



Specialist Bee Species Are Larger and Less Phylogenetically Distinct Than Generalists in Tropical Plant–Bee Interaction Networks

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Bee pollinators are key components of terrestrial ecosystems. Evidence is mounting that bees are globally in decline, and species with a higher degree of specialization are the most vulnerable to local extinction. However, ecological features that could explain bee specialization remain poorly tested, especially in tropical species. Here, we aim to determine the most specialized bee species and their associated ecological traits in tropical plant–bee interaction networks, answering three questions: (1) Which bees in the interaction networks are specialists? (2) Is body size related to their role as specialists in interaction networks? (3) Are there phylogenetic relationships between the bee species identified as specialists? We used fifteen quantitative plant–bee interaction networks from different Brazilian biomes covering 1,702 interactions (386 bee and 717 plant species). We used the normalized degree (standardized number of partners) as a metric to determine trophic specialization of bee species. Body size was estimated by measuring intertegular distance (ITD), i.e., the distance between the bases of the wings on the thorax. Evolutionary distinctiveness (ED) was used to quantify species uniqueness, i.e., the singularity of species in the phylogenetic tree. Relationships between dietary specialism, ITD and ED were assessed using generalized linear models. We detected 34 specialist bee species (9% of total species), distributed in 13 genera, and four families. ITD and ED were important variables explaining the specialization of tropical bee species. Specialists were larger and less phylogenetically distinct than expected by chance. Based on a large data set covering some of the main tropical biomes, our results suggest that loss of specialist bees from Brazilian plant–bee networks could have deleterious consequences for native plant species preferentially pollinated by large-bodied bees. Moreover, by affecting more evolutionarily distinct species, i.e., those with fewer extant relatives, the loss of specialist bees will likely affect few clades but can result on considerable loss of evolutionary history and phylogenetic diversity in the Brazilian bee communities. The results are important for decision-making concerning conservation measures for these species and may also encourage the development of sustainable management techniques for bees.

Keywords: pollinators, mutualism, trophic niche, response traits, phylogeny, biodiversity, conservation

INTRODUCTION

Pollination between bees and plants is one of the key mutualistic interactions structuring ecosystems (Potts et al., 2016). This interaction is necessary for the reproduction of most plants, allowing fruit and seed formation in natural areas (Laura et al., 2013), agricultural lands (Klein et al., 2007), and areas under recovery (Montoya et al., 2012). Thus, pollinators are essential for the maintenance of natural communities and agricultural productivity (Potts et al., 2010, 2016; Vanbergen et al., 2014). However, several studies have indicated that the abundance and diversity of bees are declining and that some species are clearly at risk of extinction (Gallai et al., 2009; Garibaldi et al., 2009; Lever et al., 2014). In particular, specialist species (i.e., those that interact with a smaller number of partners) seem to be the most vulnerable to habitat loss (Bommarco et al., 2010; Aizen et al., 2012; Ferreira et al., 2020). Bees are considered the main taxon of pollinators, so understanding bee pollination networks and bee specialization patterns may provide effective support to conservation and restoration programs (Hallett et al., 2013).

Specialization is broadly defined as the ability of organisms to exploit a more restricted set of resources than that of related lineages (Day et al., 2016). Implicit in this concept is the idea that the subset of resources exploited is used more effectively and sometimes exclusively by specialists than by generalists (Larsson, 2005; Armbruster, 2017). Bees are usually polylectic, i.e., they collect floral resources from a great diversity of plant species (Michener, 1979), exhibiting generalist behavior (Ebeling et al., 2011). Bee specialization on a single food resource is rare (e.g., González-Varo et al., 2016) and usually, specialist species depend on generalist partners (see below; Bascompte et al., 2003). Nevertheless, oligolecty may function for reducing competition and foraging costs (Armbruster, 2017), and specialist bees can be key pollinators, i.e., network connectors (hubs) (Olesen et al., 2007; Romero et al., 2020) and crop pollinators, such as the case of *Peponapis* Robertson, 1902 that preferentially visit and pollinate cucurbit plants (Guzman et al., 2019; see also Cane, 2021). Therefore, the replacement of specialist species by generalist ones may have negative consequences on community stability and resilience (Peralta et al., 2020), as well as ecosystem functioning (Clavel et al., 2011). Moreover, visiting bees do not always act as pollinators (Popic et al., 2013), and specific methods are needed to determine the effectiveness of pollination (e.g., Dafni, 1993).

