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RESEARCH ARTICLE

Flowers with poricidal anthers and their complex interaction networks—Disentangling legitimate pollinators and illegitimate visitors

José N. Mesquita-Neto^{1,2} | Nico Blüthgen³ | Clemens Schlindwein¹

¹Departamento de Botânica, Universidade Federal de Minas Gerais, Belo Horizonte, Minas Gerais, Brazil

²Laboratorio de Ecologia de Abejas, Departamento de Ciências Biológicas y Químicas, Faculdad de Ciencias Básicas, Universidad Católica del Maule, Talca, Chile

³Ecological Networks, Department of Biology, Technische Universität Darmstadt, Darmstadt, Germany

Correspondence

Clemens Schlindwein Email: schlindw@gmail.com

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Abstract

- In flowers with poricidal anthers, pollen is not freely accessible and legitimate access is restricted to bees capable of vibrating the anthers. Despite the protection of pollen provided by poricidal anthers, numerous illegitimate, non-buzz-pollinating flower visitors rob pollen.
- 2. We aimed to quantify the influence of functional groups of floral visitors and illegitimate interactions on the network structure to disentangle the flower visitor network into its mutualistic and antagonistic components.
- 3. We delimited three functional groups of bees based on their pollen collection behaviour in poricidal flowers: large bees that vibrate entire flowers in a single buzzing position (flower buzzing), bees vibrating single anthers in different positions (anther buzzing) and non-vibrating flower-damaging or gleaning bees (nonbuzzing). Moreover, we characterized legitimate and illegitimate interactions of co-occurring and co-flowering plants and their flower visitors based on the stigma contact during a visit. Since we independently assessed the type of interaction with bee-plant species combinations, we were able to include the behavioural variations of each bee species across different flowers.
- 4. The networks were modular, with stronger interactions within subsets of species than among the subsets. All modules included a combination of flower-, anther-and non-buzzing bees, and mutualistic and antagonistic networks were intermingled. Seven bee species shifted their roles across plant species. Specialization in the subset of interactions with pollinators was higher than the overall visitation network. Flower-buzzing bees were more specialized than anther-buzzing and non-buzzing bees, which used virtually all poricidal flowers similarly.
- 5. Although plants with poricidal anthers shared a specialized mechanism of pollen release, their pollinators were highly dissimilar and formed compartments of interacting species. The interaction-level approach taken in our study confers a high specificity to the pollinator network, leading to a more complex and realistic picture of mutualistic webs versus its embedded florivory, which are otherwise confounded in pooled networks across flower visitors.

KEYWORDS

bee-plant interactions, buzz pollination, ecological Networks

1 | INTRODUCTION

Pollen, one of the richest sources of protein produced by plants. is a valuable resource and motivation for animals to visit flowers (Russell, Golden, Leonard, & Papaj, 2015). Pollen consumption or collection is self-motivated and not necessarily related to pollination (Hargreaves, Harder, & Johnson, 2009; Westerkamp, 1997a). To avoid excessive pollen loss, plants commonly present strategies to limit pollen consumption by floral visitors (Hargreaves et al., 2009; Westerkamp & Claßen-Bockhoff, 2007; Westerkamp, 1997b). In flowers with poricidal anthers, pollen is not freely accessible and its removal requires buzz-pollinating bees capable of anther vibration (Buchmann, 1974; De Luca & Vallejo-Marín, 2013; Larson & Barrett, 1999a; Michener, 1962). This restriction of pollinators facilitates the evolution of floral adaptations that enhance pollination success (e.g., enantiostyly and heteranthery; Luo, Zhang, & Renner, 2008; Vallejo-Marín, Silva, Sargent, & Barrett, 2010; Westerkamp, 2004). Thus, poricidal plants possess a highly specialized and elaborate anther morphology, in which they protect and hide the pollen (Arceo-Gómez, Martínez, Parra Tabla, & García-Franco, 2011; Buchmann & Hurley, 1978), and occur in non-related plant lineages of 65 families and represent 8%-10% of angiosperms (Buchmann, 1983).

The floral constraint imposed by poricidal anthers benefits vibrating bees by reducing the number of competing pollinators (De Luca & Vallejo-Marín, 2013). Floral sonication probably arose in a common ancestor of bees during Early Cretaceous and evolved about 45 times within bees (Cardinal, Buchmann, & Russell, 2018). Possible bee pollinators able to collect pollen by anther vibration occur within the tribes Centridini, Euglossini, Xylocopini, Bombini (Apidae), Augochlorini (Halictidae) and Caupolicanini (Colletidae) (Buchmann, 1983; Michener, 1962), among others. Large-sized bees, in general, are recognized as effective pollinators of poricidal flowers because they touch the stigma while buzzing flowers, remove more pollen per visit and intensely fly among conspecific plants (Buchmann & Hurley, 1978; Burkart, Schlindwein, & Lunau, 2014; Mesquita-Neto, Costa, & Schlindwein, 2017; Renner, 1983; Solís-Montero & Vallejo-Marín, 2017).

