



Looking beyond the flowers: associations of stingless bees with sap-sucking insects

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Abstract

The main sources of food for stingless bees are the nectar and pollen harvested from flowers, whereas one important kind of nesting material (i.e. wax) is produced by their own abdominal glands. Stingless bees can, nonetheless, obtain alternative resources of food and wax from exudates released by sap-sucking insects as honeydew and waxy cover, respectively. To date, there are no comprehensive studies investigating how diversified and structured the network interactions between stingless bees and sap-sucking insects are. Here, we conducted a survey of the data on relationship between stingless bees and sap-sucking insects to evaluate: (1) which resources are collected by which stingless bee species; (2) how diverse the interaction network is, using species degree and specialisation index as a proxy; and if (3) there would be any phylogenetic signal in the species degree and specialisation indices. Our findings demonstrate that approximately 21 stingless bee species like *Trigona* spp. and *Oxytrigona* spp. have been observed interacting with 11 sap-sucking species, among which *Aethalion reticulatum* is the main partner. From ca. 50 records, Brazil is the country with most observations ($n = 38$) of this type of ecological interaction. We found also that stingless bees harvest fivefold more honeydew than waxy covers on sap-sucking insects. However, we did not find any phylogenetic signal for the occurrence of this interaction, considering species degree and specialisation indices, suggesting that both traits apparently evolved independently among stingless bee species. We suggest that specific ecological demands may drive this opportunistic behaviour exhibited by stingless bees, because major sources of food are obtained from flowers and these bees produce their own wax.

Keywords Hemiptera · Hymenoptera · Honeydew · Interaction networks · Meliponini · Mutualism · Phylogenetic signal

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Introduction

Bees (Hymenoptera) are largely associated with flowers as they have morphological adaptations (e.g. branched hairs), which are used to harvest floral resources that they then use to feed their brood (Lunau 2004; Poinar and Danforth 2006; Cardinal and Danforth 2013). Additionally, bees are able to collect food or occasionally nesting materials from alternative sources. For example, corbiculate bees such as honeybees, bumblebees and stingless bees are known to harvest honeydew or wax from sap-sucking insects (Hemiptera; Santos 1983; Batra 1993; Bishop 1994; Almeida-Neto et al. 2003; Dimou and Thrasyloulou 2007; Oda et al. 2009; Barônio et al. 2012).

Honeydew is a sweet substance expelled by hemipterans that suck sap from plants (Way 1963; Delabie 2001). This substance is a source of carbohydrates, amino acids, vitamins, proteins and other nutrients (Auclair 1963; Simova et al.

2012). Honeydew is preferentially collected from sap-sucking nymphs but can be collected from adult sap-suckers too. These insects selectively release their exudate for specific partners, based on their potential to protect them against natural enemies (Schuster 1981; Maschwitz and Hanel 1985; Letouneau and Choe 1987; Delabie 2001; Naskrecki and Nishida 2007; Azevedo et al. 2008; Oda et al. 2009; Barônio et al. 2012). Opportunistic insects touch their antennae to the abdominal tip of a hemipteran that subsequently elevates its abdomen and exudes honeydew from its anal tube (Schuster 1981; Maschwitz and Hanel 1985; Letouneau and Choe 1987; Delabie 2001; Naskrecki and Nishida 2007; Oda et al. 2009; Barônio et al. 2012). The production and release of honeydew or wax by sap-sucking insects are intrinsic physiological requirements as well as protective products, respectively, for these hemipterans. Consequently, opportunistic insects exploit the honeydew as an alternative food source and exploit the wax as a supplementary nest material (Way 1963; Maschwitz and Hanel 1985; Letouneau and Choe 1987; Corke 1999; Delabie 2001; Camargo and Pedro 2002; Naskrecki and Nishida 2007; Kondo 2010; Sansum 2013).

