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Original article

Resin foraging interactions in stingless bees: an ecological synthesis using multilayer networks

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ABSTRACT – Stingless bees use resins for nest construction, colony defense, and production of cerumen, propolis, and geopropolis. Despite their importance, resin foraging interactions are neglected in stingless bee ecology, so a synthesis is required to map how much we currently know about this topic. In addition, what kind of networks do those interactions form? The Integrative Hypothesis of Specialization (IHS) may provide a cognitive map to generate predictions and interpret results. Specifically, resin heterogeneity, phylogeny, and geography may create interaction constraints that generate a modular or compound topology in resin foraging networks. Here we systematically reviewed resin foraging interactions with a multilayer network approach accounting for biogeographical structure. A total of 1,037 bee–plant resin foraging interactions were retrieved and Anacardiaceae and Dipterocarpaceae were identified as the most frequently visited plant families worldwide. As deduced from the IHS, we found a modular topology in most cases. A compound topology was only found with a less conservative approach considering all data. In most cases, Mantel tests revealed that interactions, modules, and layers are constrained by phylogeny and geography. Our results suggest that closely related species tend to interact with similar plant genera and from the same biogeographical region. Body size was positively correlated with centrality, indicating that larger bees use highly connected plants. We hope our findings highlight the ecological patterns and drivers that shape resin foraging interactions in stingless bees. Moreover, we discuss methodological recommendations and knowledge gaps, helping to guide future studies.

botanical sources / compound topology / meliponini / modularity / propolis

1. INTRODUCTION

Stingless bees (Meliponini) comprise the most speciose group of corbiculate bees (~ 600 spp.) distributed in the Afrotropical, Indo-Malayan-Australasian, and Neotropical biogeographic regions (Rasmussen et al. 2017; Roubik 2022; but see comments on a biogeographic classification with four regions in Salatnaya et al. 2023). Among other functions, corbiculae are used for carrying resins from plants to nests (Bassindale and Matthews 1955; Gastauer et al. 2011). Resins are mainly secreted from intercellular ducts to defend the

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plants against predators and pathogens (Foisy et al. 2019; Shanahan and Spivak 2021). In stingless bees, resins are used for nest construction, colony defense (Schwarz 1948; Duangphakdee et al. 2009; Greco et al. 2010), and production of nest materials such as cerumen and geopropolis by mixing it with wax and soil, respectively (Wille 1983; Roubik 1989; 2006). As such, resins presumably enhance the fitness of stingless bees (Drescher et al. 2014). However, although resins account for high proportions of foraging flights in some species (Roubik 1989; Lorenzon and Matrangolo 2005; Shanahan and Spivak 2021), resin foraging interactions still comprise a neglected topic in bee research.

To map knowledge gaps and point to future directions, we urgently need an ecological synthesis about resin foraging interactions made by stingless bees. Fortunately, network science may help us interpret the results of such a synthesis. Specifically, considering that resin foraging interactions occur all over the world in different biogeographic regions, a multilayer approach (sensu Pilosof et al. 2017) may help us analyze them while accounting for the biogeographical structure. First, what kind of system would be formed by resin foraging interactions? The Integrative Hypothesis of Specialization (IHS; Pinheiro et al. 2016, 2019)—proposed to explain the assembly rules of interaction networks—may help us deduce some expectations. Nested networks are expected when resources are similar to each other (Pinheiro et al. 2019). However, when resources are heterogenous (e.g. in chemically heterogeneous resins collected by stingless bees), the IHS predicts modular or compound networks (Pinheiro et al. 2019; see also Bascompte et al. 2003; Lewinsohn et al. 2006; Olesen et al. 2007; Fortuna et al. 2010; Ulrich et al. 2017). The latter is especially found in well-sampled, large systems with heterogeneous resources, in which modules are internally nested. Therefore, we expected resin foraging interactions to scale up and form modular or compound topologies, with layers and modules constrained by phylogeny and geography.

Within a resin foraging network, morphological factors could determine the centrality of different bee species (i.e., the relative importance of a node to the structure of its network, Jordán et al. 2007). Specifically, body size could influence the diversity of botanical sources that provide bees with resin, because larger bees are expected to have (1) a broader flying range (Araújo et al. 2004; Greenleaf et al. 2007; Raiol et al. 2021) and (2) allometrically larger heads to accommodate powerful jaw muscles (Grüter et al. 2012) than smaller bees, which could be used to bite resin wounds and stimulate secretion (Schwarz 1948; Howard 1985). Thus, we predict larger bees to be more central in resin foraging networks.

Currently, three main methods of botanical source determination are employed to identify plants from which resins are collected: (i) chemical analyses of resins and propolis, which are compared with chemical profiles of resins from local plants (e.g. Walker and Crane 1987; Bankova et al. 2000; Drescher et al. 2019); (ii) fieldwork, recording, or other kinds of visual observation (e.g. Wallace and Lee 2010; Gastauer et al. 2011; Reyes-González and Zamudio 2020); and (iii) palynological analysis from pollen residues in propolis (Barth 1998, 2006; Barth et al. 1999; Barth and Luz 2003). However, while the reliability of chemical and fieldwork data has never been challenged, Layek et al. (2023) questioned how accurately palynological data can determine resin sources, at least for a local population of *Tetragonula iridipennis.* As such, excluding palynological data to understand resin interactions would be a more conservative approach.

Here we provide a synthesis of the current knowledge about resin foraging interactions in stingless bees, relying on a systematic review of the literature and using a multilayer network approach. Specifically, we asked: (1) Which plants are most frequently used as resin sources by stingless bees? (2) Which topology is observed in the global resin foraging network? (3) Does phylogeny shape those interactions? (4) How does body size affect the centrality of stingless bees? To cope with Layek's et al. (2023) concerns, we contrasted results between total (with all data) and conservative (without palynological data) datasets in our analysis. In addition, we also accounted for a very conservative dataset with no palynological data considering more refined taxonomic and biogeographic resolutions.