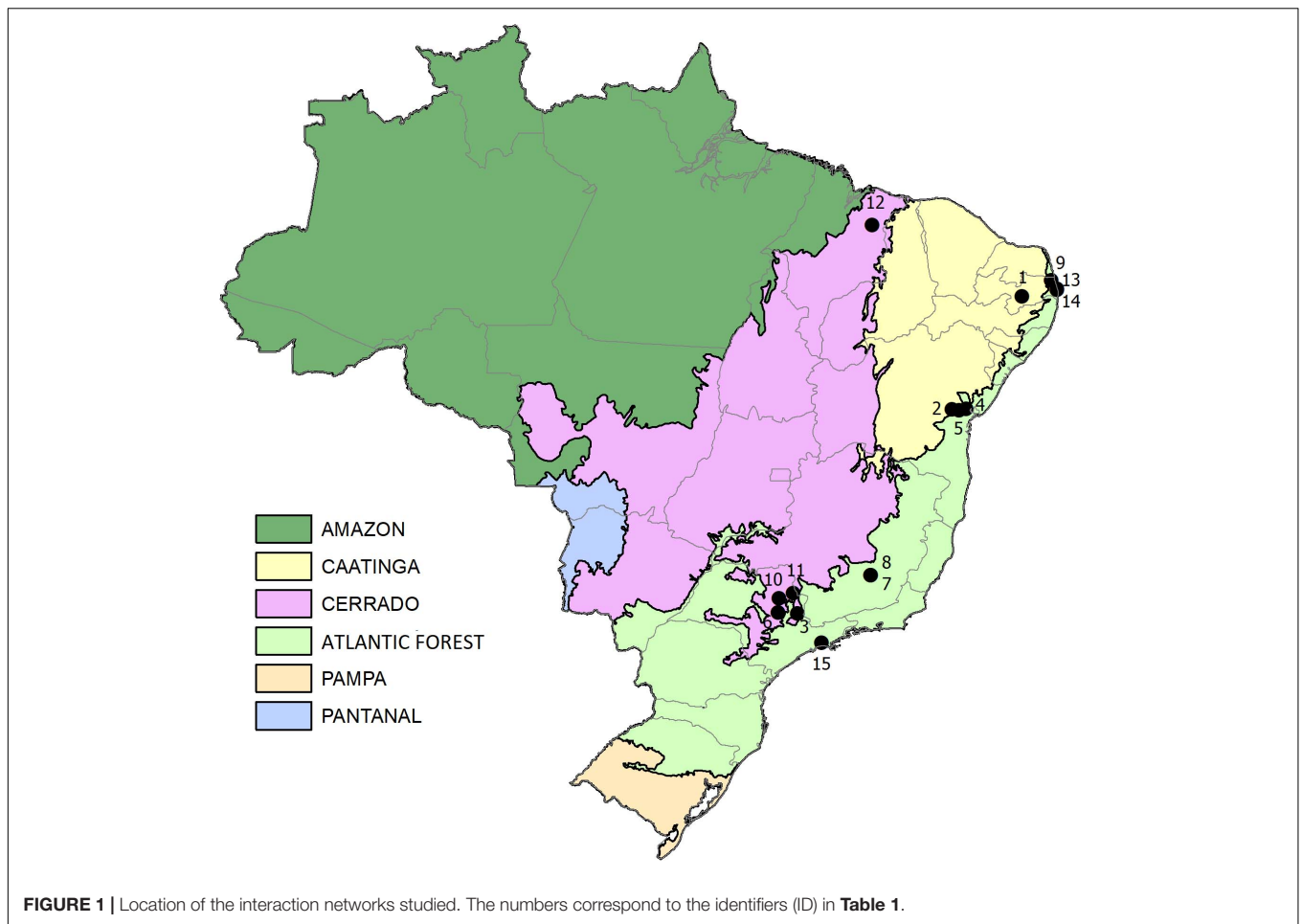
The theory of complex networks has been used to describe the structure of interspecific mutualistic interactions and the role of species within communities (Bascompte et al., 2003). Some patterns emerge from the analysis of these networks, such as nestedness, a pattern in which the interactions are asymmetric, i.e., specialist and generalist species tend to interact with the generalist ones, characterizing a core of species (Bascompte et al., 2006; Bascompte and Jordano, 2007; Aizen et al., 2012). Thus, the analysis of interaction networks is useful to characterize the level of specialization among species composing the network (Montoya et al., 2006; Weiner et al., 2014). However, such network-based approaches to determining ecological specialization are strongly influenced by sampling methods, and failure to use standard survey methods can produce

inaccurate assessments of plant–bee interactions (Vázquez and Simberloff, 2002; Vázquez and Aizen, 2003; Dorado et al., 2011). For example, in tropical regions, mainly in tropical forests with high canopies, bee sampling is usually restricted to flowers in the lower strata of vegetation (Ferreira et al., 2020).

Initially, the generalist and specialist role of species was related to their abundance (Krishna et al., 2008) but, later evidence has also shown that morphological traits are important in determining the interaction patterns of these matrices (Chamberlain et al., 2010; Gibson et al., 2012). It has been suggested that similarity in resource use is higher among species with similar body size (Cortopassi-Laurino et al., 2003; Nogueira-Ferreira and Augusto, 2007; Rabelo et al., 2014). For instance, in temperate forests, smaller bees can be more specialized foragers than larger bees (Smith et al., 2019). The authors suggested that large bees fly greater distances and thus, encounter and exploit a wider range of plant species than bee taxa with more limited dispersal abilities (Smith et al., 2019). Some controversy may be found, however, when considering bumblebees from the northern hemisphere. A previous study indicated that the foraging behavior of some large European species (genus *Bombus* Latreille, 1802) is generalist, as these species did not show fidelity in their interactions with the studied grassland plants (they can collect pollen from up to three different plant species during a foraging trip, thus having a more generalist role) (Leonhardt and Blüthgen, 2012). Another study indicated high fidelity of interactions between bumblebees and a single plant species in undisturbed forest patches of North America (Villalobos et al., 2019). Hence, further studies are required to clarify the relationship between pollinator body size and diet specialization, especially in tropical regions where still exists an important knowledge gap.

In addition to body size, specialist behavior may be related to the degree of evolutionary relationship between species because interspecific interactions are largely structured by the degree of phenotypic complementarity between mutualistic partners (e.g., long-tongued bees visit flowers with deep corolla tubes) (Vázquez et al., 2009). As related species tend to have similar characteristics due to shared ancestry (Rezende et al., 2007a), they often occupy similar positions in terms of their interactions, both with regard to the number of partners with which they interact and to the functional attributes of their partner species (Hutchinson et al., 2017). On the other hand, it is likely that competition between similar individuals is greater, and the speciation process could take place by selecting different characteristics between species, allowing them to differentiate their niches (Johnson and Hubbell, 1975). Thus, closer species could also be potentially different in terms of trophic interactions.

The present study analyzes specialization in interaction networks between plants and bees in tropical biomes, aiming to determine: (1) Which bees in the interaction networks are specialists? (2) Is the body size of bees related to their role as specialists in interaction networks? (3) Are there phylogenetic relationships between the bee species identified as specialists? Answering those questions can help understanding the ecosystem functioning in the present (but also predict future global change responses), providing support to decision-make



processes concerning pollinator's conservation and sustainable management, and identifying pathways for future research on specialist pollinator taxa in tropical ecosystems.

MATERIALS AND METHODS

Studies conducted in Brazil on interaction networks between bees and plants were compiled previously (Giannini et al., 2015). All studies followed standardized sampling procedures suggested by Sakagami et al. (1967), in which the researcher observes each plant in a pre-established transect for a fixed time (3–5 min) and collects all the bees observed using an entomological net, repeating this procedure monthly for at least one year. The interaction networks were represented as a set of nodes (species) connected through links, with each link representing an observed interaction (Bascompte and Jordano, 2007). We included surveys that determined the number of bees sampled per plant to construct fifteen quantitative networks. These networks belong to some of the most important Brazilian biomes (**Figure 1**). The nomenclature and systematic identification of the bees followed that of Moure's Bee Catalog¹, and plant identification

was in accordance with the Missouri Botanical Garden's Tropicos information system².