Sap-sucking insects are usually sedentary and gregarious, which facilitates their predation (Way 1963; Delabie 2001). Therefore, the establishment of a partnership with organisms capable of providing protection against predators/parasitoids, or even providing sanitation services, may be a good survival strategy for such insects (Way 1963; Letouneau and Choe 1987; Figueiredo 1996; Delabie 2001; Barônio et al. 2012; Oda et al. 2014). Social insects, such as ants, bees and wasps, seem to be preferred protectors because these taxa may aggressively defend their resources in a collective way (Way 1963; Letouneau and Choe 1987; Buckley and Gullan 1991; Delabie 2001; Kondo 2010; Novgorodova 2015). This behaviour benefits sap-sucking insects, which selectively reciprocate with honeydew. However, wax tends to be usurped by opportunistic insects, potentially exposing the sap-suckers to desiccation or natural enemies (Way 1963; Letouneau and Choe 1987; Buckley and Gullan 1991; Delabie 2001; Kondo 2010; Novgorodova 2015).

The interaction between sap-sucking insects and their attending ants and wasps is well documented (e.g. Way 1963; Barrows 1979; Letouneau and Choe 1987; Buckley and Gullan 1991; Delabie 2001; Novgorodova 2015); however, the interaction between stingless bees and sap-sucking insects has received little attention, and has only been anecdotally reported (Cortopassi-Laurino 1977; Almeida-Neto et al. 2003; Vieira et al. 2007; Oda et al. 2009, 2014; Koch et al. 2011; Barônio et al. 2012). To date, there are no papers comparatively and systematically investigating the interactions between stingless bees and sap-sucking insects evaluating topics as interaction network and phylogenetic perspective. Most studies on interaction networks have focused on the mutualistic relationships between plants and bees (Olesen and

Jordano 2002; Mitchell et al. 2009; Stang et al. 2009; Aidar et al. 2015; Giannini et al. 2015) but not on the relationships between bees (herein, we focus on stingless bees) and sap-sucking insects. Additionally, the phylogenetic histories of organisms may contribute to our understanding of the structure of certain patterns found in ecological networks and thus offer an important perspective (Rezende et al. 2007). When comparative phylogenetic methods are incorporated into quantitative analyses, the models are substantially improved as type I errors are avoided because differences or similarities in observed patterns can be associated to phylogenetic histories rather than ecological characteristics (Felsenstein 1985; Abouheif 1999; Rohlf and Nielsen 2015; Adams and Collyer 2018). The strength of applying comparative phylogenetic methods can be explained by the fact that closely related species are expected to retain some phenotypic similarities due to their shared evolutionary history, and this factor can be neglected when the phylogenetic history is not explicitly considered (e.g. Felsenstein 1985).

To compensate for the absence of information on the interactions between sap-sucking insects and stingless bees, we analysed this interaction network deeply by considering the phylogenetic relationships among the stingless bee species involved in such association. This approach was chosen because all stingless bees could be identified to species or genus levels, while some sap-sucking insects could not be identified by the original authors. We estimated specific parameters from the interaction network, such as species degree and specialisation index, by incorporating the phylogeny of target stingless bee species. Then, we evaluated whether these network parameters exhibited any phylogenetic signal.

Methods

Survey data

We searched Web of Science™, the Online Scientific Electronic Library (Scielo) and Google Scholar using the following terms additionally (i.e. two or more words together): stingless bees * AND honeydew * AND wax * AND Hemiptera * AND sucking-insects * AND cooperation * AND association. We then linked these words to all fields that would include items as topics, titles and abstracts to find texts in scientific journals addressing these issues. This search was performed before August 30th, 2018.

Exudates harvest from sap-sucking insects by stingless bees

When available, we recorded the types of exudate that was secreted (honeydew or wax) by sap-sucking insects and harvested by stingless bees. After that, we analysed which

exudate has been more documented being collected by stingless bees. For that analysis, we used the function *chisq.test* in R (Ihaka and Gentleman 1996; R Core Team 2016) to perform a chi-squared test. Significance was tested by calculating *p*-values using 2000 replicates with rescaling ($\alpha = 0.05$).

Ecological network

After surveying the available literature, we built a Sankey diagram of the exudates (honeydew or wax) released by a sap-sucking insects using the *geom_alluvium* function from the package ‘ggplot2’ (Wickham 2009). Subsequently, we evaluated the interactions between hemipterans and stingless bees by performing an ecological network analysis using the *species level* function from the ‘bipartite’ package (Dormann et al. 2009).

