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Food Niche Overlap Among Neotropical Carpenter Bees (Hymenoptera: Apidae: Xylocopini) in an Agricultural System

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Abstract

In the present study, we used niche overlap analysis and a network approach to investigate the use of floral resources by carpenter bees (*Xylocopa* spp.). We assessed the frequency of visit to different plant species and the activity time of carpenter bees in an agricultural system. Six species of carpenter bees were collected visiting flowers. Among the 48 interactions that were theoretically possible in the interaction network, only 19 were recorded (Connectance = 39.58%). The temporal overlap between pairs of species measured by the Shannon index (0 to 0.648) was lower than dietary overlap (0 to 0.967). The network analysis also showed that bees separated their niches more strongly in the temporal dimension ($E = 0.72$, $P < 0.001$) than in the dietary dimension ($E = 0.55$, $P < 0.001$). The levels of dietary and temporal overlap were strongly correlated with each other, as well as the time of highest frequency of visit coincided with the time of availability of resources by the most important plants (*Moringa oleifera*, *Passiflora edulis*, and *Solanum palinacanthum*). The correlation between dietary and temporal overlap is biologically explained by the presence of plants that structure the system by exerting a strong influence not only on the plant choice by foraging bees, but also on the time of resource collection.

Introduction

Most studies on bee niches have focused on the diversity of floral resources used and the partitioning of these resources (e.g., Wilms et al., 1996; Goulson & Darvill, 2004; Aguiar, 2003; Aguiar et al., 2013; Andena et al., 2012; Figueiredo et al., 2013). However, guilds of flower visitors can also be studied from other perspectives, such as activity time (Carvalho et al., 2010; Santos et al., 2013). The partitioning of temporal niches may facilitate the coexistence of ecologically similar species (Kronfeld-Schor & Dayan, 2003).

The level of complementarity or redundancy in the niches of flower-visiting insects is an important mechanism underlying the relationship between biodiversity and ecosystem functioning (Blüthgen et al., 2006; Hoehn et al., 2008; Santos et al., 2013). However, little empirical evidence exists about the level of complementarity among pollinators (Hoehn et al., 2008). Different species may have complementary niches and perform different functional roles, (Santos et al., 2010), thereby presenting different realized niches (Begon et al., 2006). Niche complementarity requires some degree of trophic or temporal specialization, whereas niche redundancy is associated with high niche overlap and functional redundancy (Blüthgen & Klein, 2011). However, two species may present redundancy on a dimension (e.g., diet) and complementarity in another dimension (e.g., temporal patterns of resource use) of their trophic niches (Santos et al., 2013).

In the present study, we used niche overlap analysis and a network approach to investigate the use of floral resources by carpenter bees (*Xylocopa* spp.). We assessed the frequency of visit to different plant species and the activity time of bees in an agricultural system. These bees are attractive candidates for crop pollination, because they have broad diet, long activity season, and are active under low illumination levels (Keasar, 2010). Indeed, several crops, such as passion fruits, tomato, and melons, can be favored by the pollination service rendered by carpenter bees (Hogendoorn et al., 2000; Sadeh et al., 2007; Benevides et al., 2009; Yamamoto et al., 2010; Keasar, 2010; Benevides et al., in press).

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Material and Methods

Study area

We collected data on bee–plant interactions in the municipality of Feira de Santana, Bahia, northeastern Brazil (12º15’25”S, 38º57’54”W). The climate of the region is semiarid, with an average annual temperature of 23.5 °C and an average annual rainfall of 867 mm (MMA 2009). The study was carried out at the Bocaiúvas Farm, that covers an area of 23.4 ha, where crops of fruits and vegetables dominate the landscape, including *Citrus sinensis* L (orange), *Citrus limonum* L. (lime), *Mangifera indica* L. (mango), *Psidium guajava* L. (guava), *Passiflora edulis* Sims (passion fruit), *Capsicum annuum* L. (papikra), *Cucurbita* sp. (pumpkin), and *Cucumis anguria* L. (bur cucumber). All plants are cultivated with no chemical additives.

Sampling

We used as a sampling unit each record of bee-plant interaction. We recorded flower-visiting bees, plants visited, visit time, temperature, relative air humidity, and luminosity each hour during each sampling. In order to characterize the guild of carpenter bees that forages on flowers in an agricultural system, we carried out monthly sampling from August 2011 to July 2012. Before the first monthly sampling, we selected a pathway crossing places rich in flowering plants. In each sampling session, two collectors captured carpenter bees visiting flowers, using entomological nets, along the same transect 1 km long. The sampling effort per specimen of plant in blossom was 5 min. We carried out sampling from 0600 to 1800, summing up 12 samples of 12 h, or 244 h of sampling per collector. All flowering plant species were sampled each hour, as collectors walked the entire transect once every hour.