To answer the first question and identify the specialist bees in the interaction networks, the following network metrics were used: (1) Degree, which describes the number of interactions of a given species with different species; thus, species with lower degree values are considered specialists because they interact with few species (Thompson, 2005; Vázquez et al., 2005; Krishna et al., 2008). (2) Strength, which is the relative frequency of interaction of a bee species with a plant species; it is represented as the number of interactions between a bee species and a plant species divided by the number of visits by all bee species to that same plant. Thus, specialist bees have lower interaction strength values (Vázquez et al., 2007; Dormann, 2011; Schleuning et al., 2011; Mello et al., 2016). (3) Closeness, which is based on the number of steps on the shortest path (in terms of interactions) that link a particular species to all other species in the network; a low closeness value for a species means that it is distant from most other species in the network, indicating specialization in interactions (González et al., 2010). (4) Betweenness, which measures the extent to which a particular species is located within the shortest paths between two other species, acting as a

¹<http://moure.cria.org.br/>

²<http://www.tropicos.org/>

central connector in the network (Newman, 2003); species with lower betweenness values are also considered more specialized (Guimarães et al., 2011). To test whether the four metrics were correlated, a Pearson's correlation test was performed. The results obtained for each metric derived from each network were scaled ranging from 0 to 1 (using $x' = x - \min x / \max x - \min x$) to reduce a possible effect of the number of interactions observed. This procedure better reflects the role of each species in the network than the raw data, avoiding any trend in the analysis of the process (Legendre and Legendre, 2012). The four metrics presented were calculated using the bipartite package (Dormann, 2019) in R (R Core Team, 2021). We selected the 5% most specialized bees in each network, aiming to determine the smallest set of species in each network, especially to help in guiding further studies and conservation programs.

To answer our second question (does body size determine bee species' roles as specialists in interaction networks?), we used a database containing intertegular distance (ITD) measurements of Brazilian bee species (Borges et al., 2020), which was complemented in the current study (46% of ITD measures). ITD is correlated with the body size of bee species (Cane, 1987; **Figure 2**), and was used as a predictor variable for the previously mentioned specialization metrics of the interaction networks.

To answer the third question (are there phylogenetic relationships between bee species identified as specialists?), a phylogeny was constructed containing all bee genera with available data recorded for Brazil, according to the TimeTree database (timetree.org, access on February 15, 2019). Species recorded in this study were inserted within the phylomatic function (Webb and Donoghue, 2005) from the software PHYLOCOM, version 4.2 (Webb et al., 2008). For tree calibration by the branch length adjustment ("bladj") algorithm from

PHYLOCOM, we used median time estimates for internal nodes, as given by the TimeTree database. The Evolutionary distinctiveness (ED) metric was used to quantify singularity of species in the phylogenetic tree (Faith, 1992; Fournier et al., 2017), being suggested to point out priority species for conservation (Veron et al., 2017). ED was computed for all species registered in this study by "evol.distinct" function using fair portions (Isaac et al., 2007) from the R package "picante" (Kembel, 2020). Additionally, phylogenetic signal, i.e., the tendency that closely related bee species resemble each other in terms of functionality, was computed as Pagel's λ and Bloomberg's K for the ITD using the "phylosig" function from the "phytools" R package (Revell, 2021). In both indices, the null expectation (high phylogenetic signal) assumes Brownian motion models of evolution (random walk). Pagel's λ measures to which degree the shared history of taxa has driven trait distribution at the tips of the phylogeny (Pagel, 1997, 1999). By definition, a lambda value of 1 results from a trait distribution as expected from Brownian motion (high phylogenetic signal), and lambda values of 0 indicate that there is no phylogenetic signal. Bloomberg's K (Blomberg et al., 2003) ranges between 0 and infinity, with $K = 1$ indicating Brownian motion evolution. Larger K indicates stronger phylogenetic signal. "phylosig" computes p -values to test if observed lambda and K value differ significantly from 0, i.e., if there is a phylogenetic signal.

To test effects of body size (ITD) and ED on bee species' specialization (normalized degree), we constructed generalized linear mixed models (GLMMs), which are considered the best tool to analyze non-normal data involving random effects (Bolker et al., 2009). We used beta models in the R package glmmTMB (Gąlecki and Burzykowski, 2013), because the data were scaled between 0 and 1, as mentioned above. Predictor variables included ITD and ED, and random variables included network and bee species, since the location where the networks were sampled can potentially affect the relationship to be tested, and some species may be more represented than others in the networks, which could increase the variability of the metrics. Candidate models were ranked by Akaike information criterion (AIC) values using the " dredge" function in the R package "MuMIn" (Barton, 2020), and selected models were those models < 2 delta AIC of the top model.

RESULTS

The database organized in the present study included 15 interaction networks belonging to three Brazilian biomes (Atlantic Forests, Cerrado and Caatinga; **Table 1** and **Figure 1**), containing 1,702 interactions between bees and plants (**Figure 3**). Data showed 814 specimens of bees distributed in 4 families, 118 genera, 386 species (**Supplementary Material**), and 869 specimens of plants distributed in 100 families, 336 genera, and 717 species.