The species level function calculates various indices for network properties at the species level. In the current study, we evaluated two indices: species degree and specialisation index. The former is the number of interactions per species (Jordano et al. 2003; Bascompte et al. 2006). Therefore, here, it was used as a proportion (normalised degree, González et al. 2010) of sap-sucking insects in which each stingless bee species interacted considering the total number of hemipteran species present in network. On the other hand, the specialisation index quantifies the degree of specialisation of a species within an interaction network (Blüthgen et al. 2006; Dormann et al. 2009). As such, it is a species-level specialisation measure (based on frequency data) adapted from Kullback–Leibler distance (*d'*) and ranges from 0 (generalist) to 1 (specialist; Blüthgen et al. 2006; Dormann et al. 2009).

To visualise the interaction network, we used the *plotweb* function (method = ‘cca’) from the bipartite package, which displays the fewest possible crossing interactions. The plot was extracted and exported as a PDF before being imported as vectors into the illustration software ‘Inkscape’ (Inkscape 2017), where the figures were tidied.

Phylogenetic comparative analyses

The phylogenetic relationships and divergence times of stingless bee species were based on the hypothesis by Rasmussen and Cameron (2010) for the 21 species included in the comparative analyses of this study. The nexus file was transformed in *phylo* using the ‘ape’ package (Paradis et al. 2004). Such a phylogeny was used to evaluate if the species degree and/or specialisation index had a phylogenetic signal. If a phylogenetic signal was found, then, the degree of relatedness between species would explain the observed pattern better than the ecological variables.

We used the function *phylosig* (with 9999 permutations) from the ‘phytools’ package (Revell 2012). The method chosen was for the continuous trait (i.e. Pagel’s λ). A λ value of

close to 0 means that the phylogenetic signal is equivalent to that which would be expected if the data arose on a star phylogeny (which has no phylogenetic signal). On the other hand, a λ value of close to 1 implies covariances among related species that match those implied by the original phylogeny (Pagel 1994). To visualise the phylogenetic signals of the species degree and specialisation index in the phylogenetic scenario, we employed the *contMap* function from the phytools package (Revell 2012). All statistical analyses were performed in R (Ihaka and Gentleman 1996; R Core Team 2016).

Results

Number of species interacting with each other and exudates harvested by stingless bees

We found that 11 hemipteran species were visited by at least 21 stingless bee species (Fig. 1; Online Resource 1). The observation that stingless bees interact with sap-sucking insects has been recorded approximately 50 times in the literature (Online Resource 1). Furthermore, our data survey showed that relationships between stingless bees and sap-sucking insects have been recorded in seven countries (Brazil, Colombia, Costa Rica, Guatemala, India, Madagascar, and Panama), Brazil having the most observations ($n = 38$). Unfortunately, some hemipteran species/genera that have been involved in these interactions are unknown (unknown taxon) because the original authors only reported family-level data. It is noteworthy that the majority of these authors were the first naturalists describing the little explored Brazilian entomofauna in the nineteenth century (Online Resource 1). Honeydew harvesting has been recorded more



Fig. 1 The interaction between *Trigona hyalinata* (Hymenoptera: Apidae: Meliponini) and *Aethalion reticulatum* (Hemiptera: Aethalionidae) on a branch of *Clitoria fairchildiana* Howard (Papilionoideae). Image use authorised by Camila Aoki. For details, see Oda et al. (2009)

times (34) than wax harvesting (7; $\chi^2 = 17.78$, p value < 0.001 ; Fig. 2). Our results also indicate that of the 12 stingless bee genera reported here, *Trigona* is the genus containing the most species (ca. 38%) interacting with sap-sucking insects.

