



Mite diversity is determined by the stingless bee host species

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Abstract – Mites can establish ecologically mutualistic and/or commensal relationships with stingless bees. In the present study, we evaluated the acarine diversity associated with colonies of three stingless bee species (*Melipona quadrifasciata quadrifasciata*, *Scaptotrigona bipunctata* and *Tetragonisca fiebrigi*) in seven localities of southern Brazil. A total of 1458 mites from 18 species/morphospecies were sampled. The colonies of *Melipona q. quadrifasciata* showed the highest richness of mites, but *T. fiebrigi* was the bee species with the highest acari diversity among the evaluated species. This information suggests a close relationship between mites and stingless bees, which has direct implications for the transport of hives and non-naturally occurring species to different regions.

Acarofauna / colonies / diversity / ecological interactions / Meliponini

1. INTRODUCTION

Ecological communities feature a great variety of species that interact with each other through amensalism, commensalism, mutualism, parasitism, or predation (Thompson 2005). Ecological interactions influence biodiversity, whereas all organisms depend on interactions for feeding, breeding and shelter (Thompson 2005; Fontaine et al. 2011). For example, bees are known for establishing a mutualistic relationship with angiosperms because they need to visit reproductive structures to collect pollen and nectar to feed their offspring (Mitchell et al. 2009). Therefore, this behaviour often promotes the pollination of

flowers and, consequently, the reproduction of plants (Mitchell et al. 2009). However, bees can establish relationships with many other organisms inside and outside their nests. Outside their hives, bees can associate with sap-sucking insects as observed with honey bees (Apini), bumble bees (Bombini), orchid bees (Euglossini) and stingless bees (Meliponini) (Bishop 1994; Dimou and Thrasyvoulou 2007; Santos et al. 2019). Inside their hives, bees' relationships are less known, although more is known about their relationships with fungi and mites (Eickwort 1990; Menezes et al. 2009; Menezes et al. 2015; Paludo et al. 2018).

Among bee-associated mites, ectoparasites such as *Varroa destructor* (Anderson and Trueman) stand out because they are associated with *Apis mellifera* Linnaeus, which causes significant losses for beekeeping worldwide and has

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reached pest status in several regions (Sammataro et al. 2000; Genersch 2010; Ramsey et al. 2019). This mite harms host bees by consuming body fat, causing direct and indirect effects, and it can be a vector of viruses (Miranda and Genersch 2010; Rosenkranz et al. 2010; Ramsey et al. 2019).

Mites of 29 families and 90 genera are reported to be associated with bees in general, and only 17 genera are recorded in stingless bees (Klimov et al. 2016). In stingless bees, *Pyemotes tritici* (LaGrèze-Fossat and Montagné) may be responsible for the deaths of colonies of *Frieseomelitta varia* (Lepelletier) and *Tetragonisca angustula* (Latreille) in Brazil, with mites parasitizing adult bees and immature individuals (Menezes et al. 2009). However, interactions between mites and bees are not restricted to parasitism and include mutualism and/or commensalism (Eickwort 1994; Sammataro et al. 2000; Okabe 2013). Most bee-associated mites are mutualistic and commensal, acting as saprophages and predators in nests (Eickwort 1990; Eickwort 1994). These activities are described as beneficial because predatory mites are responsible for the population-level reduction in harmful organisms including fungi and bacteria (Sammataro et al. 2000; Cordeiro et al. 2011; Walter and Proctor 2013). Many bee mite species are host-specific for one species or phylogenetically or ecologically close hosts (Eickwort 1994; Klimov et al. 2007; Haas et al. 2019). Some explanation for these specific interactions includes adaptations for phoresis, coexistence with the host and the evolution of physiological mechanisms (Eickwort 1990).

Several acarine species have been reported as specialists in stingless bees, with species of the genus *Melissotydeus* and the families Gaudiellidae, Laelapidae and Meliponocoptidae predominating (OConnor 2009; Okabe 2013). Little information is known about mites associated with Meliponini, but some studies suggest two types of association: mites controlling other mite species and mites removing pathogens (Okabe 2013). For example, *Proctotydaeus* (*Neotydeolus*) *therapeutikos* Flechtmann and Camargo feeds on fungi present in the nests of *Scaptotrigona postica* (Latreille) (Flechtmann and Camargo 1974).