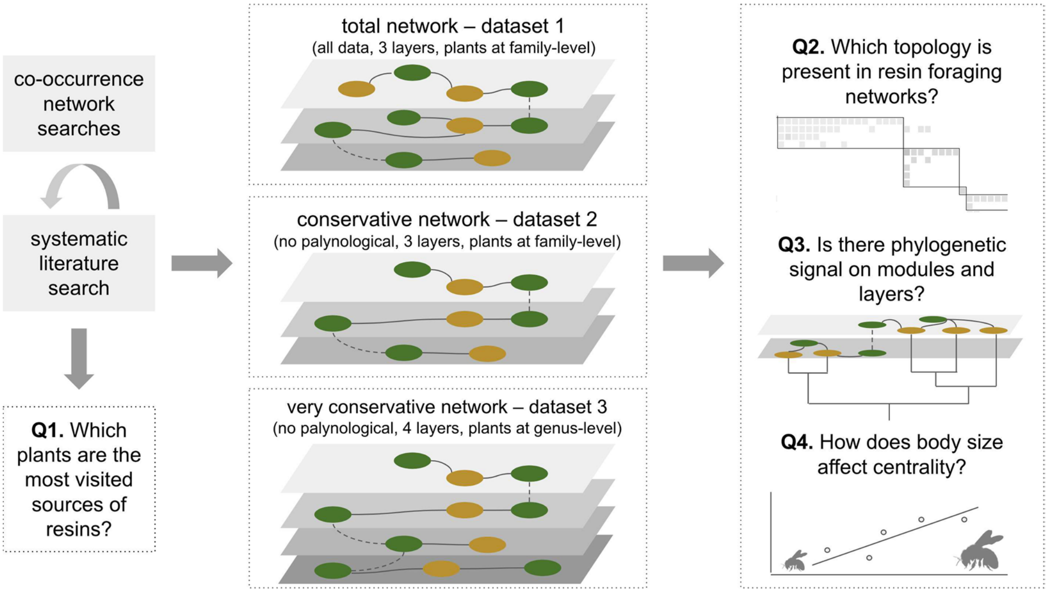

Figure 1. The workflow of our study. First, we conducted a systematic literature review using a co-occurrence network to search for additional keywords. Our dataset comprises interactions made by bees that forage on plant resins, which were used to answer our first question (Q1). We used a multilayer approach to account for the spatial structure and build three networks: a total network (using all data, three layers, and plants at family level), a conservative network (excluding palynological data, three layers, and plants at family level), and a very conservative network (excluding palynological data, four layers, and plants at genus level). Based on these networks, we answered the other three questions (Q2, Q3, and Q4) related to the Integrative Hypothesis of Specialization.

2. MATERIAL AND METHODS

2.1. Dataset

A flowchart of this study is presented in Figure 1. We conducted a systematic literature search in the Web of Science and Scopus databases using the PRISMA-EcoEvo (v1.0) extension guidelines (O'Dea et al. 2021) (Figure S1). We employed the following keywords in different combinations: 'botanical source*', 'geopropolis', 'Meliponini', 'plant source*', 'propolis', 'resin*', and 'stingless bee*'. The literature search was last performed on 19 May 2023 on titles, abstracts, and keywords. As potentially eligible articles, we also considered citations and references from publications included in the previous step. Duplicates were removed with the R-package 'litsearchr' (Grames et al. 2019). We extracted additional terms using co-occurrence network analysis, which were used in a final search to enrich our dataset (Grames et al. 2019). To fulfill objective criteria of inclusion, studies should have: (i) identified plant and stingless bee taxa at family/genus and species level, respectively; (ii) specified the plant as a resin source rather than pollen source; (iii) indicated how they infer the interaction (chemical profile, fieldwork, or palynological analyses). On one hand, several studies are only able to identify plants at the family level and thus relaxing the taxonomic resolution of plants to family level would be important to avoid a large amount of information being lost. On the other hand, considering genus level could provide valuable insights using a more refined scale. Thus, we prepared a dataset with plants at family level and another one at genus level. All sources of resin foraging data are in Table S1. In addition, plants identified at the species level were classified according to their growth forms, in order to explore which plant types are most frequently explored for resin collection (Table S2).

While body size is a theoretical variable related to flight range, intertegular distance (ITD: the distance between the two insertion points of the wings; Cane 1987) was considered its proxy (Figure S2). ITD was digitally measured with Zeiss ZEN at the Institute of Biosciences, University of São Paulo (IB-USP). Based on their availability, between three to ten specimens for each species were sampled from the Entomological Collection Paulo Nogueira Neto (CEPANN, IB-USP). ITD from species not available at CEPANN were searched in the literature (Supplementary Table S3). All taxonomic names followed the Integrated Taxonomic Information System (ITIS 2023).

2.2. Network topology

The interaction datasets were organized as node and link lists, with the latter also including information on plant family, bee species, methods of botanical source determination, and biogeographical region. Hence, in our analysis, plants and bees are nodes, the interactions between them are links, and biogeographical regions are layers. Due to the variety of methods employed in the original studies to infer bee–plant interactions (chemical, fieldwork, and palynological analyses), we decided to use binary (presence vs absence) rather than weighted data, because biases could emerge when we mix interaction frequency data collected with different methods (Mello et al. 2019). In addition, binary data are assumed to assess fundamental niches rather than realized niches (Fründ et al. 2016; Jordano 2016), which is consistent with our objective of assessing resin foraging interactions at a global scale rather than at a local scale.

Following the classification of Bueno et al. (2023), the genera of Meliponini from our dataset occur in three biogeographic regions, namely Afrotropics, Neotropics, and Indo-Malayan-Australasia. Conversely, as sensibility analysis, we also prepared an additional dataset with plants at genus level separating Indo-Malayan-Australasia into Indo-Malaya and Australia regions (Henríquez-Piskulich et al. 2024). Afrotropical data, however, were excluded from our analyses, because only a single species was present in our datasets, precluding any network analysis. To account for the geographic structure of the studied interactions, we used a multilayer network approach (Pilosof et al. 2017), in which interactions between bees and plants that occur in the same biogeographical region were considered as intralayer links (hereafter, "intralinks"), whereas nodes that occur in different biogeographical regions are connected to themselves between layers by interlayer links (hereafter, "interlinks").

To describe the network structure and estimate node centrality, all analyses were performed in the R language (R Core Team 2023) using the giant component of the multilayer network and its separate layers, following Mello et al. (2019). First, modularity (Q) measures how much the network structure contains cohesive subgroups of nodes (modules), in which the density of interactions is higher within the same module than between modules. Second, nestedness (NODF; Almeida-Neto et al. 2008) indicates to what extent the links of low-degree nodes represent a subset of the links of high-degree nodes. Finally, to test the occurrence of a compound topology (i.e., when each layer separately and the aggregated layers are formed by internally nested modules), we decomposed NODF into nestedness between pairs of species from the same module ($NODF_{sm}$) and from different modules ($NODF_{dm}$). A compound topology is present when the observed Q and $NODF_{sm}$ are significantly higher than the expected by chance and $NODF_{sm}$ is higher than $NODF_{dm}$ considering the modular structure (restricted null models). The observed Q values were calculated with the *computeModules* function, while the observed values of NODF, $NODF_{sm}$, and $NODF_{dm}$ were estimated with the *nest.smdm* function from the bipartite package for R (Dormann et al. 2008).

Statistical significance was estimated in both the absence (free null model) and presence (restricted null model) of the modular structure using a Monte Carlo procedure (1,000 random matrices), following Felix et al. (2022a). Free null models were simulated to test the significance of all network descriptors, while restricted null models were additionally performed to test the significance of NODF, NODF_{sm}, and NODF_{dm}. We did not use restricted null models to test Q, because this would make no sense (see details in Mello et al. 2019). The mean expected values were calculated for the 1,000 matrices and Z-score was calculated as Z = [observed value—mean (simulated values)] / σ(simulated values). Values were considered statistically significant when $p < 0.05$. All analyses were conducted using the R-packages bipartite (Dormann et al. 2008) and igraph (Csardi and Nepusz 2006), plus user-defined functions written by Mello et al. (2019) and Felix et al. (2022a).