Interaction network and phylogenetic signal

Overall, our interaction network analysis presented a proportion of realised vs. possible ecological interactions (i.e. connectance) of 0.09. However, since our ecological network had a small number of species investigated, such a connectance value is unreliable (Dormann et al. 2009). Concerning the normalised species degree, *Trigona spinipes* was the bee species with the highest score (0.33), followed by *Oxytrigona taira* (0.27), suggesting that these two stingless bees accounted for half of the possible interactions on the upper level of the network (Fig. 3; Table 1). However, most stingless bee species exhibited only 5% of the possible sap-sucking insects. *Parapartamona zonata*, *Plebeia droryana*, *Schwarzula coccidophila* and *Tetragonula iridipennis* showed the highest values of specialisation (i.e. 1), suggesting that they interacted with sap-sucking insects, but did not share these resources with other stingless bee species (Fig. 3; Table 1). *Trigona branneri*, *Trigona amazonensis* and *Partamona cupira* presented the lowest values of

specialisation (i.e. 0), meaning that they only interacted once with the most common partners of stingless bees (here, *Aethalion reticulatum*; Fig. 3; Table 1).

We did not find statistical significance to support the phylogenetic signal related to the normalised species degree (Pagel's $\lambda = 6.73 \times 10^{-5}$, p value = 1; Fig. 4) and specialisation index (Pagel's $\lambda = 0.40$, p value = 0.36; Fig. 4). Therefore, the relative number of interactions per species, as well the degree of specialisation of stingless bee species within the network, are more likely associated to ecological traits than to shared phylogenetic histories. This suggests that both species degree and degree of specialisation are independent of the phylogenetic history.

Discussion

Our findings show that ca. 0.013% (~ 82,000 spp., Bourgoin and Campbell 2002) of hemipteran species have been reported interacting with ca. of 3.5% (> 600 spp., Rasmussen and Cameron 2010) of stingless bee species. This proportion would certainly be higher if some species/genera of sap-sucking insects and stingless bees had been identified by original authors.