Beekeeping with stingless bees in Brazil (and other tropical regions worldwide) is a traditional activity and has increased in recent years. The transport of hives of different stingless bee species to other localities, even within their area of occurrence, is common (Cortopassi-Laurino et al. 2006; Freitas et al. 2009; Contrera et al. 2011; Jaffé et al. 2015; Jaffé et al. 2016). Given the context presented herein, it is necessary to know the composition of mites living inside the hives to understand the ecological role of these species and the risks of the hive's translocation to the community of these organisms.

Therefore, this work aims to assess the acarine diversity associated with stingless bees and analyse whether the composition of mite communities is determined by the host bee. Our main hypothesis is that bee mite communities are distinct for each species of stingless bee; in this way, we predict that each bee species presents a specific mite community.

2. MATERIALS AND METHODS

2.1. Study areas

This study was conducted in Rio Grande do Sul state (Figure 1) in southern Brazil in meliponaries of seven localities of two biomes: the Atlantic Forest (Bom Princípio (29°30'25"S 51°19'11"O), Ijuí (28°23'39"S 53°54'24"O), Panambi (28°17'20"S 53°31'24"O), Rolante (29°38'11"S 50°29'54"O), Santa Maria (29°39'7"S 53°38'54"O) and Venâncio Aires (29°33'32"S 52°10'30"O)) and Pampa (Porto Alegre 30°3'38"S 51°10'32"O). The collection sites were chosen according to the availability of beekeepers to contribute to the study and the presence of the number of colonies required for sampling.

The visited meliponaries were located in urban and rural areas, surrounded by soybean crops, corn crops and fruit orchards, with remnants of native forests. Sampling occurred in spring and summer from September 2018 to February 2019.

2.2. Sampling

For samples, three stingless bee species were selected: *Melipona quadrifasciata quadrifasciata*

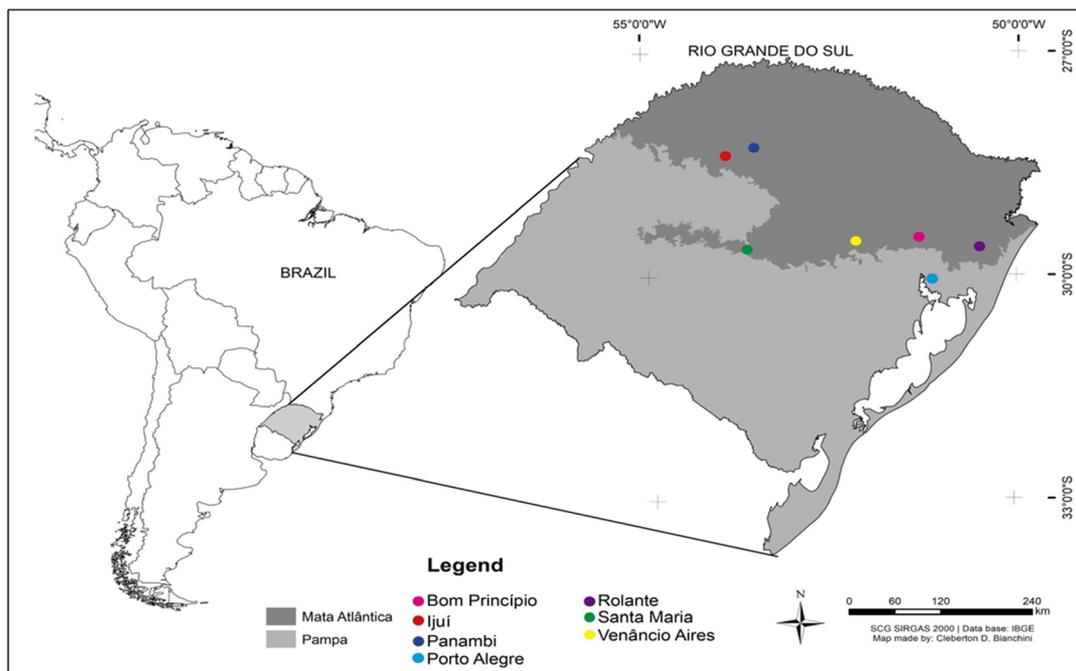


Figure 1. Map showing the state of Rio Grande do Sul with the sampling points of the colonies of stingless bees: Bom Princípio, Ijuí, Panambi, Porto Alegre, Rolante, Santa Maria and Venâncio Aires. The colours represent the boundaries of the biomes found in Rio Grande do Sul: dark grey, Atlantic Forest; light grey, Pampa.