Table 1. Carpenter bee species and plants visited for floral resources in an agricultural system.

Plant Species	Carpenter bee species					
	X. frontalis (X01)	*X. grisescens* (X02)	*X. nigrocincta* (X03)	*X. ordinaria* (X04)	*Xylocopa* sp.1 (X05)	*X. suspecta* (X06)
Anacardium occidentale L. (P01)	-	1	-	-	-	-
Bixa orellana L. (P02)	5	1	-	-	-	-
Cucurbita pepo L. (P03)	-	1	-	-	-	-
Moringa oleifera Lam. (P04)	23	3	4	-	1	7
Passiflora edulis Sims (P05)	51	-	2	1	-	4
Portulaca oleracea L. (P06)	1	-	-	-	-	-
Solanum palinacanthum Dunal (P07)	3	-	1	1	-	2
Solanum stipulaceum Willd. ex Roem.& Schult. (P08)	-	-	-	1	-	-

Data analysis

We used the importance index (Ij) to evaluate the importance of each plant species for each bee species, as well as the importance of each bee species to each plant species. This index varies from 0 to 1, and it tends to 1 when a plant species (or a bee species) has many interactions in the community or a large number of exclusive interactions (Murray, 2000).

We measured the overlap in both trophic niche dimensions (dietary and temporal) for each pair of bee species with the Schoener index (1986). This index (NO_{ih}) varies from 0 to 1, and we considered the level of overlap low when the value found was lower than 0.3, moderate when the value was higher than 0.3 and lower than 0.5, and high when the value was higher than 0.5.

Following Santos et al. (2013), we used a network approach to determine the degree of specialization in the diet and temporal activity of flower-visiting bees with the E index (Araújo et al. 2008). We organized the data on bee species and activity time as adjacency matrices and represented them as bipartite graphs using the package bipartite 2.00 for R (Dormann et al., 2009).

We used linear regressions and Spearman correlations to test for relationships between temperature, air humidity, bee richness, bee abundance, and degree of niche overlap in pairs of bee species.

Results

We collected six species of carpenter bees (113 individuals) visiting flowers of eight plant species (Table 1). In the interaction network we recorded 19 out of 48 theoretically possible bee-plant interactions (Connectance = 39.58%). The low connectance of the bee-plant network is related to singletons, as four plant species were visited only by a single bee species, and one bee species visited only one plant species (Fig. 1). *Moringa oleifera* (P04), *Passiflora edulis* (P05), and