Correlation analysis of the four network metrics showed a strong correlation between degree and the other metrics ($r > 0.70$, $p < 0.0001$) and an intermediate correlation between the other three (strength, closeness, and betweenness) ($r < 0.53$,

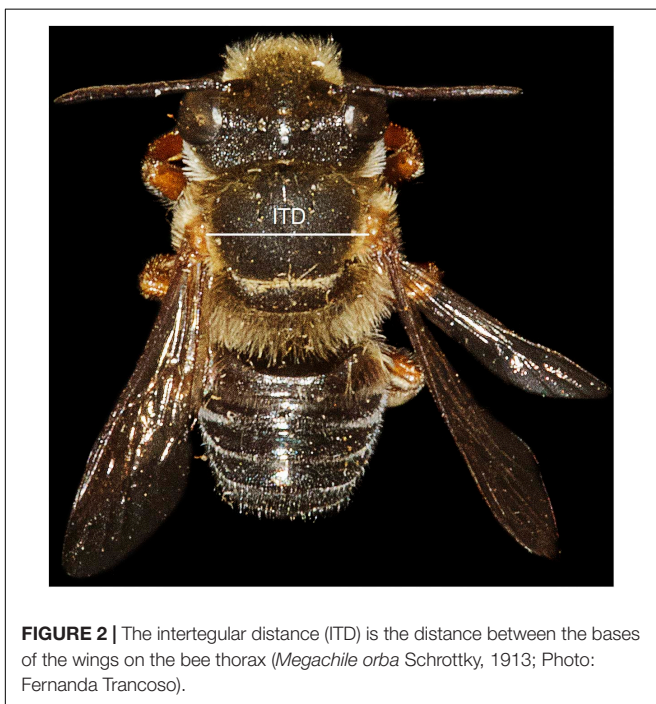


FIGURE 2 | The intertegular distance (ITD) is the distance between the bases of the wings on the bee thorax (*Megachile orba* Schrottky, 1913; Photo: Fernanda Trancoso).

TABLE 1 | Source of data for the 15 interaction networks analyzed.

ID	References	Number of bee species	Number of plant species
1.	Aguiar, 1995	23	37
2.	Aguiar, 2003; Aguiar and Zanella, 2005	39	42
3.	Andena et al., 2005	59	57
4.	Carvalho, 1993	37	19
5.	Carvalho, 1999	47	61
6.	D'Ávila, 2006	10	34
7.	Faria, 1994	46	52
8.	Faria-Mucci et al., 2003	23	42
9.	Lima, 2004	73	66
10.	Mateus, 1998	92	58
11.	Pedro, 1992	124	123
12.	Rêgo, 1998	30	26
13.	Silva, 1998; Silva and Martins, 1999	27	23
14.	Silveira, 2006 (Costa do Sol)	44	29
15.	Wilms, 1995	147	214

$p < 0.0001$). Thus, degree was used as our measure of specialism among bee taxa in the following analyses.

Specialist bees (5% of each network with the lowest degree) selected in the 15 networks totaled 34 species distributed in 13 genera and four families (Table 2). This corresponds to 8.7% of the total bee species recorded, and to 10.9% of the total bee genera in the database. The genus *Centris* (Fabricius, 1804) had the highest number of specialist bee species (10 species), followed by *Augochloropsis* (Cockerell, 1897) (6 species) and *Augochlora* (Smith, 1853) (5 species). The genera *Anthodioctes* (Holmberg, 1903), *Bombus* and *Caenohalictus* (Cameron, 1903) had two species each. *Acanthopus* (Klug, 1807), *Agapostemon* (Guérin-Méneville, 1844), *Alepidosceles* (Moure, 1947), *Ariphanarthra* (Moure, 1951), *Augochlorella* (Sandhouse, 1937), *Callonychium* (Brèthes, 1922), and *Ceratina* (Latreille, 1802) were represented with one species each.

The ITD was obtained for 85% of the analyzed bee species. A phylogenetic tree with all the genera analyzed in this study, including their branch length, can be found in Figure 4.

The best model of degree among Brazilian bee species included the predictor variables ITD and ED, with species and network held as random effects (Table 3). The resulting graphical representation of the mixed generalized linear model showed that the greater the specialization, the larger was ITD (Figure 5A). The result also shows that the greater the specialization, the lower was ED (Figure 5B). Thus, according to our data, specialist bee species are larger and less phylogenetically distinct than expected by chance. Moreover, a significant phylogenetic signal of ITD was found (Pagel's λ [p -value] = 0.9999 [<0.001]; Bloomberg's K [p -value] = 1.4069 [0.001]).

DISCUSSION

Using 15 interaction networks sampled across a range of Neotropical biomes, we identified 34 bee species that had the lowest number of interaction partners, and thus can be