Lepeletier, *Scaptotrigona bipunctata* (Lepeletier) and *Tetragonisca fiebrigi* (Schwarz). These species are representative of the meliponiculture in the state and country. In each locality, we selected three colonies of each species, totalling 21 colonies per species, except for *S. bipunctata*, of which only 16 colonies were analysed (lack of three colonies in Ijuí and two in Panambi). All stingless bee colonies were kept in wooden hives on single hive stands.

Aiming to achieve a broad analysis of each colony, we collected material from several parts of the hive. The procedure for direct sampling of mites used a paintbrush soaked in 70% ethanol that was swept across three areas of the hive: (I) inlet tube; (II) inner wall of the hive; and (III) outer wall of 1–3 honey pots. We also collected material for laboratory examination, namely, (IV) approximately 20 cm² of cerumen wrapper; (V) 1–10 g of pollen; (VI) 20 brood cells (superior position); and (VII) 10 adult bees. All collected materials were observed with a binocular stereoscopic microscope (Leica S6E), and mites were

collected with a thin paintbrush, mounted on glass slides with Hoyer's medium (Jeppson et al. 1975) and kept in a kiln between 50 and 60°C for approximately 7 days for fixation, distension and clarification of the specimens and medium drying. The specimens were examined with a phase-contrast microscope (Axio Scope, A1-Zeiss) and identified based on identification keys, descriptions and web key comparison.

All sampled bee specimens were deposited in the Science and Technology Museum of Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre, Rio Grande do Sul. The mite specimens were deposited in the reference collection of the Laboratório de Acarologia of the Universidade do Vale do Taquari – Univates, Lajeado, Rio Grande do Sul, Brazil.

2.3. Data analysis

First, we estimated the total number of non-observed mite species with the Chao equation (Chao et al. 2014) using the 'specpool' function

of the *vegan* package. Afterwards, we evaluated whether our sampling effort was enough to show the mite richness living inside the selected stingless beehives. Thus, we performed a rarefaction curve of the mite species by calculating interpolation/extrapolation according to the number of individuals sampled.

Next, we performed a diversity profile with a diversity order of Hill's series (Hill 1973). This focus allows us to dynamically compare the diversity of mites along the parameters at the scale (Rényi's diversity) between different communities (Chao et al. 2014). Thus, for example, if all the values in this scale were the greatest in a specific community, it is considered the most diverse among all analysed ones (Tóthmérész 1995). To generate these estimates, we used a matrix of mites associated with the three studied stingless bee species, framing the diversity profile with the 'renyi' function of the *vegan* package (Oksanen et al. 2016).

The composition of mite communities associated with the three stingless bee species was evaluated through a non-metric multidimensional scaling (NMDS) analysis. This method has been used to observe the dissimilarity in the composition of mites associated with stingless bee species (*M. q. quadrifasciata*, *S. bipunctata* and *T. fiebrigi*). For this, species data were standardized by the 'rank' method, which replaces the abundance values for their respective relative ranking and leaves zero values unchanged. Afterwards, our dataset was converted into a dissimilarity matrix with Gower's method, which divides all distances by the number of observations (rows) and scales each column to the reach unit. In this way, the ordered analysis was performed using the 'metaMDS' function of the *vegan* package. The resulting *stress* value was used to evaluate the ordination quality.

Posteriori, we tested whether the composition of the mite community was different according to the host bee species. Therefore, we performed an ANOVA with permutation (PERMANOVA, 1,999 permutations) controlling for sample location with the 'adonis' function of the *RVAideMemoire* package (Hervé 2019). If it was significant, we performed a pairwise comparison using the 'pairwise.perm.manova' function

of the same package, adjusting the *p*-values for corrections of 'fdr' (false discovery rate). Because PERMANOVA is sensitive to data dispersion, we analysed the homogeneity of the group dispersion with the 'betadisper' function followed by 'permutest', both in the *vegan* package. Thus, differently from PERMANOVA, which evaluates the changes in the composition of species between groups, betadisper analyses the variation inside groups.