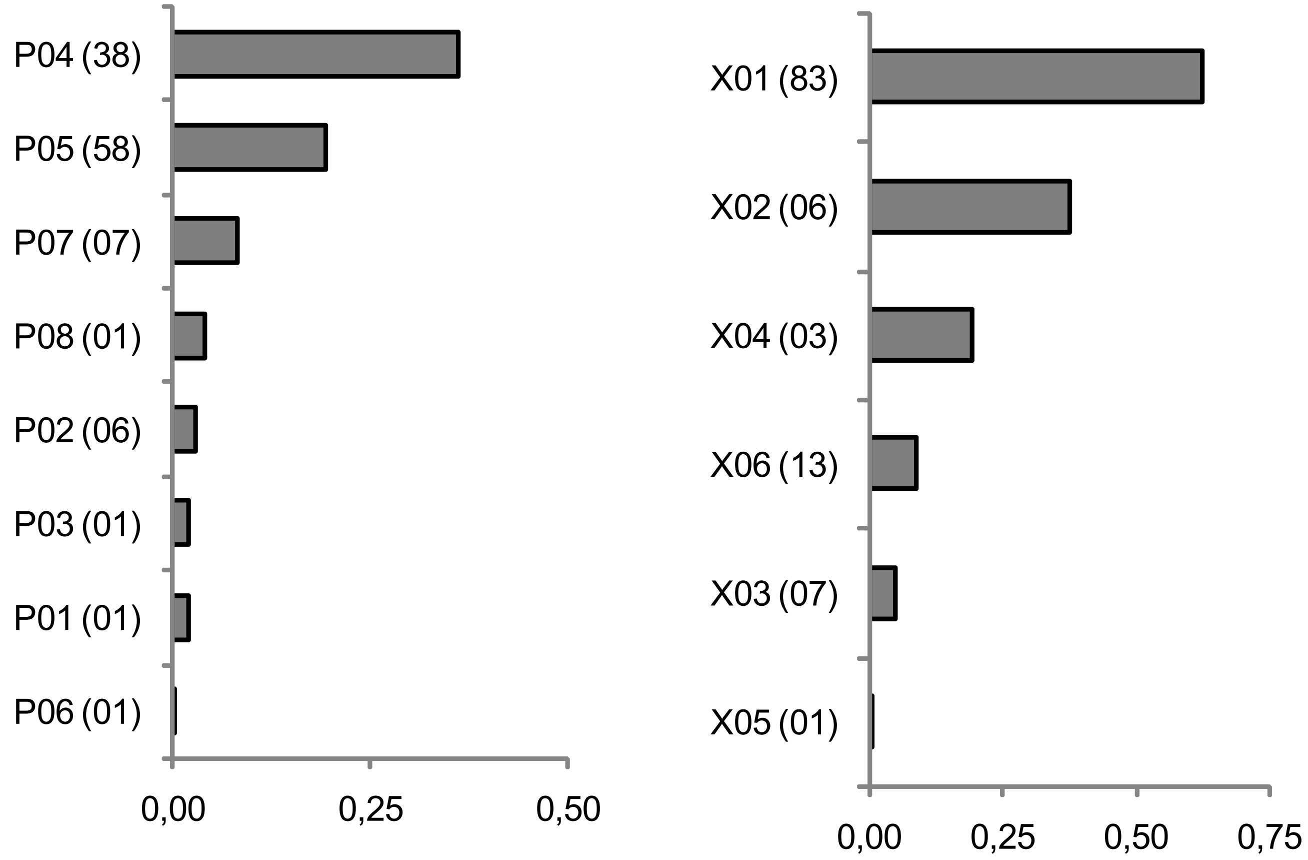

Fig. 1 - Importance index (Ij; Murray) of the plant species that provide floral resources for carpenter bees (Ij = 0.002 to 0.361) and of the flower-visiting bees (Ij = 0.004 to 0.624). Bee abundance is provided in parenthesis. Plants and Bees codes on table 1.

Table 2. Richness of visited plants (S_{pla}), abundance of individuals in each bee species (N_{bees}), and trophic niche overlap (NO_{ih}, Schoener index) between pairs of species of carpenter bees flower-visiting in an agricultural system. Temporal niche overlap dimension (upper triangle) and dietary niche overlap dimension (lower triangle).

	S_{pla}	N_{bees}	*X. frontalis*	*X. grisescens*	*X. nigrocincta*	*X. ordinaria*	*Xylocopa* sp1	*X. suspecta*
Xylocopa frontalis (Olivier, 1789)	5	83	-	0.108	0.611	0.325	0.145	0.568
Xylocopa grisescens Lepeletier, 1841	4	5	0.337	-	0.143	0.000	0.000	0.385
Xylocopa nigrocincta Smith, 1854	3	7	0.599	0.500	-	0.286	0.143	0.648
Xylocopa ordinaria Smith, 1874	3	3	0.369	0.000	0.429	-	0.333	0.308
Xylocopa sp.1	1	1	0.277	0.500	0.571	0.000	-	0.154
Xylocopa suspecta Moure & Camargo, 1988	3	13	0.621	0.500	0.967	0.462	0.538	-

Solanum palinacanthum (P07) stood out by their number of interactions with bees. These species received 91% of the bee visits. *Xylocopa frontalis* (X01) was the most abundant bee (N = 83, 73%) and visited the highest richness of plant species (Tables 1 and 2)

Carpenter bees visited flowers throughout the day, but with higher frequency of visits at three times (Fig. 2). The first peak of individuals visiting flowers occurred between 0600 and 0800 (32% of the individuals), the second between 1100 and 1300 (41%), and the third at 1500 (17%).