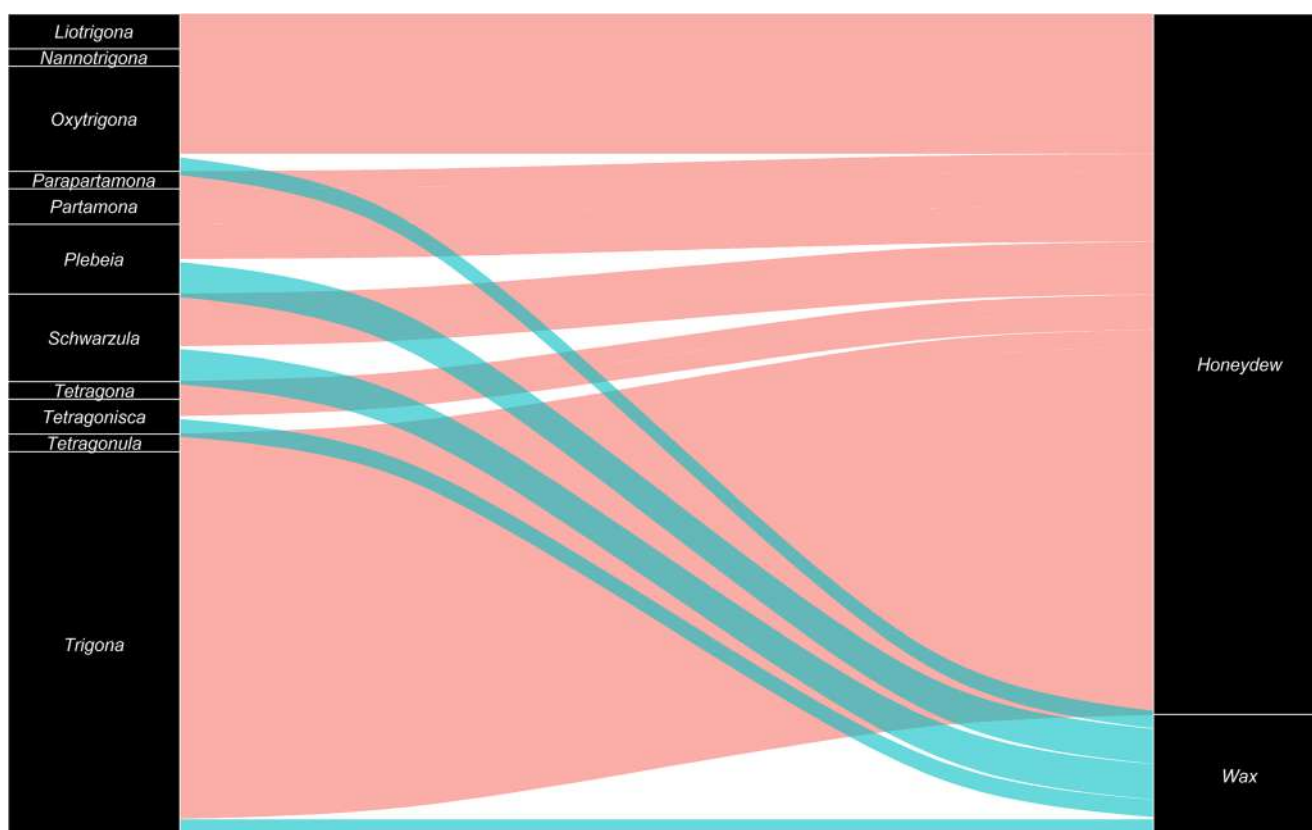


Fig. 2 Flow diagram (Sankey diagram) showing the proportion of links (width) between two entities (rectangles), including stingless bee genera (left) and sap-sucking insect exudates (right). The colours indicate whether the genera are harvesting honeydew (pink) or waxy cover (blue) from hemipterans