Despite the protection of pollen provided by poricidal anthers, numerous buzz-pollinated plant species suffer pollen theft by small bees that do not vibrate flowers. These bees cut the anthers or gnaw holes into them to remove pollen with their mouthparts (Gross, 1993; Rego, Oliveira, Jacobi, & Schlindwein, 2018; Renner, 1983). Other, usually small, bees pick up pollen grains adhering to the flower surface after visits of vibrating bees (e.g., Renner, 1983; Gross, 1993). Moreover, some small bees buzz only single anthers and, in general, do not contact stigmas during their flower visits. All these flower-visiting bees are non-effective pollinators of plants with poricidal anthers (Gottsberger & Silberbauer-Gottsberger, 1988; Gross, 1993; Hargreaves et al., 2009; Rego et al., 2018; Renner, 1983; Solís-Montero & Vallejo-Marín, 2017; Solís-Montero, Vergara, & Vallejo-Marín, 2015). Thus, we can delimit three functional groups of bees based on their pollen collection behaviour in poricidal flowers: (a) large buzzing bees that vibrate entire flowers,

(b) bees vibrating single anthers and (c) non-vibrating flower-damaging or gleaning bees.

The great diversity of buzz-pollinated plants and their bee pollinators in tropical regions offers an opportunity to characterize, in situ, the interactions between both groups. We conducted intensive sampling of flower visitors to plant species with poricidal anthers and defined the different functional groups of the bee species. This sampling design was chosen to avoid missing and forbidden links (Jordano, Bascompte, & Olesen, 2003; Olesen, Dupont, Hagen, Trøjelsgaard, & Rasmussen, 2011) due to morphological constraints, spatio-temporal uncoupling and phenological mismatching among plants and flower visitors (e.g., phenophases of potentially interacting species do not overlap; species do not co-occur in space or time). Thus, the numbers of interactions likely mirror the preferences of the bees, including unobserved links that suggest that bees avoid plant species.

Here, we aimed to quantify the influence of functional groups of floral visitors and illegitimate visits on network structure, disentangling a flower visitor network into its mutualistic and antagonistic components. We focused on the following questions: Do plant species share flower visitors? How does network structure change if illegitimate visitors are included? Do different functional groups of bee visitors also show different levels of specialization in their interactions with plant species with poricidal anthers? We expected that, (a) plant species with poricidal anthers share pollinators due to their local co-occurrence and overlap of flowering (Hypothesis 1); (b) illegitimate interactions show higher generalization than legitimate interactions because the behaviour of non-buzzing bees on poricidal flowers is not related to buzz pollination (Hypothesis 2). Thus, interaction legitimacy was independent of the functional roles. The first is related to the consequences for plant reproduction and the second to the pollen collection behaviour.

2 | MATERIALS AND METHODS

2.1 | Study site and plant species

Fieldwork was conducted in the "Parque Estadual do Rio Preto" nature reserve in the municipality of São Gonçalo do Rio Preto, Minas Gerais State, Brazil (18°05'28.3"S, 43°20'29.2"W), from September to December 2014 and 2015. The climate is tropical with dry (April-September) and rainy (October–March) seasons and a mean annual temperature ranging from 15 to 35°C (Aw, Köppen's ranking; Peel, Finlayson, & McMahon, 2007). The vegetation of the reserve is characteristic of the Cerrado (Brazilian Savannah). The study site is characterized by sandy soil with a diversified plant cover composed mainly of Melastomataceae, Fabaceae, Myrtaceae, Lythraceae, Vochysiaceae, Eriocaulaceae, Cyperaceae, Xyridaceae and Poaceae, among other families (IEF, 2004).