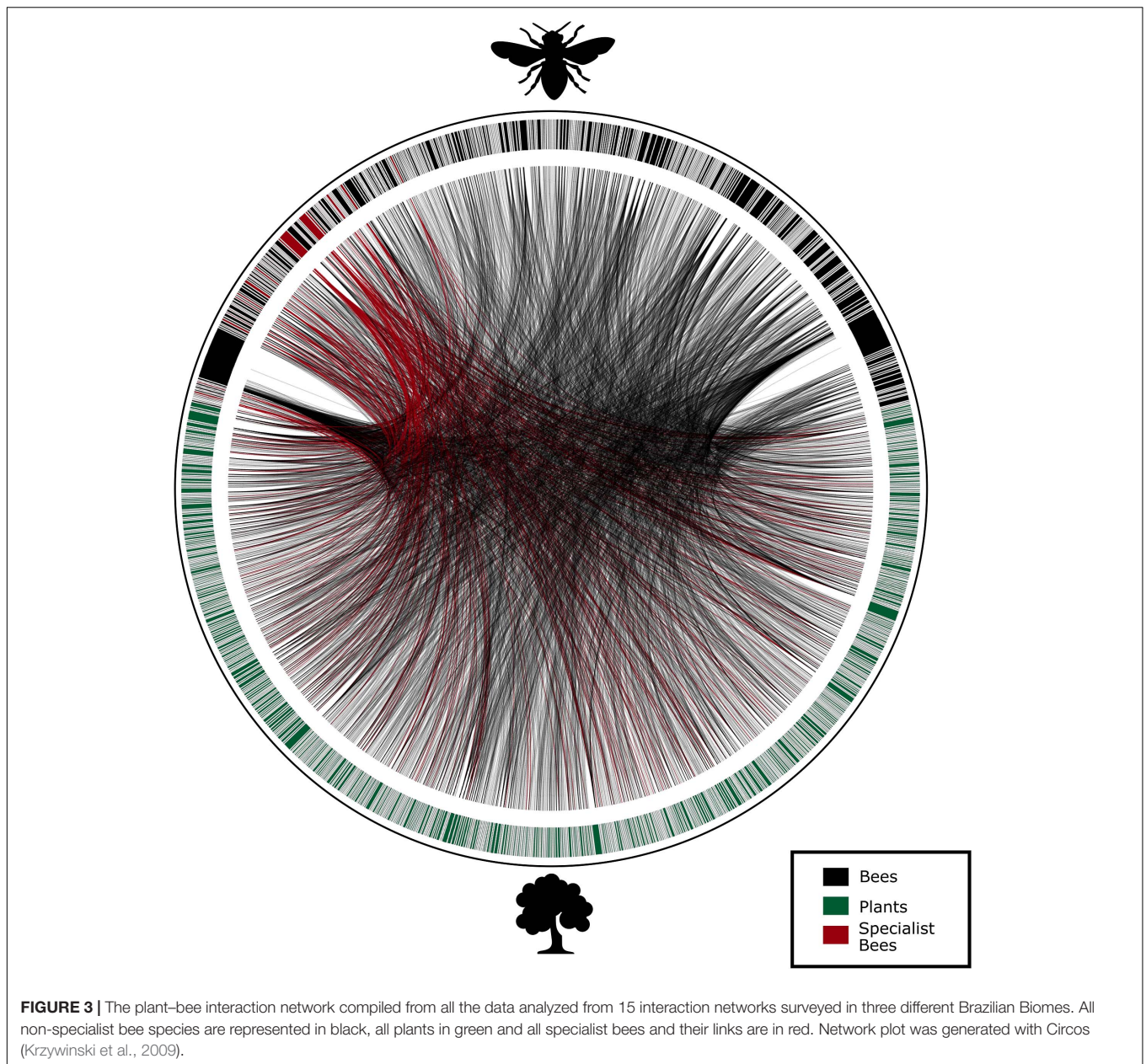
considered the most specialized. Nearly one third of them belong to the oil-collecting bee genus (*Centris*). Results also showed that more specialized bees (i.e., low degree) tend to have larger body size and lower ED than more generalist species. Also, we found a phylogenetic signal for body size (ITD). Our study is the first with such quantitative assessment of specialization for Neotropical bees, and based on more than 1,700 plant–bee interactions.

Specialist Bees in the Interaction Networks

The highly specialized mutualistic relationships between the solitary bees of the genus *Centris* and families of plants whose flowers produce oil are well known (Machado, 2004; Mello et al., 2013; Rabelo et al., 2014; Pacheco-Filho et al., 2015). The main sources of floral oils with recorded interactions with these bees belong to the following botanical families: Calceolariaceae, Iridaceae, Krameriaceae, Malpighiaceae, Orchidaceae, and Plantaginaceae (Giannini et al., 2013; Martins et al., 2015). The species *Centris burgdorfi* (Friese, 1900) was previously indicated as a specialist on a local scale (Sabino et al., 2019). Species of some subgenera of *Centris* (especially *Paracentris* and *Wagenknechtia*) are notably specialists (Giannini et al., 2013), and two species from the list obtained here belong to *Paracentris* [*C. burgdorfi* Friese (1900) and *Centris klugii* Friese (1899)]. For other species cited as specialists, *Augochlorella ephyra* (Schrottky, 1910) was classified as rare in interactions with flowers of the plant *Ludwigia sericea* (Cambess.) H. Hara (Onagraceae) in South Brazil (Gonçalves and Buschini, 2017). One species of the genus *Caenohalictus* was cited as a specialist in an interaction network study conducted in South Brazil (Diniz and Buschini, 2015), although the species quoted was different from the two species recorded in the present study. Bees in the genus *Alepidosceles* (including *A. imitatrix* Schrottky, 1909) are all components of an oligolectic clade (Michener, 2007), therefore demonstrating the strength of the methods applied here to determine specialist bees from Neotropical interaction networks. The bee *Acanthopus excellens* (Schrottky, 1902) is a cleptoparasite of *Centris*, subgenus *Ptilotopus*, although none of the *Centris* in this subgenus is specialist in our study. *Acanthopus* visits on flowers are likely an unusual event, as they are not required to provide food for their offspring. For the other species of bees identified as specialists, there are no published studies on their mutualistic interactions patterns, demonstrating the important knowledge gap. Available data are limited to the degree of rarity, record and frequency of occurrence (Schlindwein, 1998; Imperatriz-Fonseca et al., 2011; Boff et al., 2013; Mouga et al., 2015; Gostinski et al., 2016). It is also noteworthy that most of the specialist species emphasized here exhibit non-eusocial behavior, for which there are little data available in the literature and/or an expressive taxonomic impediment, especially for species in the Halictidae family (16 out of the 34 specialist species belong to this family).

Specialism and Body Size

The results of the present study also showed that bee specialization is positively related to body size, i.e., the larger



the bee, the higher the specialization. Although these results contradict two previous studies (Leonhardt and Blüthgen, 2012; Smith et al., 2019), it is also in accordance to the finds of one study in undisturbed forests of North America (Villalobos et al., 2019). The study of Leonhardt and Blüthgen (2012) compared *Apis mellifera* L. and two species of *Bombus* [*B. pascuorum* (Scopoli, 1763) and *B. terrestris* (Linnaeus, 1758)]. Although *Bombus* species have large body sizes (Borges et al., 2020), this variable was not specifically evaluated. The study of Smith et al. (2019), conducted on forests in the mid-Atlantic United States, analyzed a much smaller number of bee species (56 species). This reinforces the importance of the results obtained in the present study, since they address several tropical and subtropical climate sites in Brazil, and a large number of species. Warmer

climates might support the evolution of specialist behavior among pollinators, given the high resource supply and the costs for resources competition (Classen et al., 2020), which may explain the opposite relations between broad scale studies from temperate and tropical climates (see also Orr et al., 2021).

Body size directly influences foraging capacity and resource exploitation in bees (Rabelo et al., 2015) because larger bees have a larger flight range (Greenleaf et al., 2007). Our result may indicate that larger bee species, presenting a greater flight capacity, can most likely preferentially exploit the most rewarding food sources and thus, be more prone to specialize in these sources. Larger body size bees can maximize exploitation of a sparsely distributed food plant, becoming more efficient at resource collection on a single species or collection of closely

TABLE 2 | Specialist bee species selected on 15 Brazilian plant–bee networks (representing 5% of each network) and their degree.