2.3. Centrality metrics

We followed the protocol for estimating centrality metrics from multilayer networks using the EMLN package for R (Frydman et al. 2023). First, we created a multilayer graph object using the *create_multilayer_network* function, considering its bipartite structure. Then, we obtained the supra-adjacency matrix (SAM) with the *get_sam* function and converted it to an 'igraph' object. The following centrality metrics were estimated: (1) normalized degree, (2) betweenness, and (3) eigenvector centrality. Normalized degree is the number of plant families with which each bee interacts scaled by the total number of plant families in the network, and may be biologically interpreted as the fundamental niche breadth (Nooy et al. 2005; Mello et al. 2015, 2019). Betweenness centrality is the proportion of shortest paths (i.e., geodesics) wherein a given bee species is present (Freeman 1977), and may be biologically interpreted as the magnitude of a species in binding different guilds within the network (Mello et al. 2019). Finally, eigenvector centrality is calculated as the contribution of each bee species to the main eigenvector of the network (Taylor et al. 2017), and may be biologically interpreted as a combination of niche breadth and role in binding guilds (that is, a bee may have a high eigenvector value either due to a high degree or when it is connected with a high degree plant; Mello et al. 2019).

2.4. Statistical analyses

Mantel tests with 10,000 permutations were performed to test for phylogenetic signals in the interactions, modules, and layers (biogeographical regions). We converted the most comprehensive phylogeny of Meliponini (Quezada-Euán et al. 2019) into a phylogenetic distance matrix using the function *cophenetic.phylo* from the 'ape' package (Paradis and Schliep 2019). Interactions, modules, and layers were converted to distance matrices through a Jaccard algorithm using the function *vegdist* from the vegan package for R (Dixon 2003). We performed mixed effects models to test the correlation between centrality metrics (response variables) and body size (predictor variable). To control for the spatial non-independence of data, we included the network layers (biogeographic regions) as a random factor. All analyses were performed with the glmmTMB package for R (Brooks et al. 2017).

2.5. Sensibility analysis

We considered datasets accounting for the variation in methods of botanical source determination (total = with all data; conservative = excluding palynological data), biogeographical delimitation (with three regions = Afrotropical, Indo-Malayan-Australasian, and Neotropical; with four regions = separating Indo-Malaya from Australia), and taxonomic resolution (plants at genus and family levels). Thus, three datasets were generated: Dataset 1 (total with all data, three regions, and plants at family level), Dataset 2 (conservative with no palynological data, three regions, and plants at family level), and Dataset 3 (very conservative with no palynological data, four regions, and plants at genus level). All network and statistical analyses were repeated for each dataset.

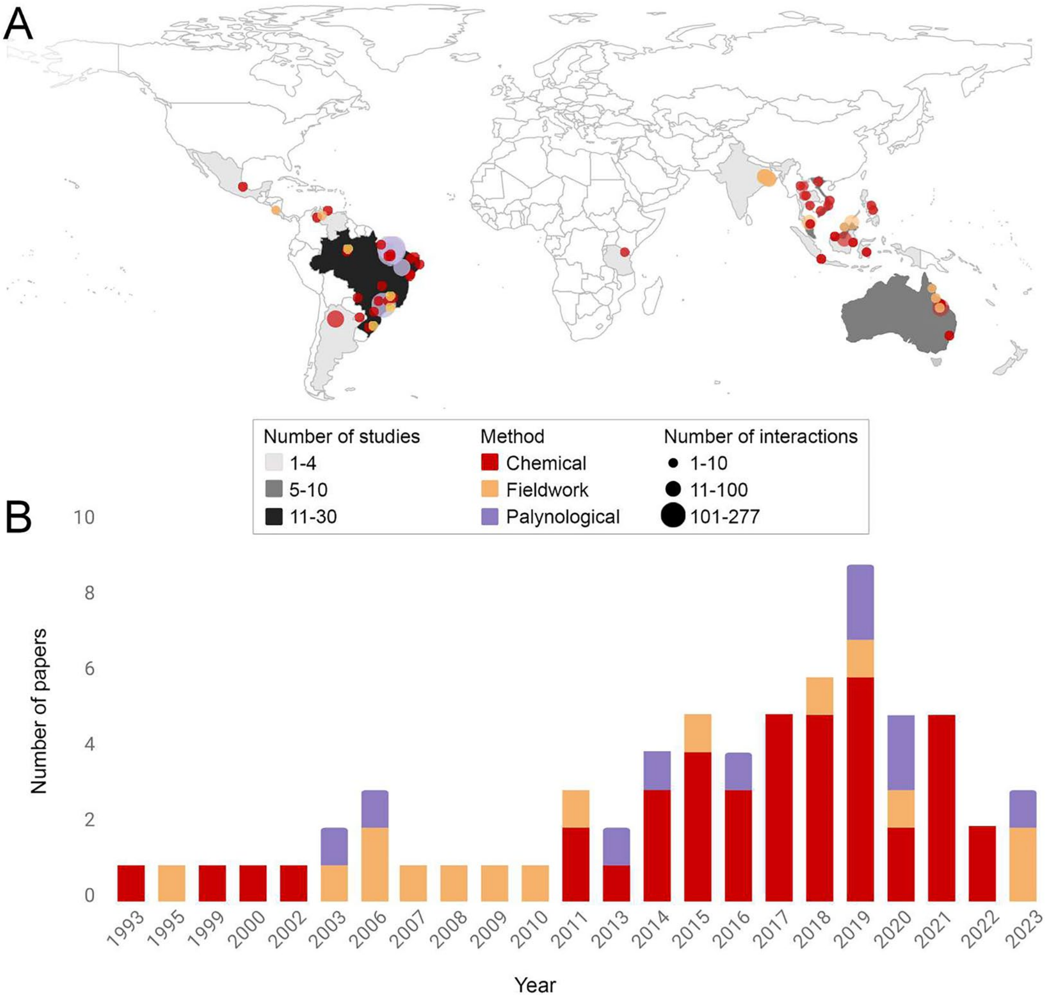

Figure 2. Geographical and temporal literature synthesis for resin foraging interactions made by stingless bees. (A) Geographical distribution of studies reporting the botanical origin of resins, separated by methods of botanical source determination (chemical, fieldwork, or palynological), number of studies, and number of interactions. (B) Variation in the number of papers on the topic over the years.

3. RESULTS

We recovered 1,037 bee–plant resin foraging interactions from 62 studies (Table S1; see details on each step of literature search in Figure S1), in which 48% (30) were located in the Neotropics, 50% (31) in the Indo-Malayan-Australasia, and 2% (1) in the Afrotropics (Figure 2A). Particularly, 45% of studies are concentrated in Brazil (28), 11% in Australia (7), 10% in Vietnam (6), and 8% in Malaysia (5; Supplementary Table S1). Contrasting different methods of botanical source determination, our systematic literature search revealed that 15% of the interactions were determined through chemical profile (156), 12% through fieldwork (125), and 73% through palynological analyses (743). The number of papers reporting resin foraging interactions through chemical profiles has been increasing since 2011, with occasional decreases (e.g. 2020 and 2022; Figure 2B).