Finally, we performed a percentage similarity (Simper) analysis to evaluate which species contributed to the composition dissimilarity of the mite species. This analysis was performed with the 'simper' function of the *vegan* package (Oksanen et al. 2016). All analyses were performed in R (R Core Team 2019).

3. RESULTS

Overall, we collected 1,458 mites associated with *M. q. quadrifasciata*, *S. bipunctata* and *T. fiebrigi*, with the occurrence of 18 species per morphospecies belonging to 14 genera and ten families (Table I), including five new species. The bee species that presented the highest mite abundance was *M. q. quadrifasciata* ($n = 938$), followed by *S. bipunctata* ($n = 408$) and *T. fiebrigi* ($n = 112$). The greatest mite abundance was found on the inner wall of the hive ($n = 769$), cerumen wrapper ($n = 504$), honey pots ($n = 67$) and brood cells ($n = 64$).

The most abundant species of mites were *Hypoaspis alfabetica* Berlese (Laelapidae) ($n = 773$), *Melissotydeus bipunctata* Da-Costa et al. (Tydeidae) ($n = 363$), *Lorryia meliponarum* Da-Costa et al. (Tydeidae) ($n = 127$) and *Tyrophagus putrescentiae* (Schrank) (Acaridae) ($n = 47$). The most abundant species in *M. q. quadrifasciata* were *H. alfabetica* ($n = 773$) and *L. meliponarum* ($n = 61$); in *S. bipunctata*, they were *M. bipunctata* ($n = 363$) and *Proctotydaeus (Neotydeolus) lasaroi* Da-Costa, Rodighero and Ferla ($n = 21$); and in *T. fiebrigi*, the most abundant species were *L. meliponarum* ($n = 66$) and *T. putrescentiae* ($n = 16$) (Figure 2C).

Although we found 18 acarine species/morphospecies associated with stingless bees in southern Brazil, the Chao estimator suggests that,

Table I. List of mite species found in the colonies of the three stingless bee species in southern Brazil

Species	M	S	T	
Superorder Parasitiformes				
Order Mesostigmata				
Blattisociidae	<i>Lasioseius</i> sp.	3	0	0
Laelapidae	<i>Eumellitiphis</i> sp.	0	0	9
	<i>Hypoaspis alfabetica</i> Berlese	773	0	0
Superorder Acariformes				
Order Trombidiformes				
Cheyletidae	<i>Cheletomimus (Hemicheyletia) gracilis</i> Fain, Bochkov and Corpuz-Raros	3	0	1
	<i>Eutogenes</i> sp.	0	1	0
Iolinidae	<i>Proctotydaeus (Oriolella) dorsoreticulatus</i> Da-Costa, Rodighero and Ferla	0	0	15
	<i>Proctotydaeus (Oriolella) quadrifasciatae</i> Da-Costa, Rodighero and Ferla	27	0	0
	<i>Proctotydaeus (Neotydeolus) lasaroi</i> Da-Costa, Rodighero and Ferla	0	21	0
Raphignathidae	<i>Raphignathus</i> sp.	0	0	1
Tarsonemidae	<i>Tarsonemus (Tarsonemus)</i> sp.	0	1	1
Tydeidae	<i>Lorryia meliponarum</i> Da-Costa et al.	61	0	66
	<i>Lorryia</i> sp.	0	1	0
	<i>Lorryia reticulata</i> (Oudemans)	3	0	1
	<i>Melissotydeus bipunctata</i> Da-Costa et al.	0	363	0
Order Sarcoptiformes				
Acaridae	<i>Forcellinia</i> sp.	27	2	2
	<i>Tyrophagus putrescentiae</i> (Schrank)	12	19	16
Gaudiellidae	<i>Platyglyphus</i> sp.	24	0	0
Glycyphagidae	<i>Glycyphagus</i> sp.	5	0	0
	Total	938	408	112

M, *Melipona quadrifasciata quadrifasciata*; *S*, *Scaptotrigona bipunctata*; *T*, *Tetragonisca fiebrigi*

if more hives were sampled, we would likely find more mite species ($\text{Chao} = 22 \pm 5$) (Figure 2A). According to the sample effort analysis, we have evidence that *M. q. quadrifasciata* was optimally sampled since approximately 1000 collected mites do not increase the probability of sampling more mite species. However, rarefaction curves for *S. bipunctata* and *T. fiebrigi* suggest that the richness must be greater than that found in this study.