Family	Genus	Species	Degree
Apidae	<i>Acanthopus</i>	<i>Acanthopus excellens</i> (Schrottky, 1902)	0.0345
Halictidae	<i>Agapostemon</i>	<i>Agapostemon chapadensis</i> (Cockerell, 1900)	0.0175
Apidae	<i>Alepidosceles</i>	<i>Alepidosceles imitatrix</i> (Schrottky, 1909)	0.0081
Megachilidae	<i>Anthodioctes</i>	<i>Anthodioctes megachiloides</i> (Holmberg, 1903)	0.0175
		<i>Anthodioctes vernoniae</i> (Schrottky, 1911)	0.0081
Halictidae	<i>Ariphanarthra</i>	<i>Ariphanarthra palpalis</i> (Moure, 1951)	0.0047
Halictidae	<i>Augochlora</i>	<i>Augochlora caerulior</i> (Cockerell, 1900)	0.0175
		<i>Augochlora foxiana</i> (Cockerell, 1900)	0.0081
		<i>Augochlora perimelas</i> (Cockerell, 1900)	0.0172
		<i>Augochlora michaelis</i> (Vachal, 1911)	0.0047
		<i>Augochlora thalia</i> (Smith, 1879)	0.0047
Halictidae	<i>Augochlorella</i>	<i>Augochlorella ephyra</i> (Schrottky, 1910)	0.0164
Halictidae	<i>Augochloropsis</i>	<i>Augochloropsis callichroa</i> (Cockerell, 1900)	0.0192
		<i>Augochloropsis cockerelli</i> (Schrottky, 1909)	0.0164
		<i>Augochloropsis crassigena</i> (Moure, 1943)	0.0385
		<i>Augochloropsis electra</i> (Smith, 1853)	0.0172
		<i>Augochloropsis nigra</i> (Moure, 1944)	0.0047
		<i>Augochloropsis rotalis</i> (Vachal, 1903)	0.0047
Apidae	<i>Bombus</i>	<i>Bombus brevivillus</i> (Franklin, 1913)	0.0238
		<i>Bombus morio</i> (Swederus, 1787)	0.0238
Halictidae	<i>Caenohalictus</i>	<i>Caenohalictus curticeps</i> (Vachal, 1903)	0.0047
		<i>Caenohalictus incertus</i> (Schrottky, 1902)	0.0172
Andrenidae	<i>Callonychium</i>	<i>Callonychium brasiliense</i> (Ducke, 1907)	0.0152
Apidae	<i>Centris</i>	<i>Centris aenea</i> (Lepelletier, 1841)	0.0081
		<i>Centris analis</i> (Moure & Seabra, 1960)	0.0081
		<i>Centris burgdorfi</i> (Friese, 1900)	0.0152
		<i>Centris decolorata</i> (Lepelletier, 1841)	0.0385
		<i>Centris discolor</i> (Smith, 1874)	0.0047
		<i>Centris ferruginea</i> (Lepelletier, 1841)	0.0152
		<i>Centris klugii</i> (Friese, 1899)	0.0192
		<i>Centris lutea</i> (Friese, 1899)	0.0152
		<i>Centris mocsaryi</i> (Friese, 1899)	0.0081
		<i>Centris spilopoda</i> (Moure, 1969)	0.0526
Apidae	<i>Ceratina</i>	<i>Ceratina paraguayensis</i> (Schrottky, 1907)	0.0435

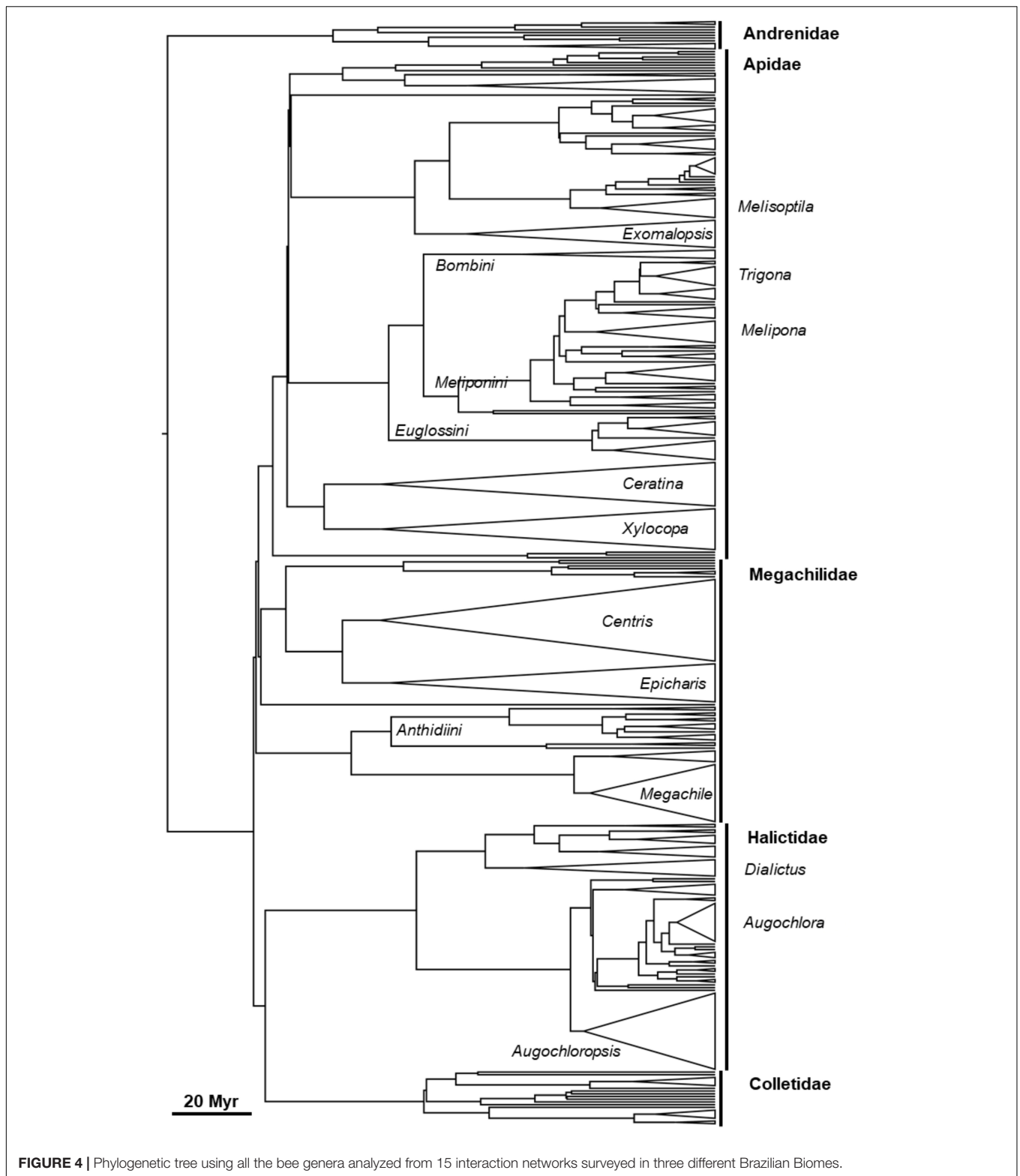
related plant species than bee species with more generalized diets, thus gaining a fitness advantage. But this is only possible in large species that can overcome energetic costs of such a strategy. In fact, preferences based in nutritional benefits have already been shown. The amount of amino acids in