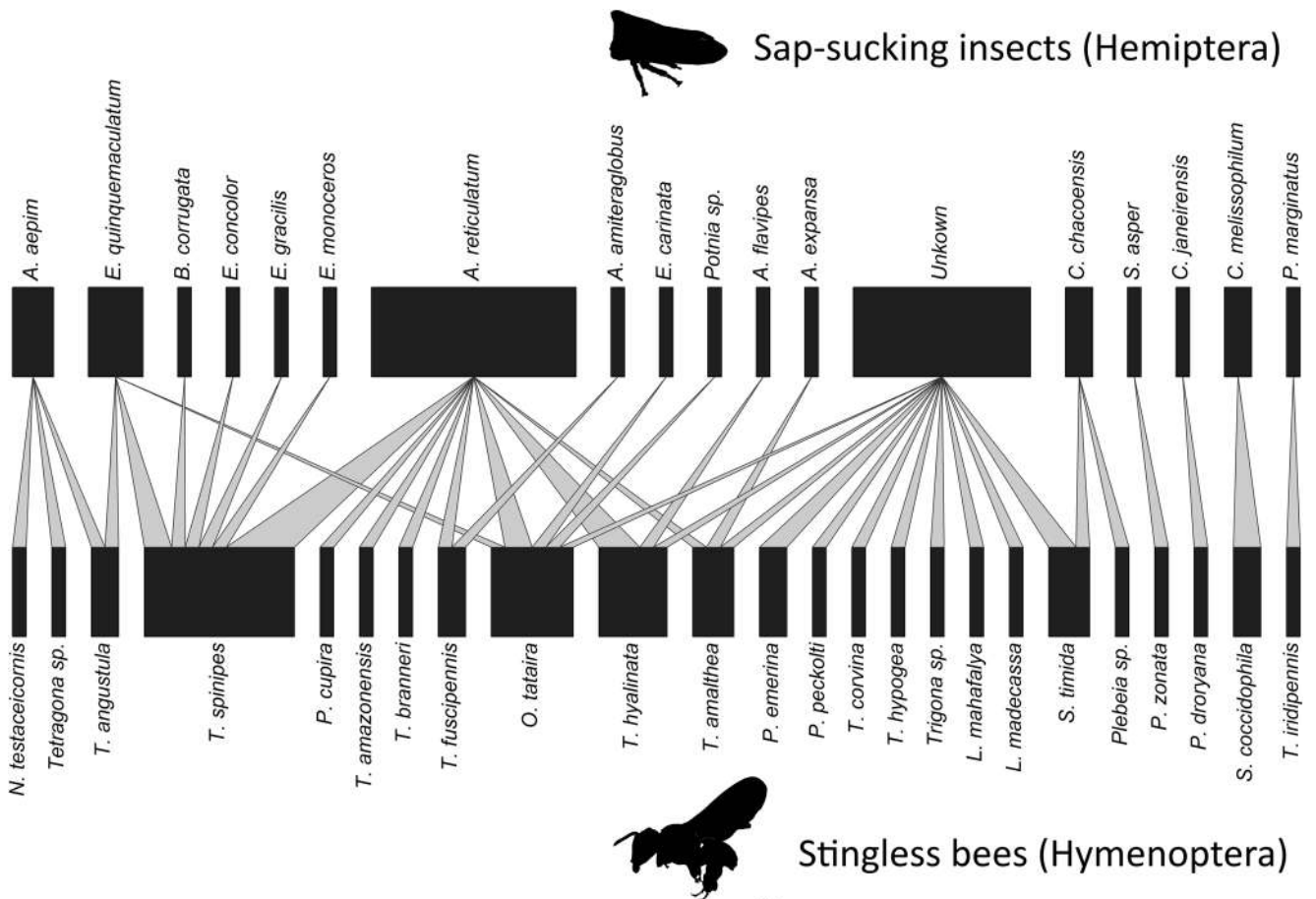


Fig. 3 Bipartite ecological network plotted as weighted parallel coordinates showing the interactions between sap-sucking insects (upper level) and stingless bees (lower level). Rectangle width is proportional to the sum of the interactions involving each species

Stingless bee species harvest more honeydew than wax as they opportunistically visit sap-sucking insects. This fact reveals that alternative sources of food are in higher demand by their colonies than complementary nest materials are.

The strong association of the stingless bee genera *Trigona* (mainly *T. spinipes*) and *Oxytrigona* (*O. taira*) with sap-sucking insects is noteworthy, and particularly their interaction with *A. reticulatum*, a very common agricultural pest. It is known that *A. reticulatum* is sedentary and gregarious and often occurs at high population densities (e.g. Brown 1976; Hamity et al. 2003). They are prone to intense predation and parasitism (Brown 1976; Hamity et al. 2003), and as a result, females (mothers) provide maternal care by protecting her eggs or nymphs against natural enemies and desiccation (Brown 1976). Consequently, the most common interactions between sap-sucking insects with *Trigona* and *Oxytrigona* may be because these stingless bees of these genera exhibit territorial and aggressive behaviour when visiting hemipterans, whereas other stingless bees do not display such behaviour (Cortopassi-Laurino 1977; Schuster 1981; Figueiredo 1996; Almeida-Neto et al. 2003; Vieira et al. 2007; Azevedo et al. 2008; Oda et al. 2009; Barônio et al. 2012).

Trigona bees have strong-toothed mandibles that are used for, among other things, attacking their competitors and enemies (Schwarz 1948; Slaa et al. 2003; Shackleton et al. 2015). As a result, sometimes, only the presence of *Trigona* workers around sap-sucking insects suffices to indirectly ward off competitors or potential enemies of the sap-sucking insects (Schuster 1981; Almeida-Neto et al. 2003). Furthermore, *Trigona* workers may assume threat postures by opening their mandibles and wings towards opponents (Vieira et al. 2007; Oda et al. 2009; Schorkopf et al. 2009; Barônio et al. 2012), or may release repelling substances able to deter potential predators or competitors (such as ants) from sap-sucking insect aggregations (Schorkopf et al. 2009). On the other hand, fire bees (*Oxytrigona* spp.) may expel formic acid from their mandibular glands onto their natural enemies (Bian et al. 1984; Roubik et al. 1987), a strategy that potentially helps these bees to successfully defend aggregates of sap-sucking insects (Cortopassi-Laurino 1977; Oda et al. 2014). The aggregates of sap-sucking insects releasing honeydew may occur randomly in nature, which in turn may hinder encounters with stingless bees for making their detection by these bees more challenging (Chamorro et al. 2013; Wolff et al. 2015).

