Review Article

Generalist Bee Species on Brazilian Bee-Plant Interaction Networks

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Determining bee and plant interactions has an important role on understanding general biology of bee species as well as the potential pollinating relationship between them. Bee surveys have been conducted in Brazil since the end of the 1960s. Most of them applied standardized methods and had identified the plant species where the bees were collected. To analyze the most generalist bees on Brazilian surveys, we built a matrix of bee-plant interactions. We estimated the most generalist bees determining the three bee species of each surveyed locality that presented the highest number of interactions. We found 47 localities and 39 species of bees. Most of them belong to Apidae (31 species) and Halictidae (6) families and to Meliponini (14) and Xylocopini (6) tribes. However, most of the surveys presented *Apis mellifera* and/or *Trigona spinipes* as the most generalist species. *Apis mellifera* is an exotic bee species and *Trigona spinipes*, a native species, is also widespread and presents broad diet breadth and high number of individuals per colony.

1. Introduction

Bees are important keys to global diversity providing vital ecosystem services such as pollination [1]. For bees, plants species are basically their main food sources, where they collect pollen and nectar and eventually other resources, such as oil. Plants are those which have interest on bees' skills to achieve successful reproduction. They have to deal with different foraging techniques employed by bees [2–4] to reach their main reward, reproduction.

In Brazil, until the end of 1960s, information about bee-plant interactions came mostly from observations made by naturalists of the early 20th century. However, the study of [5] proposed a standardized methodology to perform bee surveys that was subsequently applied to most of them, allowing further comparisons between the different surveyed localities.

The studies of [6–8] made previous synthesis of Brazilian surveys. The first one only compared information about species richness found in different biomes. The other two studies used only data from eusocial Apidae found on the surveys. Until now, no attempt was made to determine the

generalist bee species in interaction networks of different localities using all Apoidea species found on them.

Interaction networks are built as a matrix of interacting species and have been justified mainly because networks involving plants and pollinators are generalists and form complex systems bringing additional challenges to their study [9].

In plant-pollinator interactions, species are commonly seen as generalists when they interact with many species of different taxa, and specialists if they interact with one or a few closely related species [10]. Reference [11] showed that in pollination systems the most generalized species are usually network keystone species. Since they interact with most plant species, they play an important role to maintain the whole network.

The main goal of this study was to determine the most generalist bee species on bee surveys conducted on different localities in Brazil.

2. Material and Methods

We searched the academic literature for bee surveys on flowering plants on different localities of Brazil, aiming to

FIGURE 1: Brazilian localities where the bee surveys were conducted.

build a matrix of bee-plant interactions to each locality. We considered the surveys that used the standard procedure suggested by [5] and whose observations were made for at least one year. In this procedure a fixed amount of time is spent at each flowering plant (or patch) and the coverage of transects is randomized in time, order, and direction. On most of these surveys, the interactions were not detailed and could include effective pollination and/or nectar, pollen, or oil foraging.

Many survey datasets have been published only in M.S. or Ph.D. thesis and are only available to the public at their universities. When these works were subsequently published as a paper, both datasets were compared and both were cited on the reference list.

The bee taxonomic names were updated according to [12]. We discarded the observations that were taxonomically unresolved.

We used the bipartite package [13] for R 2.11.1 (The R Foundation for Statistical Computing) to analyze each matrix. Each cell of the matrix represents a single bee-plant interaction and can have a value of 0 if the interaction is not observed, or 1, if observed [14]. With this tool we determined the first three bee species with the highest number of interactions.

The declared coordinate point of each survey was also used to build a map with ArcGIS 10 software (Esri Inc.).

3. Results

We found 47 localities whose surveys fulfilled the requirements previously quoted on the methodology section. Most surveys were done on South, Southeast, and Northeast regions of Brazil, either on urban areas, on seasonally dry areas of Tropical Dry Forest (Brazilian Caatinga) and Tropical Shrublands (Brazilian Cerrado), or on Tropical Moist Forest (Brazilian Atlantic Forest) biomes (Figure 1, Table 1). We did not find any bee survey on the North region and only one on the Midwest region of Brazil.