An intense sampling effort was done during the period of coflowering of plants with poricidal anthers. We included plant species in a radius of about 500 m from a given point (18°05'28.3"S,

43°20'29.2"W). The criteria for choosing the sampling area was its richness of co-flowering plant species with poricidal anthers. We selected 10 co-flowering plant species from three families with poricidal anthers that were represented by at least 10 individuals at the site (Figure 1): Chamaecrista debilis (Vogel) H.S.Irwin & Barneby (Fabaceae), shrub, up to 120 cm in height, yellow asymmetric flowers (diameter 19 mm); Chamaecrista desvauxii (Collad.) Killip. (Fabaceae), subshrub, up to 50 cm in height, yellow asymmetric flowers (diameter 29 mm); Comolia stenodon (Naudin) Triana (Melastomataceae), subshrub, up to 50 cm in height, purple zygomorphic flowers (diameter 21 mm): Lavoisiera imbricata DC., shrub (Melastomataceae). up to 150 cm in height, pink-white zygomorphic flowers (diameter 19 mm); Leandra aurea (Cham.) Cogn. (Melastomataceae), shrub, up to 60 cm in height, purple zygomorphic flowers (diameter 6 mm); Macairea radula (Bonpl.) DC. (Melastomataceae), shrub, up to 250 cm in height, pink-white zygomorphic flowers (diameter 19 mm); Miconia albicans (Sw.) Steud. (Melastomataceae), shrub, up to 90 cm in height, white zygomorphic flowers (diameter 9 mm); Pterolepis alpestris Triana (Melastomataceae), herb, up to 40 cm in height, purple zygomorphic flowers (diameter 21 mm); Tococa guianensis Aubl. (Melastomataceae), shrub, up to 200 cm in height, white actinomorphic flowers (diameter 15 mm); Ouratea floribunda Engl. (Ochnaceae), shrub, up to 250 cm in height, yellow actinomorphic flowers (diameter 17 mm).

2.2 | Functional groups of bees

In 10 labelled plants per species, floral visitors were sampled and had their behaviour recorded on 25 sunny days in 2014 and 31 sunny days in 2015, from 04:30 to 19:00 hr. A collector with an entomological net remained for about 15 min at a single individual plant of a species, sampling all flower visitors. After this time interval, the collector passed to another individual of another plant species and so on throughout the day. We performed a total of 672 hr of sampling effort with around 67 hr per plant species.

We delimited three functional groups of visiting bees based on their pollen collection behaviour, according to Renner (1983), Solís-Montero et al. (2015) and our own observations: (a) *flower-buzzing* bees: bees buzz the entire flower applying one or more buzzes; these bees vibrate all anthers in a unique position; (b) *anther-buzzing bees*: bees buzz single anthers or a set of a few anthers of a flower; these bees change their position in the flower between buzzes; (c) *nonbuzzing bees*: bees collect pollen without buzzing the anthers; these bees may collect pollen with their mouthparts, after cutting or perforating anthers, or by gleaning residual pollen that adhered on different floral parts after pollen extraction by vibrating bees.

We independently assessed the functional role of a given bee visit on a given plant species. During each flower visit, we noted the pollen extraction behaviour (entire flower buzzing, single anther buzzing or non-buzzing). Thus, the same bee species could show different functional roles during different visits on the same plant, and/or among different individuals of the same plant species and/or among different species. After the bee visits, we collected and killed the individuals to identify the species in the laboratory. When we were not able to collect an observed individual bee, the data were not considered. The interaction data were assembled into a quantitative bipartite network using the bipartite package (Dormann, 2011; Dormann, Gruber, & Fründ, 2008) in R version 3.3.3 (R Core Team, 2017). Each pairwise interaction frequency in the network represents the number of visits of a given floral visitor to a poricidal plant species. The nodes of bee species were classified according to the three functional groups.

To calculate the effect of each functional group of visitors on plant specialization, we compared the complementary specialization index (d' index) of the plant species across the three subnetworks (i.e., network that only includes flower-buzzing, anther-buzzing, or non-buzzing interactions). The d' index (Blüthgen, Menzel, & Blüthgen, 2006) describes each species' deviation in flower visitation from the distribution of all visitors. High values, closer to 1, indicate strong niche partitioning and specialization. We calculated the mean d' of all plant species, with each species being weighted by its total number of observations.

A Generalized Linear Model (GLM) with quasibinomial distribution was constructed to search for any significant influence of visitor groups on variation in plant species d'. The GLM was calculated using the *stats* package in R version 3.3.3 (R Core Team, 2017).