Table 1 Network parameters of stingless bee species

Species	Species degree*	Specialisation
<i>Liotrigona madecassa</i>	0.055	0.053
<i>Liotrigona mahafalya</i>	0.055	0.053
<i>Nannotrigona testaceicornis</i>	0.055	0.594
<i>Parapartamona zonata</i>	0.055	1.000
<i>Partamona cupira</i>	0.055	0.000
<i>Partamona peckolti</i>	0.055	0.053
<i>Plebeia droryana</i>	0.055	1.000
<i>Plebeia emerina</i>	0.055	0.290
<i>Schwarzula coccidophila</i>	0.055	1.000
<i>Schwarzula timida</i>	0.111	0.334
<i>Tetragonisca angustula</i>	0.111	0.529
<i>Tetragonula iridipennis</i>	0.055	1.000
<i>Oxytrigona tataira</i>	0.277	0.222
<i>Trigona amalthea</i>	0.166	0.208
<i>Trigona amazonensis</i>	0.055	0.000
<i>Trigona branneri</i>	0.055	0.000
<i>Trigona corvina</i>	0.055	0.053
<i>Trigona fuscipennis</i>	0.111	0.486
<i>Trigona hyalinata</i>	0.166	0.193
<i>Trigona hypogea</i>	0.055	0.053
<i>Trigona spinipes</i>	0.333	0.493

*Normalised species degree: the proportion of sap-sucking insects with which each stingless bee species could theoretically interact

Honeydew harvesting is more common than wax harvesting by stingless bees, and this phenomenon can certainly be explained by the fact that these bees produce their own wax from their abdominal glands (Cruz-Landim 1967). Furthermore, with the exception of rare cases of mutualism between stingless bee species (*Schwarzula* spp.) and coccids (*Cryptostigma* spp.; Camargo and Pedro 2002; Kondo 2010; Roubik 2006), the removal of wax from hemipterans is usually detrimental for them. This waxy cover of hemipterans functions as a protective layer against predators, so its removal by stingless bees may make them more vulnerable to natural enemies (Peronti et al. 2013).

In our comparative analyses, we did not indicate any phylogenetic signal concerning to species degree and specialisation. Therefore, on this latter trait, for example, even though *Trigona* spp., *Partamona* spp. and *Liotrigona* spp. are generalists, this shared trait may not be attributed to the phylogenetic history of the species because it probably evolved multiple times independently. We suggest that this mutualistic behaviour exhibited by stingless bees appears to be opportunistic and may be driven by ecological demands, as indicated by the fact that relationships between stingless bees and sap-sucking insects are not explained by the phylogenetic history. Scarcity of flowering plants within locality may favour the alternative foraging strategies, such as the interaction with sap-sucking insects. Similarly, periods when the number of bee workers producing wax is