Hill's diversity profile demonstrates that acarine richness is higher in *M. q. quadrifasciata* than in *S. bipunctata* and *T. fiebrigi*. When observing the Shannon-Wiener index, *T. fiebrigi* seems to be superior in this diversity index, suggesting the presence of rare species, followed by *S. bipunctata*. When analysing the Simpson

index, the dominance index is higher in *T. fiebrigi* than that in *M. q. quadrifasciata* and *S. bipunctata*. These results suggest that *M. q. quadrifasciata* shows higher richness, but for the other indices that use abundance values, *T. fiebrigi* shows higher diversity than the other two taxa (Figure 2B).

The quality of the ordination analysis (NMDS) was considered good and had a low stress value (0.05). We may say that the three stingless bee species have a discrete mite community and that there is a difference among the sampled locations (PERMANOVA, $F_{(2,87)} = 14.5$; $R^2 = 0.25$; $p < 0.001$, Figure 2D; Table II). Using only the abundance matrix of mite species, including the variable location, the generated ordination explains $\frac{1}{4}$ of the difference in the composition of the mite

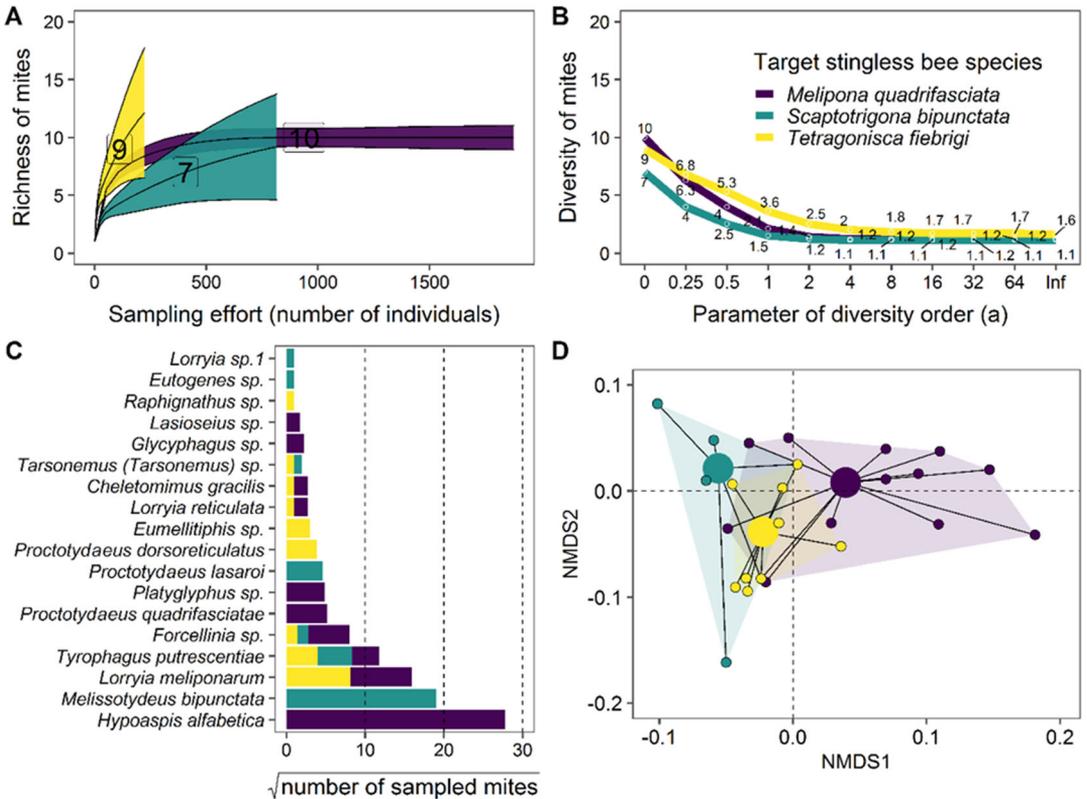


Figure 2. **A** Rarefaction curves of mite species: x-axis, number of individuals per sampling unit; y-axis, interpolation (before value) and extrapolation (after value) of the Hill number with order $q = 0$ exhibiting the species richness found and the number of expected species against the average. The shadow indicates the confidence intervals (95%). **B** Diversity profile of the Hill numbers. The x-axis shows the change in diversity indices over the Hill numbers; the y-axis displays the level of diversity for measures on the x-axis. The left-hand side of the x-axis is more sensitive to rare species, whereas the right-hand side is more sensitive to the abundance of mite taxa. This continuum of values allows inferring the contributions of rare vs. abundant species in a community. Some diversity indices on the x-axis can be inferred: 0 species richness; 1, Shannon-Wiener index; 2, Simpson index; inf, Berger-Parker index. **C** Number of mites sampled according to stingless bee species. Note: The total number of mites was transformed into the square root to facilitate visualization. The approximate value in the x-axis can be retrieved with the square power. **D** Non-metric multidimensional scaling (stress = 0.05): Community composition of mites sampled according to stingless bee species. Note: Larger points are the centroids; smaller points are the sampling units. Colours in all panels represent the stingless bee host (see legend in **B**). The full species names are shown in Table I.

community relative to the bee species studied and the locations sampled. Therefore, even though there is some overlap in the mite community of different bee species, bees are associated with distinct mite communities. In the pairwise analysis, all stingless bee species differed from each other (PERMANOVA, pairwise analyses, $p < 0.001$). There was no difference in dispersion homogeneity within groups ($F_{(2,87)} = 1.50$; $p =$