Chamaecrista debilis Comolia stenodon Lavoisiera imbricata Leandra aurea Macairea radula Miconia albicans Pterolepis alpestris Ouratea floribunda Tococa guianensis

Chamaecrista desvauxii



FIGURE 1 Floral phenology of the poricidal plants co-occurring in the *Rio Preto* park in Cerrado, Brazil. Note that plants are co-flowering during the sampling period of our study (Sept-Dec)

2.3 | Legitimate and illegitimate interactions

In addition to pollen collection behaviour, we also noted if a bee contacted the stigma during each flower visit. When a visitor touched the stigma, we considered the interaction legitimate, and illegitimate when it did not. We independently assessed the legitimacy of the interaction for each bee-plant species combination, as we did to evaluate the functional role (previous section). However, interaction legitimacy was independent of functional roles. The interaction legitimacy is related to stigma contact and functional roles to pollen collection behaviour of bees. Thus, a same bee species can be legitimate visitor of a given plant species and non-buzzing bee, for example.

To simulate the effect of incorporating illegitimate interactions on the set of interactions, we built two different bipartite networks grouping the interactions according to legitimacy: (a) the visitation network, including all flower visits, legitimate and illegitimate; and (b) the mutualistic subnetwork, including only legitimate visits. We evaluated variation in the network metric values and its significance in relation to the null model. Thus, for the visitation and mutualistic networks, we calculated the following metrics to illustrate structural properties: (a) Connectance: the ratio between the number of realized links to the number of possible links in the network; (b) Niche overlap: measure of similarity in interaction pattern between species. Niche overlap was calculated using the Morisita-Horn index, which varies from 0 to 1 (Horn, 1966); (c) Nestedness: quantifies the chances of the network to present a nested pattern wherein specialists interact with proper subsets of the species interacting with generalists (Bascompte, Jordano, Melián, & Olesen, 2003). We calculated the weighted nestedness using wNODF (Almeida-Neto & Ulrich, 2011); (d) Complementary specialization: estimated by the H_2' index, which measures specialization in quantitative networks (Blüthgen et al., 2006). Specialization and generalization were defined by the number of interactions established by the species in relation to all possible interactions in the system. H_2' describes how much the interactions of each species differ from those of other species in the network, which has the advantage of not being influenced by network size and number of observations per species (Blüthgen, Menzel, Hovestadt, Fiala, & Blüthgen, 2007); (e) Modularity: quantifying the prevalence of interactions within modules (i.e., subunits in the community), in relation to the interactions among modules. Weighted Modularity (Q,,) was estimated using the QuanBiMo optimization algorithm (Dormann & Strauss, 2014). This algorithm computes modules based on a hierarchical representation of species link weight and optimal allocation to modules through swapping in a "Simulated Annealing-Monte Carlo" approach (Dormann & Strauss, 2014). The level of modularity (Q) measures the extent to which species interact mainly within their module, ranging from 0 to 1. As the QuanBiMo algorithm is stochastic, the values found can be slightly different between runs; we accounted for this by choosing the higher values from 10 independent runs set to 10^7 swaps to each network (see, for example, Maruyama, Vizentin-Bugoni, Oliveira, Oliveira, & Dalsgaard, 2014; Vizentin-Bugoni et al., 2016). Values of Q in the randomizations

were then used to calculate the *z*-score, which is the number of standard deviations a datum is above the mean of the 100 randomized networks using the functions r2dtable and vaznull in the bipartite package (Dormann et al., 2008). *Z*-score values of \geq 2 were considered significantly modular (Dormann & Strauss, 2014).

The significance of the Connectance, Niche Overlap, Nestedness and H_2' were assessed by comparing the observed values to those obtained by 1,000 randomized networks generated by the null model r2dtable (Patefield, 1981) in the R-package bipartite (Dormann et al., 2008). We consider the r2dtable algorithm more adequate in our study because it maintains the marginal totals and thus the total number of observations per species (which directly limit the number of links per species and most other metrics). This algorithm is widely used in other studies, making our results comparable to other pollination networks. Metric values were considered significant if they did not overlap the 95% confidence intervals of the randomized values. Although no formal tests were conducted to compare the metric values across different types of interactions, which were impaired by the lack of replicates, these procedures are consistent with those of previous studies, which compared subsets of interactions (e.g., illegitimate and legitimate visitors) of the same network (Genini, Morellato, Guimarães, & Olesen, 2010; Maruyama, Vizentin-Bugoni, Dalsgaard, & Sazima, 2015; Yoshikawa & Isagi, 2013).

2.4 | Species-level analysis

We calculated *z*- and *c*-values to describe the role of each species in the modularity of the network (Guimera & Amaral, 2005; Olesen, Bascompte, Dupont, & Jordano, 2007). The *z*-value refers to within-module and the *c*-value to the among-module connectivity, which defines how the species is positioned within its own module and with respect to other modules. Following Olesen et al. (2007), we sorted all species into: (a) peripheral species (low $z \le 2.5$; low $c \le 0.62$), have few links inside its own module and rarely any to other modules; (b) module hubs (high z > 2.5; low $c \le 0.62$), species that should be important for the coherence of their own modules; (c) connectors (low $z \le 2.5$; high c > 0.62), species that should be important for the coherence of their own modules; and (d) network hubs (high z > 2.5; high c > 0.62) should be important for the coherence of both the network and its own module.