3.1. Botanical sources of resins

Considering our total analysis (Dataset 1), stingless bees were reported to forage for resins from 101 plant families (70 genera) worldwide: 88 (24) in the Neotropics, 41 (52) in Indo-Malayan-Australasia, and one family (from the genus *Pinus*) in the Afrotropics. Considering Indo-Malayan-Australasia as different regions, resin foraging was found in 43 plant genera in Indo-Malaya and nine in Australia. Each stingless bee species was reported to forage on 2 ± 11.3 plant families (range: 1–45, with the maximum value reported for *Tetragonisca angustula*). The plant families with the highest degree scores were Dipterocarpaceae (degree = 34), Anacardiaceae (33), Myrtaceae (26), Fabaceae (22), Clusiaceae (20), Euphorbiaceae (19), and Araucariaceae (19). In the conservative analysis (Dataset 2), the plant families with the highest degree scores were Dipterocarpaceae (degree = 22), Anacardiaceae (17), Clusiaceae (15), Araucariaceae (14), and Myrtaceae (10). In the very conservative analysis (Dataset 3), the plant genera with the highest degree scores were *Shorea* (degree = 25), *Agathis* (14), *Dipterocarpus* (14), *Dryobalanops* (11), *Mangifera* (11), *Parashorea* (11), and *Clusia* (10). A complete comparison of the number of interactions for stingless bee species, plant families and genera is reported in Figures S3, S4, and S5 respectively.

When comparing botanical sources across methods of determination, 28, 18, and 70 plant families were reported through chemical profile, fieldwork, and palynological analyses, respectively. The most foraged plant families were Anacardiaceae, Myrtaceae and Fabaceae in palynological data (degree = 14), and Dipterocarpaceae in both chemical (degree = 14) and fieldwork data (degree = 19). At the genus level, *Shorea* (degree = 15) and *Mangifera* (10) were the most visited sources according to chemical data, whereas *Dipterocarpus* (11) and *Shorea* (10) were the most reported through fieldwork.

Plant identification at the species level was available for 149 species. Most of these species were represented by trees (65%), with fewer records for other growth forms (Table S2). Even though few interactions were reported for each plant species, a high number of records was reported for species from the Dipterocarpaceae family (*Dryobalanops lanceolata*, n = 13; *Agathis borneensis,* n = 14; *Rubroshorea parvifolia,* n = 16), *Mangifera indica* (mango tree, n = 15), and *Schinus terebinthifolia* (Brazilian pepper tree, n = 17).

3.2. Network topology and phylogenetic signal

The total resin foraging multilayer network of stingless bees from the Dataset 1 (Figure 3A) comprises 169 nodes (68 bees and 101 plants) and 534 links (508 intralinks and 27 interlinks), with one link in Afrotropics, 101 links in Indo-Malayan-Australasia, and 404 links in Neotropics. We found a compound topology in the multilayer network, that is, a modular structure different from expected by null models ($Q = 0.41$; $P_{free} < 0.001$) with internally nested modules ($NODFsm = 0.62$; $P_{res} = 0.02$; $NODFdm = 0.27$; $P_{res} < 0.001$; Figure 4A; Table I). Similar patterns are significant for the Neotropical layer but not for the Indo-Malayan-Australasian layer (Table I). Mantel tests revealed significant associations between phylogeny, interactions, modules, and layers (Table II). For instance, closely related species of stingless bees are usually from the same module ($r = 0.07$; $P = 0.01$) and layer ($r = 0.08$, $P = 0.01$), exhibiting similar interactions ($r = 0.1$; $P = 0.004$). Likewise, species from the same biogeographical region are likely from the same module ($r = 0.2$; $P < 0.001$).

The conservative network from the Dataset 2 (Figures 3B and 4B) comprises 95 nodes (61 bees and 34 plants) and 146 links (137 intralinks and 8 interlinks), with one link in Afrotropics, 82 in Indo-Malayan-Australasia, and 52 in Neotropics. In the multilayer ($Q = 0.55$; $P_{free} < 0.001$) and Neotropical layer ($Q = 0.59$; $P_{free} < 0.001$), we found modular topologies different from expected from null models whose modules are not internally nested (Table III). However, the Indo-Malayan-Australasian layer exhibits modularity ($Q = 0.46$; $Pf_{ree} < 0.001$) and nestedness ($NODF = 0.35$; $P_{res} = 0.01$) different from expected by null models,

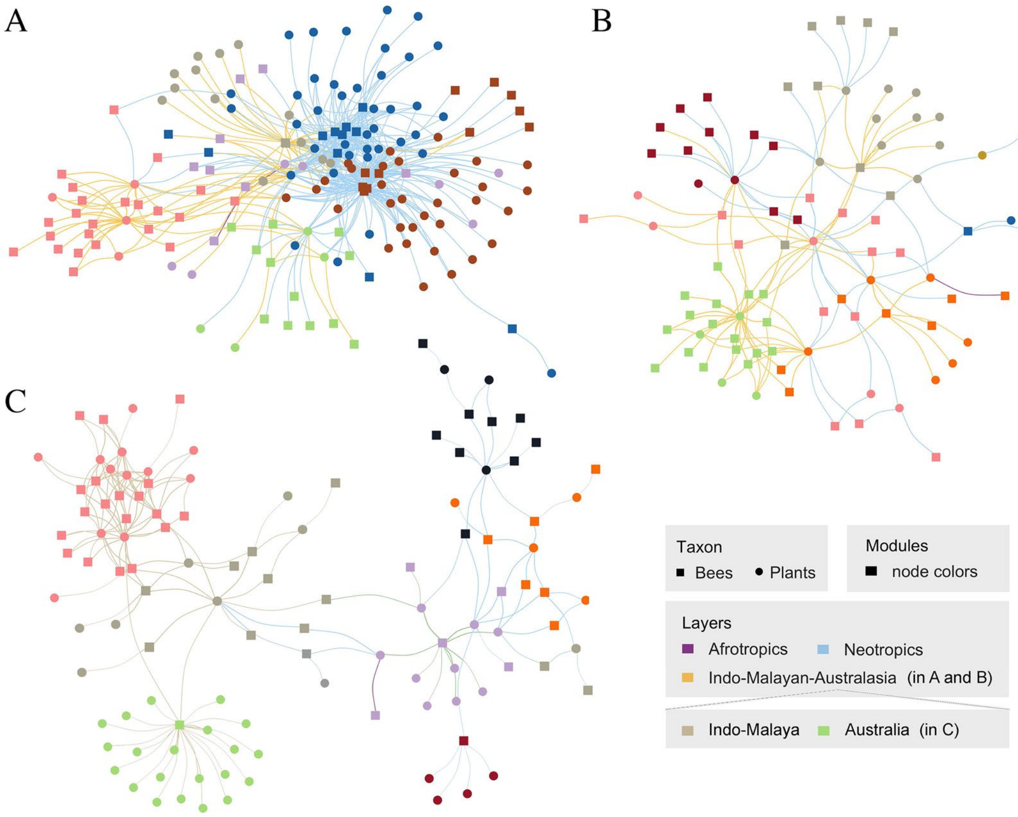

Figure 3. Multilayer networks of resin foraging interactions made by stingless bees, considering bipartite (bees vs plants), spatial, and modular structures. (A) Total network (Dataset 1: all data, three layers, plants at family level). (B) Conservative multilayer network (Dataset 2: no palynological data, three layers, plants at family level). (C) Very conservative multilayer network (Dataset 3: no palynological data, four layers, plants at genus level). The Indo-Malayan-Australasia layer is separated into Indo-Malaya and Australia in (C). Bees are represented as squares; plants as circles. Node colors represent modules. Link colors represent layers.