We compared niche overlap (dietary and temporal) for six *Xylocopa* species (Table 2). The values calculated for species with few individuals should be interpreted with caution, since they may not reflect the real local overlap in the use of the resources. The dietary overlap varied from 0 to 0.967. Out of 15 pairs of species analyzed, three pairs showed low overlap

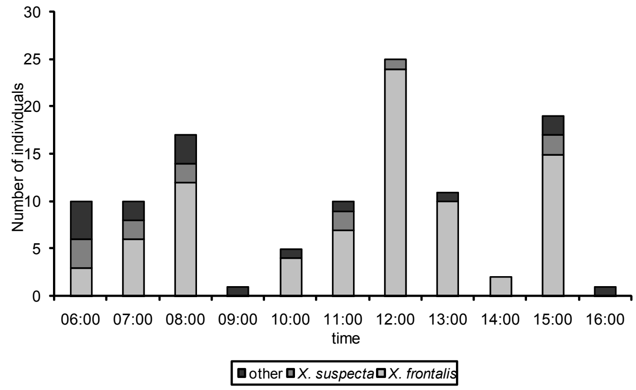

Fig. 2 – Number of individuals of carpenter bees (Xylocopa spp) captured visiting flowers in an agricultural system at each sampling time.

($NO_{ih} < 30\%$), seven pairs showed intermediate overlap ($30\% < NO_{ih} < 50\%$), and five pairs showed high overlap ($NO_{ih} > 50\%$). Temporal overlap was lower than dietary overlap, varying from 0 to 0.648. Out of 15 pairs of species analyzed in terms of temporal overlap, eight showed low overlap ($NO_{ih} < 30\%$), four pairs showed intermediate overlap ($30\% < NO_{ih} < 50\%$), and only three pairs showed high overlap ($NO_{ih} > 50\%$; Table 2). The highest value of overlap in the dietary niche (0.967) was found between *X. nigrocincta* and *X. suspecta*, which resulted primarily from the concentration of visits both in the flowers of *M. oleifera* and *P. edulis*.

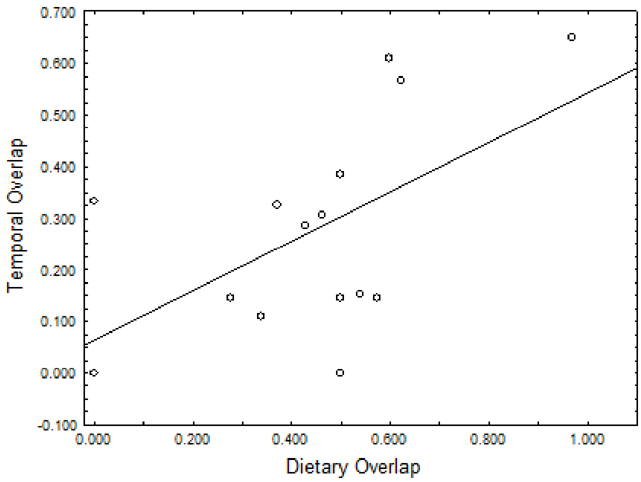

Fig. 3 – Correlation between dietary and temporal overlap among carpenter bees (Xylocopa spp) (y = 0.063 + 0.4815*x; r = 0.5557; p = 0.0315) in an agricultural system.