pollen seems to influence floral preference in *A. mellifera* (Cook et al., 2003); similarly, the ratio between pollen proteins and lipids affects the preference of bumblebees (Vaudo et al., 2016). The discrimination capacity presented by bees seems to have a genetic basis, i.e., certain genes have an effect on the preference of pollinators and may therefore have played an important role in floral evolution (Schemske and Bradshaw, 1999). As mentioned above, there are few studies available on bees, but a previous study involving ants and their interactive plants showed an equally positive relationship between species body size and specialization in trophic interaction networks (Chamberlain and Holland, 2009).

Specialism and Evolutionary Distinctiveness

The interactions between plants and bees may exhibit phylogenetic components that direct the preferences of a group of bees toward a particular group of plants (Pacheco-Filho et al., 2015). In fact, specialism seems to be an ancestral trait in bees, since the earliest branches of their phylogenetic tree include specialists (Danforth et al., 2006). Some bees developed convergent traits specialized in the exploitation of floral resources, forming functional groups (Fenster et al., 2004), especially in highly specialized interactions. One example is orchid bees (Euglossini), which through coevolutionary processes exhibit specialized morphological and behavioral modifications for the collection of aromatic compounds from orchids flowers (Ramírez et al., 2010, 2011). Body size, as showed by our results, presented a strong phylogenetic signal indicating that closely related species tend to resemble each other considering this trait. This was already showed for insects (Chown and Gaston, 2010; Pallarés et al., 2019), as well for vertebrates (Smith et al., 2004; Diniz-Filho et al., 2007). However, complex interactions between ecological function, environment, natural history and phylogenetic evolution likely play a joint role in body size (Smith et al., 2004), and how significant is specifically the phylogenetic signal in its variation remains unclear (Chown and Gaston, 2010).

As mentioned earlier, highly specialized mutualistic interactions are rare in nature (Hoeksema and Bruna, 2000), and our study showed that species with more specialized behavior have lower ED in the bee phylogeny. Together with the concentration of most specialist within few genera from mainly two families, this may indicate that, depending on how these species respond to environmental changes (climatic, land use, for example), the loss of evolutionary history and phylogenetic diversity within certain clades would be much higher than if there was a more heterogeneous distribution of specialist species in the phylogeny. Rezende et al. (2007b) tested whether simulated coextinctions in plant–animal mutualistic interaction networks involved phylogenetically related species more frequently than expected at random. The authors obtained evidence that phylogeny is partially responsible for the propensity of species to interact in more than one-third of the analyzed networks and that phylogenetically related species tend to interact with a similar set of species and tend to have similar roles in interaction networks.



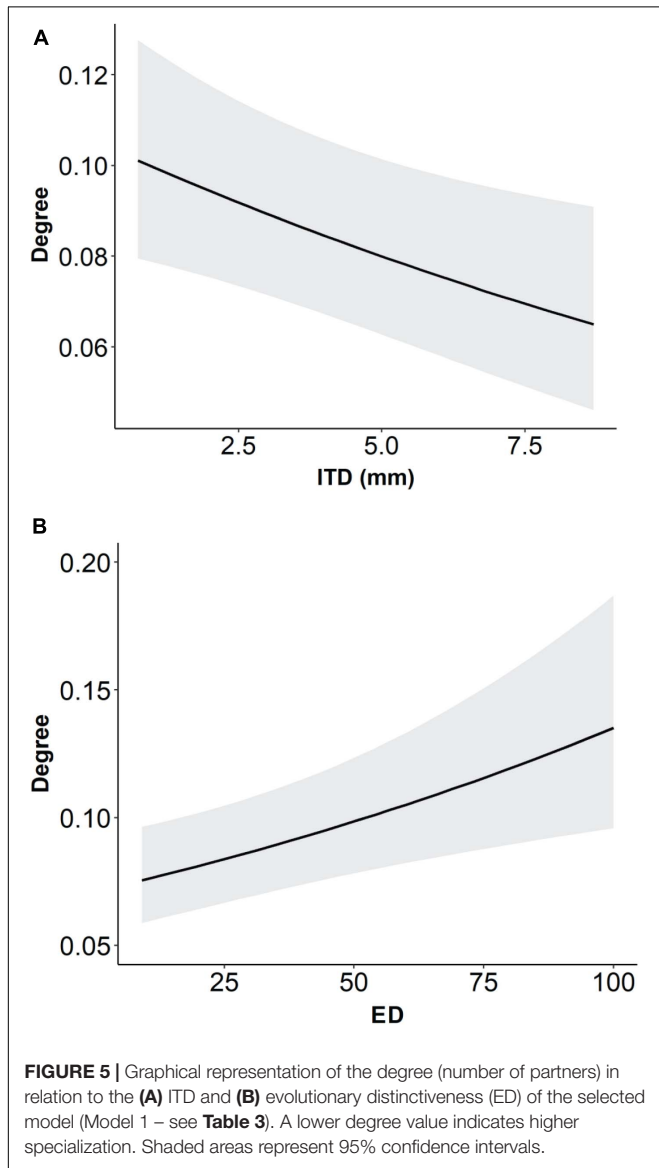
Our results also showed that none of the 34 specialist bee species highlighted here exhibit eusocial behavior. Social species (some degree of sociality, i.e., from cooperative working to eusociality) represent 10–15% of all extant bees and are

