0.33	0.74	0.78	0.62	0.57	0.55	0.73	0.54	0.61	0.75	0.44	0.62	0.72	0.52				
B73		0.75	0.52	0.65	0.39	0.73	0.72	0.53	0.70	0.53	0.37	0.68	0.58	0.43	0.27	0.27	0.27	0.61	0.61	0.46	0.67	0.58	0.69	0.55	0.45	0.36	0.38	0.51	0.57	0.69	0.55			
B74		0.70	0.76	0.67	0.29	0.72	0.77	0.56	0.76	0.54	0.42	0.58	0.42	0.55	0.23	0.29	0.42	0.54	0.55	0.54	0.80	0.68	0.68	0.48	0.57	0.33	0.42	0.45	0.63	0.74	0.55	0.67		
B76		0.73	0.48	0.56	0.28	0.77	0.66	0.63	0.73	0.64	0.51	0.68	0.65	0.43	0.33	0.34	0.16	0.77	0.72	0.61	0.65	0.59	0.75	0.58	0.41	0.54	0.41	0.57	0.72	0.64	0.69	0.73	0.59	
B77		0.75	0.48	0.75	0.36	0.71	0.75	0.65	0.78	0.52	0.47	0.59	0.57	0.43	0.22	0.27	0.26	0.61	0.63	0.53	0.67	0.55	0.71	0.46	0.47	0.36	0.39	0.46	0.73	0.58	0.81	0.73	0.73	

The codes used for bees are listed in Table I

**Figure 2.** Flower-visiting network of bees in the Caatinga of Castro Alves, northeastern Brazil. Bees are represented as *rectangles* on the *right-hand side* and plants are represented as *rectangles* on the *left-hand side*. The *thickness of each line* (flower visiting interaction) is proportional to the number of bees observed visiting each plant species. The *size of each rectangle* is proportional to the number of visits observed for each species of bee or plant. Species codes are listed in Table I.



**Figure 3.** Foraging time network of flower-visiting bees in the Caatinga of Castro Alves, northeastern Brazil. Flower-visiting bees are represented as *rectangles* on the *left-hand side* and visit times are represented as *rectangles* on the *right-hand side*. The *thickness of each line* (foraging activity) is proportional to the number of bees observed foraging at each time. The *size of each rectangle* is proportional to the number of visits observed for each species of bee or for each time. Species codes are listed in Table I.



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**Chevauchement des niches trophique et temporelle dans une guilde d'abeilles (Hymenoptera, Apoidea), visitant les fleurs d'une forêt sèche tropicale**

**Niche trophique/ niche temporelle/ Apoidea/ Caatinga/**

**Überlappung von trophischen und zeitlichen Nischen in der blütenbesuchenden Bienengilde (Hymenoptera, Apoidea) eines tropischen Trockenwalds**

**Trophische Nische/ zeitliche Nische/ Nischenüberlappung/ Bienengilde/Apoidea**

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