but with no modules internally nested (Table III). The Mantel test results from the conservative dataset are congruent with those from the total dataset (Table II), except for phylogeny vs modules ($r = 0.08$; $P = 0.07$).

The very conservative network from the Dataset 3 (Figures 3C and 4C) comprises 129 nodes (60 bees and 69 plants) and 195 links (189 intralinks and 6 interlinks), with one link in Afrotropics, 10 in Australia, 122 in Indo-Malaya, and 53 in Neotropics. Network analyses revealed a modular pattern different from expected by null models in the multilayer ($Q = 0.62$; $P_{free} < 0.001$), Neotropical ($Q = 0.65$; $P_{free} < 0.001$), and Indo-Malayan layers ($Q = 0.45$; $P_{free} < 0.001$), but with no modules internally nested (Table IV). In contrast, the Australian layer is not modular ($Q = 0.11$; $P_{free} = 0.3$). The Mantel tests were congruent with those from the total dataset (Table II).

3.3. Effect of body size on centrality

Corroborating our expectations (Figure 5), the mixed model from the total multilayer network (Dataset 1) revealed a significant effect of body size on normalized degree ($\beta = 0.08$; std. error $= 0.02$; $z = 3.89$; $P < 0.001$) and betweenness ($\beta = 100.11$; std. error $= 22.65$; $z = 4.42$; $P < 0.001$) but not for

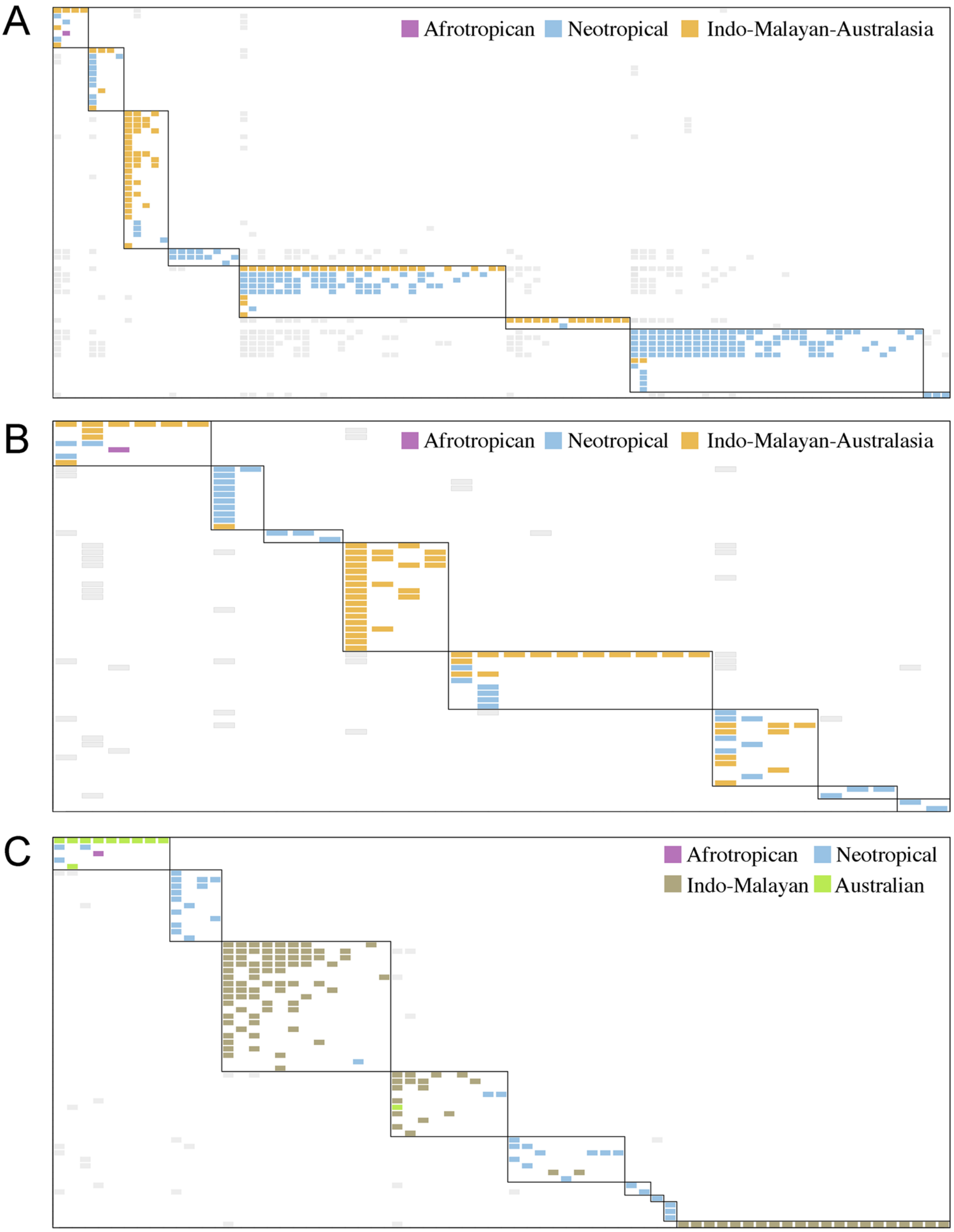

Figure 4. The compound topology of the aggregated networks represented as incidence matrices. (A) The total matrix (Dataset 1). (B) The conservative matrix (Dataset 2). (C) The very conservative matrix (Dataset 3). Note that interactions that occur in the same module are mostly from the same biogeographical region. Columns = plants; rows = stingless bees.