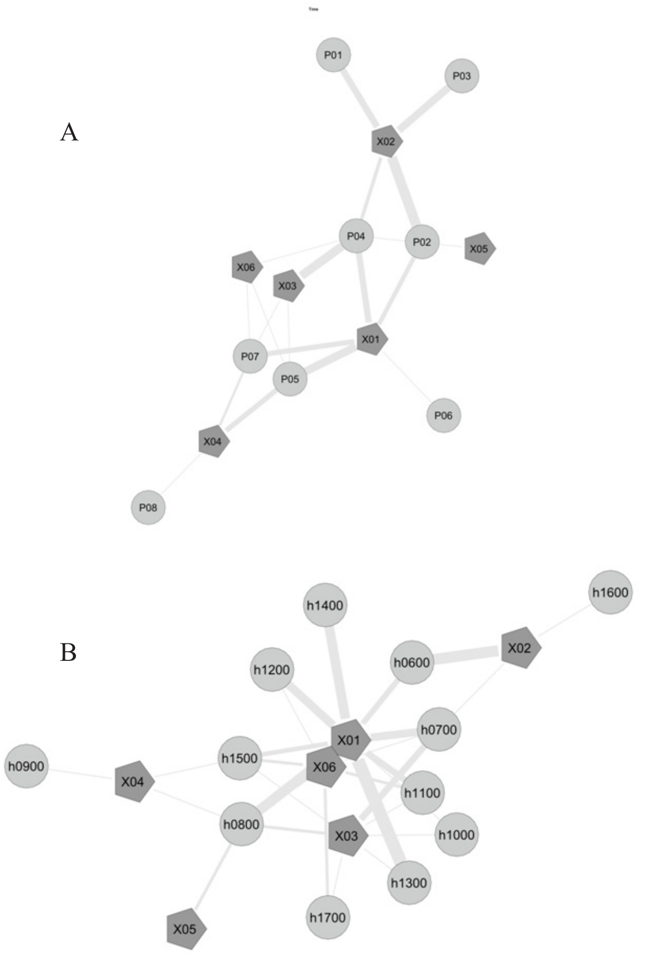

Fig. 4 – Graphs showing a larger weighted clustering coefficient in the bee-plant network than in the bee-time network. Dark gray pentagons represent carpenter bees (Xylocopa spp), light gray circles represent in graph A the plants visited, and in graph B the time of visit. Lines represent links and their thickness is proportional to the number of observations. Plants and Bee codes on table 1.

There was no significant relationship between bee abundance, bee species richness, plant species richness, temperature, and relative air humidity. However, we found a significant positive relationship between the level of temporal overlap and the level of dietary overlap (y = 0.063 + 0.4815*x; r = 0.56; p = 0.03) (Fig. 3). The network analysis showed similar results; bees separated their niches more strongly in the temporal dimension ($E = 0.72$, $P < 0.001$) than in the dietary dimension ($E = 0.55$, $P < 0.001$; Fig. 4).

Discussion

Among *Xylocopa* bees, *X. frontalis* was the species with the highest number of interactions and with the broadest trophic niche. This species is known for its generalistic foraging behavior and for exploring a relatively broad diversity of floral resources (Silva, 2009; Yamamoto et al., 2012).

However, an analysis of the pollen collected by female *X. frontalis, X. grisescens*, and other carpenter bee species revealed that, in spite of being generalistic, carpenter bees tend to explore more intensively a subset of the floral resources available, which contributes to the narrowing of their dietary niche and increases dietary overlap between species (Silva, 2009).

The three peaks of carpenter bee foraging on flowers observed in the present study and the high overlap in bee activity at these times seem to be related to the temporal availability of the floral resources of three important plants. In the morning, the foraging activity of bees was more intensive at early hours, a period that coincides with the opening of *M. oleifera* flowers, which occurs from 0300 on (Jyothi et al., 1990) and of *S. palinacanthum* flowers, whose anthesis begins around 0600 (Carvalho et al., 2001). The second peak was recorded around midday, which coincides with the anthesis and availability of the resources of *P. edulis* flowers at 1200 (Benevides et al., 2009; Siqueira et al., 2009). In the mid afternoon, there was an increase in the frequency of carpenter bees on flowers, which is consistent with the observations made by Carvalho et al. (2001), who studied the visitors of *S. palinacanthum.*

The availability of floral resources by *P. edulis* from midday on strongly influenced the overlap of carpenter bee niches, since this plant received the highest number of visitors. As in our study, Benevides et al. (2009) recorded the highest frequency of bee visits to *P. edulis* flowers between 12:30 and 13:30 in passion fruit crops in southeastern Brazil, in which *X. frontalis* and *X. ordinaria* were the most frequent carpenter bees. On the other hand, Varassin et al. (2010) found a constant visit rate of *X. frontalis* to *P. edulis* flowers between 14:00 and 18:00, and concluded that the visit rate of this carpenter bee was not influenced by anthesis timing or nectar volume or concentration.

At times of low visit frequency of *Xylocopa* to the monitored plants, we presume that the females changed their foraging routes to explore other plants in the surroundings. Likewise, Jyothi et al. (1990) observed that the temporal activity of *Xylocopa* on *M. oleifera* depended not only on the availability of nectar provided by this plant, but also on the availability of resources produced by other plants in the surroundings, which could be more attractive to foraging females at some times of the day. As pointed out by Silva (2009) and Yamamoto et al. (2012), in agricultural systems, *Xylocopa* species interact with both cultivated and wild plants.

In the present study, abiotic factors (temperature and relative humidity) did not affect the visit frequency of carpenter bees or the overlap in dietary and temporal niches. Although there are several examples of a relationship between the foraging activity of bees and abiotic factors, there are also examples of the daily activity of bees explained by the temporal availability of floral resources. According to Stone et al. (1999), the time of resource production by plants represents a window of opportunity for foraging bees and may also be a driver of bee activity.

In the studied system, the levels of dietary and temporal overlap were strongly correlated with each other, as well as the time of highest visit frequency of bees coincided with the time of availability of resources by most important plants. The correlation between dietary and temporal overlap is biologically explained by the presence of plants that structure the system by exerting a strong influence not only on the plant choice by foraging bees (bee diets), but also on the time of resource collection.

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