0.20). Therefore, the mite community is more influenced by the difference in composition between the respective species of stingless bee hosts than by the variation within them.

The following acarine species were (cumulatively) the most influential for the dissimilarity of the communities among bee species in at least 70%. For the dissimilarity between *M. q. quadrifasciata* and *S. bipunctata*, the species were *M. bipunctata*

Table II. PERMANOVA parameters and subsequent paired comparison of the composition of the mite community associated with stingless bee colonies in southern Brazil

	Degrees of freedom	Sum of squares	Mean squares	F	R ²	p
Stingless bee species	2	0.16	0.080	14.5	0.25	< 0.001
Residuals	87	0.48	0.005		0.74	
Total	88	0.64			1.00	
Pairwise comparisons showing the p of PERMANOVA						
		<i>Melipona quadrifasciata</i>			<i>Scaptotrigona bipunctata</i>	
<i>Scaptotrigona bipunctata</i>		< 0.001			< 0.001	
<i>Tetragonisca fiebrigi</i>		< 0.001				

(0.38), *H. alfabetica* (0.30) and *T. putrescentiae* (0.07). For the differentiation between *M. q. quadrifasciata* and *T. fiebrigi*, the species that contributed were *H. alfabetica* (0.40), *T. putrescentiae* (0.14), *Platyglyphus* sp. (0.08) and *Proctotydaeus (Oriolella) dorsoreticulatus* Da-Costa, Rodighero and Ferla (0.08). For the dissimilarity between *S. bipunctata* and *T. fiebrigi*, the most influential species were *M. bipunctata* (0.49), *T. putrescentiae* (0.12) and *P. (Neotydeolus) lasaroi* (0.10).

4. DISCUSSION

Our initial expectations that the mite community was different in each bee species were corroborated in this study. Our results show that stingless bees harbour a high diversity of mites and that acarine species can increase according to samples and bee species.

We found 14 genera and 18 species/morpho-species, with approximately 17 genera previously recorded in stingless bees (Klimov et al. 2016). Five of the identified species are likely new to science (Da-Costa et al. 2019; Da-Costa et al. 2020). In this study, we did not observe any species with parasitic behaviour. The mite community was different in each host bee species, which suggests that the structure and composition of these bee nests, and possibly some biological characteristics (e.g. behaviour), determine the community of mite species. These organisms find a suitable and specific ecological niche to colonize, and external factors (e.g. vegetation and climate) as well as nesting and body size (Haas et al. 2019) can help differentiate the community.

The predominance of *H. alfabetica* in *M. q. quadrifasciata* may be related to the high habitat diversity already recorded for representatives of this family. Laelapidae features a high diversity of species that may be parasites of invertebrates and vertebrates, inhabiting soil and nests of vertebrates and arthropods (Faraji and Halliday 2009; Joharchi and Shahedi 2016). This species was found only in association with *M. q. quadrifasciata*, demonstrating an apparent co-specific association. This information reinforces the association between these two groups, supporting the suspicion that several Laelapidae genera are specialists on stingless bees (Okabe 2013).