The first, second, and third most interacting species on each surveyed locality are found on Table 1. We found a total number of 39 different species. Most of them belong to Apidae (31 species) and Halictidae (6) families, and to Meliponini (14) and Xylocopini (6) tribes (both from Apidae family). The genus with the highest number of interacting species was *Xylocopa* (5 species). The genera *Trigona*, *Exomalopsis*, and *Augochloropsis* presented each three interacting species.

TABLE 1: Number of times bee species were quoted as the first, second, or third most interacting species on the Brazilian bee surveys.

Family	Tribe	Species	1st	2nd	3rd	Biome (<i>sensu lato</i>)	References
Andrenidae	Oxaeini	<i>Oxaea flavescens</i>		1	1	Tropical Shrublands	[15, 16]
Apidae	Apini	<i>Apis mellifera</i>	20	15	2	Various	[15, 17–56]
	Bombini	<i>Bombus morio</i>		1		Tropical Shrublands	[26]
	Centridini	<i>Bombus pauloensis</i>	2	4	3	Tropical Shrublands, Tropical Moist Forest and Urban Area	[26, 33, 36, 57–62]
		<i>Centris klugii</i>			1	Tropical Shrublands	[26]
		<i>Centris lepreuri</i>			1	Tropical Shrublands and Tropical Moist Forest	[45, 46]
		<i>Melissoptila cneomala</i>		1		Tropical Shrublands	[26]
	Euglossini	<i>Eulaemia nigrita</i>	1			Tropical Moist Forest	[27]
	Exomalopsini	<i>Exomalopsis analis</i>			1	Dune	[22]
		<i>Exomalopsis auropilosa</i>	1			Urban Area	[62]
	Meliponini	<i>Exomalopsis fulvofasciata</i>	1		1	Tropical Shrublands	[41, 63, 64]
		<i>Cephalotrigona capitata</i>		1		Tropical Moist Forest	[65]
		<i>Melipona scutellaris</i>			1	Tropical Moist Forest	[51–53]
		<i>Mourella caerulea</i>	1			Tropical Shrublands	[61]
		<i>Paratrigona lineata</i>	2			Tropical Dry Forest and Tropical Shrublands	[32, 57]
		<i>Paratrigona subnuda</i>	1	1	1	Urban Area and Tropical Moist Forest	[34, 35, 42, 43, 55, 56]
Tetrapediini Xylocopini		<i>Plebeia droryana</i>		1	1	Urban Area and Tropical Shrublands	[50, 66]
		<i>Plebeia emerina</i>		1	1	Tropical Moist Forest	[39]
		<i>Scaptotrigona bipunctata</i>			1	Tropical Shrublands	[66]
		<i>Scaptotrigona tubiba</i>			1	Tropical Moist Forest	[67]
		<i>Tetragona clavipes</i>			1	Tropical Shrublands	[38]
		<i>Tetragonisca angustula</i>		1	6	Various	[17, 27, 28, 40, 48, 50, 54, 63, 64]
		<i>Trigona fulviventris</i>	1		2	Tropical Moist Forest	[37, 39]
		<i>Trigona pallens</i>				Tropical Shrublands	[44]
		<i>Trigona spinipes</i>	16	14	11	Various	[15–21, 24–56, 61, 63–67]
		<i>Tetrapedia rugulosa</i>			2	Tropical Shrublands	[23–25, 30]
		<i>Ceratina maculifrons</i>			2	Urban Area and Tropical Shrublands	[16, 62]
		<i>Xylocopa carbonaria</i>	1			Dune	[22]
		<i>Xylocopa cearensis</i>			1	Urban Area	[49]
		<i>Xylocopa grisescens</i>			1	Tropical Dry Forest	[29]
		<i>Xylocopa ordinaria</i>			1	Urban Area	[49]
		<i>Xylocopa suspecta</i>			1	Tropical Moist Forest	[47]
Halictidae	Augochlorini	<i>Augochlora esox</i>			1	Tropical Dry Forest	[57]
		<i>Augochloropsis callichroa</i>		1		Tropical Moist Forest	[67]
		<i>Augochloropsis crassiceps</i>			1	Tropical Moist Forest	[65]
		<i>Augochloropsis illustris</i>		1		Urban Area	[62]
Megachilidae	Halictini	<i>Ceratalictus theius</i>		1		Tropical Shrublands	[58–60]
		<i>Dialictus opacus</i>		3		Urban Area, Tropical Dry Forest and Tropical Shrublands	[18–21, 49, 58–60]
	Anthidiini	<i>Hypanthidium divaricatum</i>			1	Tropical Moist Forest	[39]