Table I Description of the resin foraging network topology, considering the total multilayer structure from Dataset 1 (all data, three regions, and plants at family level) The Afrotropical layer is not shown because calculation of modularity and nestedness was inapplicable (only a single bee species from Africa is present in our dataset)

	Obs	E_{free}	Z_{free}	P_{free}	E_{res}	Z_{res}	P_{res}
Multilayer							
Q	0.41	0.21	30.44	**<0.001**	NA	NA	NA
NODF	0.34	0.31	13.18	**<0.001**	0.32	-1.28	**<0.001**
NODF_{sm}	0.62	0.29	42.49	**<0.001**	0.57	31.94	**0.02**
NODF_{dm}	0.27	0.31	5.61	<0.001	0.24	-6.29	**<0.001**
Neotropical layer							
Q	0.28	0.21	7.77	**<0.001**	NA	NA	NA
NODF	0.44	0.44	21.72	0.46	0.41	6.36	**<0.001**
NODF_{sm}	0.69	0.45	48.66	**<0.001**	0.62	37.37	**<0.001**
NODF_{dm}	0.34	0.44	13.18	<**0.001**	0.32	-0.46	**<0.001**
Indo-Malayan-Australasian layer							
Q	0.52	0.26	18.30	**<0.001**	NA	NA	NA
NODF	0.29	0.25	21.69	0.07	0.29	11.01	**0.37**
NODF_{sm}	0.36	0.21	30.29	**<0.001**	0.37	20.08	0.38
NODF_{dm}	0.25	0.29	16.97	0.12	0.23	11.90	0.2

Significant P values are in bold. All statistics were estimated using free and restricted null models, except for M whose significance cannot be tested using restricted null models (see the rationale in Mello et al. 2019)

E expected score, *Q* modularity, *NODF* nestedness in the whole network, $NODF_{sm}$ nestedness within the same module, $NODF_{dm}$ nestedness in different modules, *Obs* observed values

eigenvector centrality ($P > 0.05$). We found a significant effect of body size on eigenvector centrality for the conservative network (Dataset 2: $\beta = 0.05$; std. error $= 0.02$; $z = 2.41$; $P < 0.05$) and the very conservative network (Dataset 3: $\beta = 0.06$; std. error $= 0.02$; $z = 2.57$; $P < 0.01$), but no significant effect was found for normalized degree and betweenness in both networks ($P > 0.05$).

Table II Mantel tests using 10,000 permutations to detect phylogenetic signals in layers (biogeographic regions), modules, and interactions in the total (Dataset 1), conservative (Dataset 2), and very conservative (Dataset 3) multilayer resin foraging networks

	Total		**Conservative**		**Very conservative**	
	r	**p**	**r**	**p**	**r**	**p**
Phylogeny vs Interactions	0.10	**0.004**	0.09	**0.009**	0.11	**0.004**
Phylogeny vs Modules	0.07	**0.01**	0.08	0.07	0.12	**0.005**
Phylogeny vs Layers	0.08	**0.01**	0.09	**0.01**	0.11	**0.008**
Modules vs Layers	0.20	**<0.001**	0.24	**<0.001**	**0.36**	**<0.001**
Interactions vs Layers	0.31	**<0.001**	0.28	**<0.001**	0.44	**<0.001**

Significant p-values are in bold ($p < 0.05$)

r Mantel correlation coefficient

Table III The conservative multilayer structure from Dataset 2 (no palynological data, three layers, and plants at family level)

	Obs	E_{free}	Z_{free}	P_{free}	E_{res}	Z_{res}	P_{res}
Multilayer							
Q	0.55	0.31	16.78	**< 0.001**	NA	NA	NA
NODF	0.19	0.25	8.98	**< 0.001**	0.18	-0.62	0.3
NODFsm	0.55	0.26	47.36	**< 0.001**	0.53	34.85	0.24
NODFdm	0.12	0.25	2.04	**< 0.001**	0.11	-1.48	0.38
Neotropical layer							
Q	0.59	0.48	0.03	**< 0.001**	NA	NA	NA
NODF	0.13	0.17	5.49	**0.01**	0.14	3.79	0.3
NODFsm	0.36	0.15	31.68	**< 0.001**	0.38	28.15	0.39
NODFdm	0.09	0.17	1.75	**< 0.001**	0.95	1.43	0.24
Indo-Malayan-Australasian layer							
Q	0.46	0.25	12.89	**< 0.001**	NA	NA	NA
NODF	0.35	0.35	26.91	0.46	0.31	19.82	**0.01**
NODFsm	0.61	0.33	54.61	**< 0.001**	0.58	44.04	0.2
NODFdm	0.26	0.35	17.69	**0.01**	0.21	14.58	**0.02**

Significant P values are in bold

E expected score, *Q* modularity, *NODF* nestedness in the whole network, *NODFsm* nestedness within the same module, *NODFdm* nestedness in different modules, *Obs* observed values

4. DISCUSSION

Our study provides a synthesis of resin foraging interactions made by stingless bees worldwide, made possible by combining a systematic review with a multilayer network approach. Our results shed light on four questions. First, we identified Anacardiaceae and Dipterocarpaceae as the most important resin sources at family level, and *Agathis*, *Dipterocarpus*, and *Shorea* at genus level. Second, a modular structure was detected in most cases, whereas a compound topology was only observed in the total multilayer network and its Neotropical layer. Third, there was a phylogenetic signal in the interactions, modules, and layers in most cases. Fourth, body size and some centrality metrics were positively correlated. Together, our results point to knowledge gaps and provide insights into resin foraging interactions, which we discuss below.

4.1. Insights from the multilayer network

As deduced from the IHS (Pinheiro et al. 2019), first we found a modular topology when analyzing the Indo-Malayan-Australasian separately, excluding palynological data (the conservative network), or considering a data set with four regions and plants at the genus level (the very conservative network). Second, we found a compound topology in the multilayer and its Neotropical layer from the resin foraging network based on the total dataset.

The phylogenetic constraints revealed by Mantel tests seem to explain the emergence of modules, in which closely related stingless bees likely forage similar resin plants. Besides, internally nested modules found in the total multilayer and Neotropical layer could emerge from consumer adaptations to forage on a particular resource that also favor the use of other similar

Table IV The very conservative multilayer structure from Dataset 3 (no palynological data, four layers, and plants at genus level)

	Obs	E_{free}	Z_{free}	P_{free}	E_{res}	Z_{res}	P_{res}
Multilayer							
Q	0.62	0.39	18.25	**< 0.001**	NA	NA	NA
NODF	0.08	0.12	-1.55	**< 0.001**	0.9	-9.99	0.17
NODFsm	0.29	0.11	21.94	**< 0.001**	0.32	13.61	0.15
NODFdm	0.04	0.12	-5.83	**< 0.001**	0.04	-9.22	0.36
Neotropical layer							
Q	0.65	0.52	6.03	**< 0.001**	NA	NA	NA
NODF	0.10	0.13	3.99	0.06	0.10	0.87	0.47
NODFsm	0.43	0.13	39.65	**< 0.001**	0.46	34.58	0.31
NODFdm	0.06	0.13	-0.22	**< 0.001**	0.05	-1.27	0.27
Indo-Malayan layer							
Q	0.45	0.34	8.09	**< 0.001**	NA	NA	NA
NODF	0.19	0.24	10.28	**0.02**	0.18	-0.71	0.09
NODFsm	0.27	0.17	19.84	**< 0.001**	0.25	13.69	0.27
NODFdm	0.16	.27	7.68	**< 0.001**	0.15	-5.88	**0.05**
Australian layer							
Q	0.11	0.12	-0.92	0.3	NA	NA	NA
NODF	0.26	0.37	19.91	0.12	NA	NA	NA