Tydeid mites, namely, *L. meliponarum* and *M. bipunctata*, were also abundant in hives and may be related to the presence of fungi in stingless bee nests. It is known that some fungi proliferate in the nests and benefit the bees, as in the case of *Zygosaccharomyces* sp., which is a source of sterols and helps in the larval development of *Scaptotrigona depilis* (Moure) (Paludo et al. 2018). Tydeid mites show diverse feeding behaviours, but most species are fungivorous (Silva et al. 2014; Silva et al. 2016). In Brazil, two species of *Melissotydeus* are reported to be associated with bees, *M. bipunctata* and *Melissotydeus macrosolenus* (André 1985; Da-Costa et al. 2019), and it is accepted that this genus is mutualistic (Eickwort 1994). *Tyrophagus putrescentiae* was found in the three bee species and shows generalist habits, feeding on fungi, pollen debris and nematodes (Klimov et al. 2016). This species was already found infesting

A. mellifera hives in Brazil (Teixeira et al. 2014). However, in this study, it was found in relatively small populations, and no damage was noticed.

Iolinid mites were also abundant in the nests of stingless bees, with the most representative species being *Proctotydaeus (Oriolella) quadrifasciatae* Da-Costa, Rodighero and Ferla. In this study, it was possible to observe the specificity of the members of this family with the host bees. *P. (Oriolella) dorsoreticulatus* was found only in the colonies of *T. fiebrigi*; *P. (Neotydeolus) lasaroi* only in *S. bipunctata*; and *P. (Oriolella) quadrifasciatae* only in the colonies of *M. q. quadrifasciata*. Members of this family can be found in plants and soil and are associated with insect nests. It is suggested that *P. (Neotydeolus) therapeutikos* feeds on fungi in the nests of *S. postica* (Flechtmann and Camargo 1974; Theron et al. 2012). Flechtmann and Camargo (1974) highlight losses of 50% in brood cells of *S. postica* without the presence of mites due to a fungal disease that quickly develops in brood cells. The authors observed that after introducing *P. (Neotydeolus) therapeutikos*, there was a decrease of approximately 3% in the mortality level.

There is little ecological information about mites associated with Meliponini, but this study demonstrates that the composition of the mite community is quite variable and is determined by the bee species. As our data indicate, at least for *S. bipunctata* and *T. fiebrigi*, there is an important diversity of mites to be found. In the three studied stingless bee species, mites show high ecological and functional diversity, including detritivorous, saprophagous and predatory habits, which suggests that these organisms can assist in the health of bee colonies by controlling fungus proliferation as well as other mites and insects that may be harmful to bees.

Overall, it is possible that acarofauna contributes—when at appropriate populational levels—to the well-being of native bee colonies, but more studies are necessary to increase the knowledge about these associations. Finally, we conclude that stingless bee species are associated with multiple mite species that form specific communities. However, most stingless beekeepers commercialize their hives to diverse people that inhabit different localities or even distinct biomes. Therefore, transport (sale and exchange) of

colonies should be conducted carefully by considering geographic range or the biome in which the species is inserted. If they are transported to very different places, the mite composition of the hives may change, and the implications for bee health under this scenario are unknown.

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AUTHOR CONTRIBUTION

TDC, NJF and BB conceived this research and designed the experiments. TDC and LFR performed the collection and identification. TDC and CFS analysed the data. TDC, CFS, NJF and BB wrote the paper and participated in the revisions. All authors read and approved the final manuscript.

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DATA AVAILABILITY

The dataset is available with the corresponding author.

CODE AVAILABILITY

Not applicable

DECLARATIONS

Ethics approval Not applicable

Consent to participate Not applicable

Consent for publication Not applicable

Competing interests The authors declare no competing interests.

La diversité des acariens chez les abeilles sans dard dépend de l'espèce d'abeille et de la proximité géographique des colonies.

Acarofaune / colonies / diversité / interactions écologiques / Meliponini.

Die Milbendiversität bei stachellosen Bienen hängt ab von der Bienenspezies und der geographischen Nähe der Kolonien.

Acarofauna / Kolonien / Diversität / ökologische Interaktionen / Meliponini.

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