FIGURE 2: Percentage of Brazilian bee surveys presenting *Apis mellifera* or *Trigona spinipes* as (a) the first species with highest number of interactions and (b) the second species with highest number of interactions.

On most surveys *Apis mellifera* and/or *Trigona spinipes* were the most interacting species (Table 1). Considering the first and second species with the highest number of interactions, *A. mellifera* was present on 75% of the Brazilian surveys and *T. spinipes* on 64% (Figure 2).

Other important interacting species were *Bombus pauloensis* that was quoted nine times on the different localities and on different ranks (first, second, or third interacting species), *Tetragonisca angustula* (7 times), *Dialictus opacus*, and *Paratrigona subnuda* (3 times each) (Table 1).

Halictidae and Xylocopini species as well as *A. mellifera* and *T. spinipes* were found on different biomes (Table 1). Most of Meliponini species were found on Tropical Moist Forest and on Tropical Shrublands.

4. Discussion

Apidae is a large family of bees, whose species are mostly generalist foragers. It is widely distributed, occurring on different biomes under different environmental characteristics [68]. Bee species from the Meliponini tribe live in tropical and subtropical regions of the world and are considered to be important pollinators of plant species on different environments [69].

T. spinipes, one of the most generalist stingless bee species according to our results, presents colonies with a huge number of individuals and wide diet breath, and it shows widespread distribution over the Brazilian territory. Moreover, they build aerial nests, being independent of any kind of holes to nidify. Independence of holes and the great availability of workers may determine the degree of dispersion over the countryside and the generalist interacting behavior [70].

A. mellifera is an exotic bee species also widespread in different biomes. It is well adapted to different climatic conditions and presents a generalist foraging behavior. Despite the potential negative impact on native pollinator

species [71], it was already recognized as the most important pollinator of natural environments and also of agricultural crops [72].

Although we are not aware of any study comparing *A. mellifera* and *T. spinipes* pollinating performance, they are probably important resource competitors, due to their similar colony size and widespread distribution. The efficient communication system exhibited by *Apis mellifera* and the aggressive behavior on flowers, already reported to *T. spinipes*, complete this scenario [73, 74].

Recent reports of the colony collapse disorder syndrome of *Apis mellifera* species arouse the awareness of the importance of this species [75], especially due to its importance to agriculture. At the same time, it also brings the attention to the native pollinators and their importance to local crops, and international initiatives have been suggested to protect them [76].

Far from the number of interactions found for the two main species, two other generalist bee species were *B. pauloensis* (9 interactions) and *T. angustula* (7 interactions). Both species were found in distinct biomes, including urban areas, thus suggesting a broad ability to survive at different environmental conditions. But unlike *T. spinipes* both depend on cavities to nidify and do not present an efficient communication system as *A. mellifera* and its ability to leave for other places when conditions become hard [77], or the aggressive behavior on flowers reported to *T. spinipes*. Besides, their colonies are much smaller than those of these two species. All these factors together are responsible for the lower number of interactions presented by them in comparison to the two main species.

In summary, we demonstrated the importance of a native bee species (*T. spinipes*) and of an exotic one (*A. mellifera*) to interaction networks on surveys conducted in Brazil. As already mentioned, their populous colonies, broad distribution, and aggressive behavior probably are the most important contributors to these results. Comparisons involving their pollinating performance and resource

partitioning are suggested as important lines for further research.

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