usually regarded as generalists (Michener, 2007), however, this may not be true for all species. Worldwide, few social species have been studied (Smith et al., 2019), being bumblebees and honeybees the most represented taxa. Solitary species represent

TABLE 3 | Model selection results based on Akaike information criterion (AIC) for beta GLMMs of bee species' specialization, as measured using degree (D).

Model	Structure	AIC	ΔAIC	Wgt
1	D ~ ITD + ED	-2165.43	0.00	0.87
2	D ~ ED	-2160.90	4.53	0.09
3	D ~ ITD	-2158.61	6.81	0.03
NULL	D ~ 1	-2157.44	7.98	0.02

Table shows that Model 1 is the most parsimonious model ($\Delta AIC < 2$). Predictor variables included body size as measured using intertegular distance (ITD), and evolutionary distinctiveness (ED). Random effects included network and bee species.



85% of extant bees (Michener, 2007) (they are about 75% of the species in our study), but despite being the majority (Wcislo and Cane, 1996), the knowledge on solitary species biology is even more scarce. Generalist trends within eusocial bees have

been hypothesized as a response to the (1) high number of individuals in the nest (high demand for resources in the nest and high abundances in the field), (2) eusocial colonies are active throughout the year (especially in tropical zones), and (3) labor division supports a higher diversity of interactions (independent search combined to recruitment foraging behavior) (Lichtenberg et al., 2010; Maia et al., 2019). From the 13 genera of specialist bees identified in the present study, one is a cleptoparasitic (*Acanthopus*), one is a representative of an oligolectic and solitary clade (*Alepidosceles*), four are solitary (*Anthodioctes*, *Arriphanarthra*, *Centris*, and *Ceratina*) and seven present some degree of sociality, from the formation of aggregated nesting sites (*Caenohalictus* and *Callonychium*), communal behavior (*Agapostemon* and *Augochlora*), variable social behavior (*Augochlorella* and *Augochloropsis*), and the primitively eusocial bumblebees (genus *Bombus*) (Janjic and Packer, 2003; Alves dos Santos, 2004; Coelho, 2004; Michener, 2007; Gonçalves, 2016; Gonçalves, 2019). Although most specialist species are solitary, some are also social, as found in undisturbed forests of north America (Villalobos et al., 2019); thus, both social and solitary bees are prone to adopt specialist behavior (Classen et al., 2020).

Specialism apparently has multiple independent evolutionary origins, being more common on Colletidae, Andrenidae, Megachilidae, and non-social Apinae, but most genera within these families contain also generalist species (Wcislo and Cane, 1996). Multiple drivers are likely related to trophic specialism on both social and solitary bees, such as, a larger or smaller suit of foraging behaviors (Portman et al., 2019), the plasticity to respond to floral resource coverage (Petanidou et al., 2008; Fründ et al., 2010; Baude et al., 2016; Kelly and Elle, 2021), seasonal or phenological change of nutritional value on available floral resources (Seitz et al., 2020), resource competition (Johnson and Hubbell, 1975; Sáez et al., 2017) specially related to nectar-robbing processes (Irwin et al., 2010), and also, can be based on the biology of individual-level interactions and not only on species-level (Brosi, 2016; Smith et al., 2019). Since bees are a megadiverse group (Orr et al., 2021), further studies are still necessary for understanding the roles of sociality and specialization on foraging behavior and species evolution.

Caveats and Future Steps

As previously stated, it is necessary to consider that methodological survey biases may interfere with the results obtained here, especially because high canopy forests cannot be surveyed using the standard methodology analyzed. There remains a big gap regarding studies of interaction networks with standardized methods in tropical regions, as well as studies on phylogenetic and functional traits, which makes comparisons even more difficult. However, the present work is an important contribution considering current empirical data in tropical regions, and aims to help pave the way for a deeper understanding of the mechanisms driving specialization patterns in tropical environments.

Future studies should prioritize new surveys of plant-bee interaction in places not yet sampled and test other interaction network metrics to identify specialist species

(e.g., Blüthgen et al., 2006; Kaiser-Bunbury and Blüthgen, 2015; Vargas et al., 2017). They also should deepen the ecological knowledge on bee species here identified as specialists to help devise conservation programs. A possible investigation is to determine if specialism is related to bee phenology and flight activity period. Additionally, it would be important to determine the geographical distribution of specialist species to protect their natural habitats, ensuring future habitat availability. Studies that involve conservation genetics for maintenance of the genetic viability of natural populations of specialist species are also urgently required.

CONCLUSION

Based on a data set covering some of the main tropical biomes, we demonstrate that interaction network metrics are useful for identifying the bees that have specialized interactions with plants and that these species have a larger body size and lower ED. These species deserve attention because they act as effective pollinators and are more vulnerable to environmental change. Our results can serve as support to decision-making and the implementation of conservation measures for these species, and may also encourage future studies. Given increasing human impacts on tropical ecosystems, evidence-based approaches to conserving specialist bees are urgently needed to safeguard their populations and functions in tropical plant–pollinator communities.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author.

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AUTHOR CONTRIBUTIONS

TG and RR: conceptualization. RR, MG, MA, RB, and TG: data curation. RR, AC, MG, and MA: formal analysis. TG: funding acquisition. RR and TG: writing – original draft. All authors reviewed and edited the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fevo.2021.699649/full#supplementary-material>

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