Significant P values are in bold

E expected score, *Q* modularity, *NODF* nestedness in the whole network, *NODFsm* nestedness within the same module, *NODFdm* nestedness in different modules, *Obs* observed values. Note that NODFsm and NODFdm are inapplicable for the Australian layer due to the non-significant modularity

resources, but hinder using dissimilar resources (Pinheiro et al. 2016, 2019, 2022; see also Crestani et al. 2019; Mello et al. 2019; Queiroz et al. 2021; Felix et al. 2022a, b). However, given that we found evidence either favoring or contradicting the detection of a compound architecture in resin foraging networks, we should interpret our findings cautiously based on two characteristics of the current available data. According to the IHS, modular topologies are expected for networks with high resource heterogeneity. In addition, when those systems are also larger and have been well sampled, compound topologies might also be detected (Pinheiro et al. 2019; Mello et al. 2019). Considering those conditions, first, sample size is reduced when we consider each layer separately, exclude palynological data, or use only data of plants identified at genus level. Second, using palynological data in the total multilayer network could mix up different types of interactions (pollination and resin collection) and thus the compound topologies may be resulting from contamination, as suggested by Layek et al. (2023). As such, forthcoming resin foraging data from chemical and fieldwork methods with plants at genus or species level should be appended to our very conservative dataset to conduct a new test of the IHS in the future.

Currently, most data available on resin interactions by stingless bees is based on plant identification at family and genus level. According to Guimarães Jr. (2020), "there is no intrinsically correct scale for describing the structure of ecological networks [...] because the appropriate spatial, temporal, and organizational scales depend on the question being addressed". Interactions may scale up to form new patterns in upper levels of taxonomic resolution and give fingerprints of processes

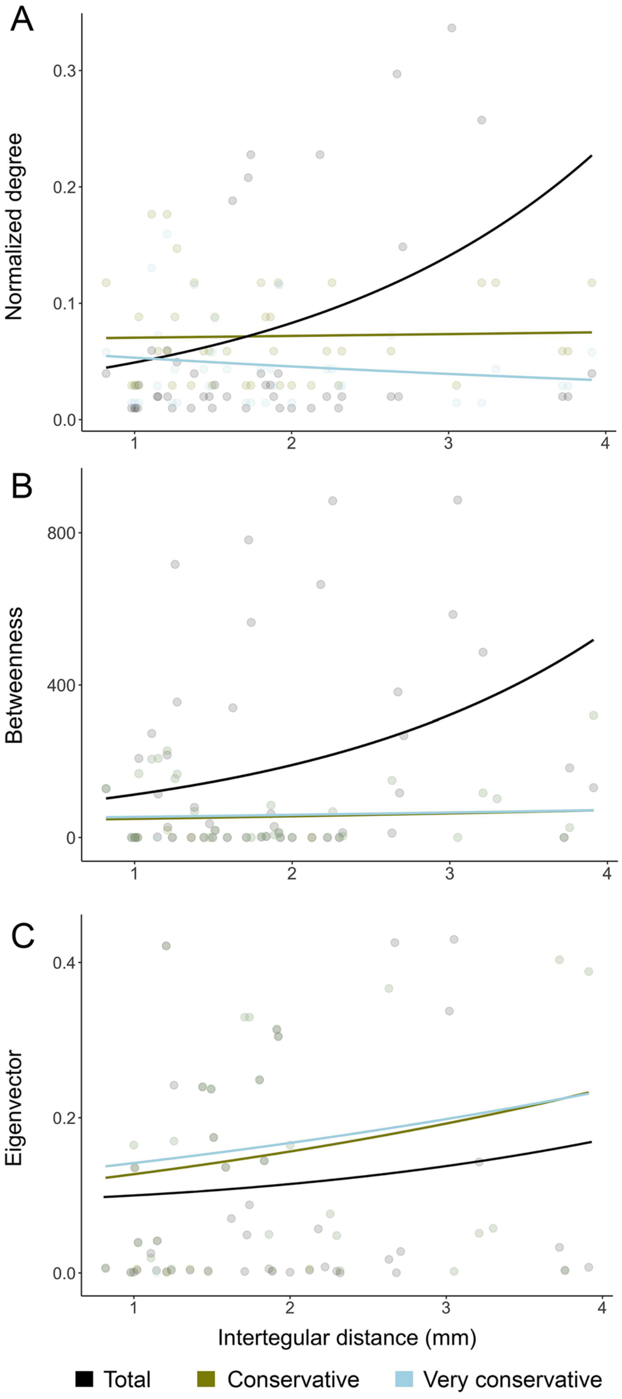

Figure 5. Effect of body size (using intertegular distance as a proxy) on centrality metrics. (A) Normalized degree; (B) betweenness centrality; and (C) eigenvector centrality. See Results for details.

not detectable in lower organization levels (Niquil et al. 2020). Accordingly, plants identified at family level may indicate patterns at a macroevolutionary scale (Braga et al. 2018; e.g. fingerprints from resin foraging interactions between ancestral plants and bees). However, plants identified at genus or species level may be a better approach to indicate the current ecological patterns found in nature. In this regard, although a compound topology is only found in the total multilayer network (Dataset 1), we still found a modular structure in the conservative (Dataset 2) and very conservative (Dataset 3) multilayer networks, as deduced from the IHS. Noteworthy, when we separate the Indo-Malayan-Australasia into different regions and increase taxonomic resolution of plants from family to genera in the very conservative analysis, an association between phylogeny and interactions, layers, and modules is still found. That is, closely related species tend to interact with similar plant genera from the same module and from the same biogeographical region.

On the node level, morphological traits might influence the centrality of bees, which is consistent with the ecomorphology theory (Stevan 1983). As predicted, we found that body size is positively correlated with eigenvector centrality in the conservative and very conservative network. This means that larger bees forage resins from either a high number of plant genera or a high number of highly connected plants. Thus, larger bees with a broader flying range (Araújo et al. 2004; Greenleaf et al. 2007; Raiol et al. 2021) and a stronger bite to stimulate resin secretion (Schwarz 1948; Howard 1985) could access more diverse plant sources. On the other hand, smaller bees could be constrained by the accessible plants close to their nest that are naturally secreting exudates, since they are not expected to mechanically induce resin secretion. In addition, small bees are less likely to use highly connected plants in the network, suggesting that they do not benefit from resin secretion induced by other bees or that they are excluded from the most explored resources. This must be experimentally tested in the future.