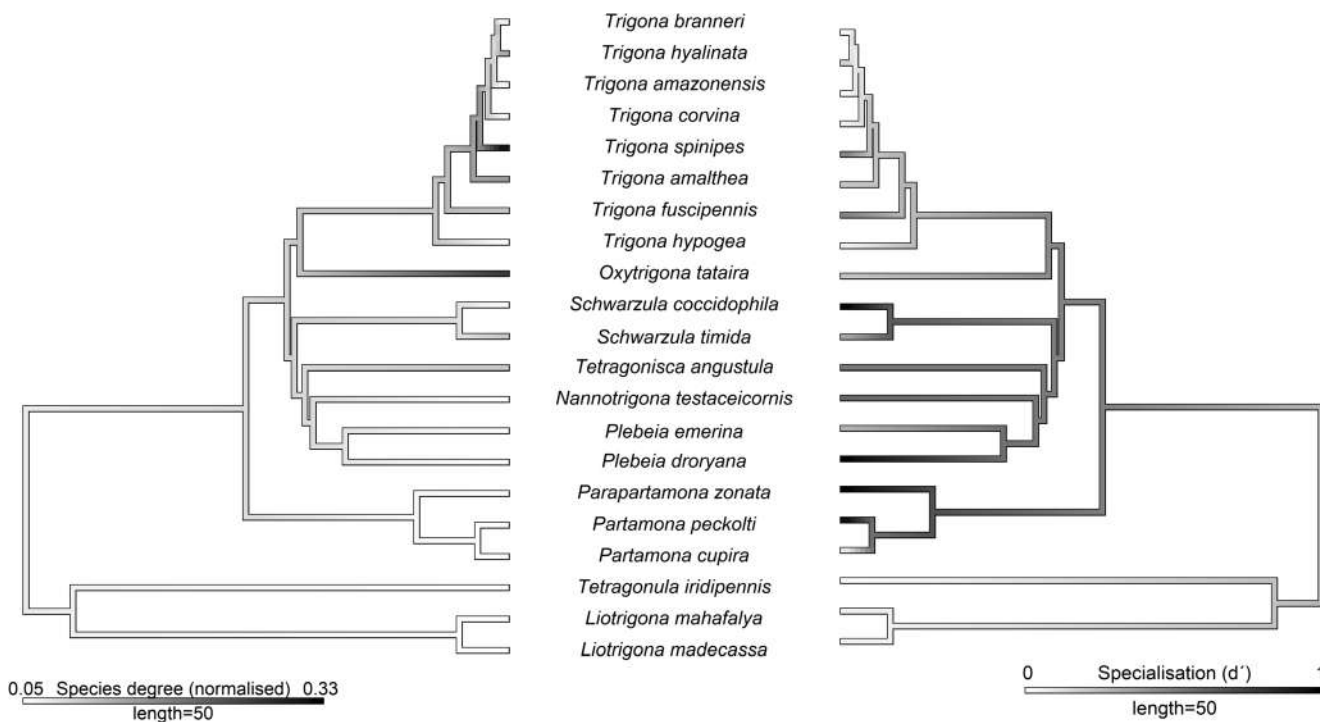


Fig. 4 Continuous character maps of two network parameters for 21 stingless bee species: left—species degree (i.e. number of interactions per species); right—specialisation index (i.e. degree of specialisation of a species within an interaction network). Trait changes are shown as

colour scale. Phylogenetic relationships among stingless bee species were adapted from the Meliponini time-tree from Rasmussen and Cameron (2010). Branch lengths are proportional to divergence times among lineages

low may trigger nestmates to harvest any material resembling their own wax. Furthermore, we have shown that sap-sucking insects which interact with the genera *Trigona* and *Oxytrigona* may benefit from the stingless bees' protection from natural enemies, whereas sap-sucking insects interacting with waxy cover robbers may be further exposed to desiccation and natural enemies. These two genera should be further investigated because of their broad range of interactions with sap-sucking insects. In particular, the visitation of flowers by *Oxytrigona* is rarely documented (Camargo and Pedro 2013). We suggest that when entomologists observe sap-sucking insects interacting with stingless bees (for example, *Oxytrigona* spp.), they should also inspect whether the bees are also visiting flowers at the same locality. This would further the analysis of such relationships and help determining the role of alternative sources of food (like honeydew) within plant-pollinator networks. Additionally, the relative amounts of both nectar and honeydew present within honey could be analysed using, e.g. physicochemical and microscopic tools, because honey produced by stingless bees is commonly consumed by people.

In summary, the Hymenoptera is a relevant insect order for ecological relationships established by various of its taxa with sap-sucking insects. Not only ants and wasps (Maschwitz and Hanel 1985; Letouneau and Choe 1987; Delabie 2001), but also, certain groups of bees have in hemipterans' exudates an alternative food source (Barônio et al. 2012; Batra 1993; Bishop 1994b; Dimou and Thrasylvoulou 2007; Herrmann et al. 2003; Konrad et al. 2009; Oda et al. 2014, Vieira et al. 2007). Even though the bees are insects widely associated to flowers, from which they obtain most of their food provisions (particularly nectar and pollen), their ecological interactions are not restricted to these reproductive structures of plants. Their food and or nest material needs can be obtained from sources as honeydew and waxy cover from sap-sucking insects, which turn out to be very special and interactions, although largely neglected so far.

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