Previous studies testing the relationship between body size and centrality of plant–bee pollination networks made by different bee groups are either consistent (Smith et al. 2019) or inconsistent (Raiol et al. 2021) with our results for resin foraging interactions. Raiol et al. (2021) found that larger bees from the tropics were more specialized in plant-bee networks, which could be related to their potential to access the most rewarding resources or to avoid competition. In contrast, our results suggest that large bees do not avoid competition for resin collection, since they interact with highly connected plants which likely provide rewarding resources (in quantity or quality; Armbruster 1984). In addition, resin diversity is known to be beneficial for bees, with synergistic defensive effects when different sources are combined (Drescher et al. 2014). Future studies could thus explore the factors influencing resin foraging and contrast availability versus benefits for stingless bees.

4.2. Systematic synthesis and future directions

Our systematic literature synthesis highlights the most visited botanical sources of resins in Meliponini. Although botanical sources of resins have been determined for several stingless bee species, our synthesis revealed that 29 out of 48 bee genera have no data on the botanical sources of resins. Additionally, six bee species (*Lestrimelitta limao, Melipona flavolineata, Melipona mandacaia, Nannotrigona testaceicornis, Trigona recursa,* and *Trigona ungulata*) have botanical sources determined only through palynological data, but chemical and fieldwork data should be obtained as well. Moreover, gaps in knowledge are concentrated in the Afrotropics (only a single African bee is present in our dataset, *Axestotrigona ferruginea*; Popova et al. 2021), which precludes any analysis for this biogeographical region. In contrast, several Neotropical studies seem concentrated in Brazil, especially in the Maranhão State. As such, the continuous efforts to collect resin foraging interactions data for the above-mentioned genera and those endemic to the Afrotropics or from Neotropical countries other than Brazil should be priorities to advance our knowledge on resin collection of stingless bees.

Among the seven most frequently visited resin sources for stingless bees, Anacardiaceae, Euphorbiaceae, Fabaceae, and Myrtaceae are also reported as the most frequently visited for flower resource collection (Bueno et al. 2023). The partial overlap between food and resin networks could indicate that foraging in general may be affected by similar eco-evolutionary mechanisms in stingless bees. Despite this congruence, it is not expected that the same individual collects food and resin from the same plant, due to individual specialization in foraging (Sommeijer et al. 1983). Trees were the most frequently reported plant type explored for resin collection, as suggested by previous studies (Leonhardt et al. 2011; Chui et al. 2023). Even though shrubs, herbs, and other growth forms were also visited for resin collection, our results indicate that trees are highly relevant as resin sources for stingless bees, which can help future conservation plans that also consider non-floral resources (Requier and Leonhardt 2020).

Each method of botanical source determination has its pros and cons. Chemical and fieldwork methods are advantageous due to a high taxonomic resolution (plants are usually identified at genus or species level), but the mean number of botanical sources of resins identified per study is usually low (e.g. Chui's et al. 2023 fieldwork focused on a single plant family). In contrast, palynological studies are characterized by the identification of grains from several species of plants stuck in propolis or resin from a few bee species (e.g. Barth 2006 found 44 families of plants in propolis and geopropolis samples from six species of Meliponini), generating large datasets. Among some disadvantages, palynological studies usually identify plants at the family level (low taxonomic resolution), and sometimes pollen can wrongly derive from three types of contaminations. Specifically, (1) nectar/pollen foragers may become latex/resin foragers, changing their social functions but leaving remnant pollen from pollination interactions within the corbicula (Layek et al. 2021); (2) pollen adhered to the internal tunnel surface of nests can stick to resins from returning foragers (Layek et al. 2023); and (3) pollen is added to resins during propolis production (Armbruster 1984). These behavioral processes underlying pollen contamination in resins are the reasons why we contrasted total and conservative networks.

Based on our extensive review, we recommend below four future directions to advance knowledge on resin foraging interactions. First, methods other than chemical, fieldwork, and palynological analyses could be employed in the future. For instance, metagenomics may sequence millions of environmental DNA fragments (eDNA reads) present in resins and map them against a database of local bees to determine foraging interactions (Wilson et al. 2013). Second, future efforts could also be directed to increase chemical studies, since resins have been chemically described for 49 out of ~ 600 spp. of Meliponini (data available for only 15 out of 52 genera). Third, among resin sources found in our review, there are currently native and introduced plants. For instance, Kustiawan et al. (2015) reported *Wallacetrigona incisa* foraging resins from *Anacardium occidentale* (cashew tree) and *Mangifera indica* (mango), which are two plants introduced for cultivation in Samarinda, Indonesia. Likewise, *Trigona spinipes* has been reported to forage resins from *Corymbia citriodora*, which is native from Australia and introduced in Brazil (Freitas et al. 2008). Further studies identifying more plants at species or genus level could improve our classification of plants as native or introduced to understand the effect of exotic plants in resin foraging networks. Finally, the plant organ from which resins are collected has been poorly documented (Table S4). This could be relevant to distinct commensalistic (e.g. when resins are exudates collected from tree bark and leaves, presumably increasing bee—but not plant—fitness) from mutualistic interactions in resin collection (e.g. when resins are collected as flower resources, resins are suggested to be beneficial for plants by enhancing the attractiveness of flowers; Armbruster 1984). Future fieldwork studies should record the plant organ from which resins are collected, and when enough data will be available to distinguish commensalistic from mutualistic interactions, multilayer networks may be employed to consider each type of interaction as different layers of this complex system (e.g. Mello et al. 2019).

5. CONCLUSION

Using a systematic literature search and multilayer networks, here we explored the ecological patterns and underlying processes that shape the resin foraging interactions made by stingless bees. We highlighted the importance of further investigating resin interactions because they are involved in key mechanisms of stingless bee communication, nest building, and defense against predators and pathogens (Shanahan and Spivak 2021), and sometimes also seed dispersal (Bacelar-Lima et al. 2006). Furthermore, there is a growing interest in exploring the pharmacological properties of propolis produced by stingless bees (Popova et al. 2021), so unveiling the botanical sources of resins may help advance this field. Despite these factors, there are still large gaps in knowledge, so future studies could invest in recording these interactions for poorly known groups, preferably employing chemical and fieldwork methods, which are more reliable. Encouraging records of resin collection through citizen science projects could also be promising (Koffler et al. 2021). Thus, further studies on the neglected topic of resin interactions may expand our knowledge on patterns and mechanisms underlying bee interactions beyond pollination, while also contributing to potential applications on beekeeping, health, and conservation.

SUPPLEMENTARY INFORMATION

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AUTHOR'S CONTRIBUTIONS

Conceptualization: DYMN and SK. Methodology: DYMN, SK, and MARM. Formal analysis and investigation: DYMN. Writing – original draft preparation: DYMN. Writing – review and editing: SK, MARM, and TMF. Funding acquisition: TMF. Supervision: SK.

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DATA AVAILABILITY

Body size data are provided in Supplementary Information. Binary incidence matrices and phylogenetic tree are available at https://github.com/danimelsz/ResinNetwork.

CODE AVAILABILITY

R codes are available at https://github.com/danimelsz/ResinNetwork.

DECLARATIONS

Ethics approval This study only used literature data and thus an ethics approval is not applicable.

Consent for publication Not applicable.

Competing interests The authors declare no competing interests.

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