3 | RESULTS

3.1 | Functional group level

The poricidal plant flower visitor network at the study site comprised 584 interactions among nine poricidal plant and 55 bee species (Figure 2; Supporting Information Table S1). No floral visitors were recorded on *L. aurea* flowers. Flower buzzing characterized the majority of the interactions with poricidal plants (54.5%) followed by non-buzzing (24.4%) and anther-buzzing (24.1%) flower visits. Anther buzzing and non-buzzing together accounted for 45.5% of the visits (266 visits). Non-buzzing visits



FIGURE 2 Bipartite network representing the interactions of poricidal plant species and bee visitors in Cerrado, Brazil. The bottom nodes (grey) representing the poricidal plant species and the upper coloured nodes represent the species of flower-visiting bee. Links are coloured according to the bee functional group on flowers: flower-buzzing bees (blue); anther-buzzing bees (green); non-buzzing bees (red). Note that visitor nodes with two colours are bee species that belong to different functional groups in different plant species

were composed of 114 destructive visits (90.4%) and 11 gleaning visits (9.6%).

Not all species of bees belonged to a single functional group. The species of *Bombus* spp., *Melipona quinquefasciata*, *Augochloropsis* sp. 4 and *Pseudaugochlora pandora* (nodes with two different colours in Figure 2) shifted their behaviour across different plant species. They collected pollen by buzzing entire flowers (flower buzzing) in one species and by anther buzzing in another (see details in Species level).

After excluding flower-buzzing interactions from the network, the complementary specialization (d' index) decreased significantly. Non-vibrating bees reached the lowest d' plants, close to zero (Figure 3). Anther buzzing had a d' index intermediate between flower-buzzing and non-buzzing bees.

3.2 | Legitimate and illegitimate visits

Both the visitation network and the mutualistic subnetwork showed niche overlap and nestedness (NODF) lower than expected by chance (<95% lower confidence interval of the null model) and a higher degree of complementary specialization H_2' (Table 1). In addition, the networks were modular, with interactions stronger within subsets of species than among subsets, although visitation and mutualistic networks contained plant species placed into different modules (Figure 4). However, modularity increased in the mutualistic subnetwork ($Q_w = 0.46$) in relation to the visitation network ($Q_w = 0.36$) with a higher *z*-score (pollination network: r2d-table: 22.91; vaznull: 934.05; visitation network: r2dtable: 10.76; vaznull: 41.00) with more modules and higher H_2' (Figure 2; Table 1).



FIGURE 3 Box plots of *Complementary Specialization* of plants (*d'* index) related to functional groups of bees (flower-buzzing, anther-buzzing and non-buzzing subnetwork). Different letters indicate significant differences ($p \le 0.01$) by Generalized Linear Model (GLM) with *quasibinomial* distribution

All modules contained a mix of flower-buzzing, anther-buzzing and non-buzzing bees, without apparent prevalence of one of the groups (Figure 4). Flower-buzzing, anther-buzzing, and non-buzzing bees had legitimate visits, touching the stigma in 97%, 28% and 8% of all visits, respectively.

Network metrics	Visitation network			Mutualistic subnetwork		
	Observed index value	95% lower Cl	95% upper Cl	Observed index value	95% lower Cl	95% upper Cl
Niche overlap	0.23	0.56	0.61	0.25	0.52	0.54
H ₂ '	0.36	0.10	0.10	0.45	0.12	0.13
Weighted NODF	21.02	39.81	40.80	18.23	37.83	38.96
Connectance	0.29	0.40	0.41	0.28	0.41	0.42

TABLE 1 Network metrics for the floral visitation network, in which all bee visits (legitimate and illegitimate) with poricidal flowers were included and for the mutualistic subnetwork, in which only legitimate visits were considered

Note. Metric values were considered significant if they did not overlap the 95% confidence intervals (CI) of the randomized values in 1,000 networks generated by the null model r2dtable. The networks are significantly non-random when the CIs do not overlap with the observed values.



FIGURE 4 Modules in the poricidal plant-bee visitor network from Rio Preto Park, Cerrado, Brazil. The top matrix, the entire visitation network, includes all interactions; the bottom matrix, mutualistic subnetwork, excludes illegitimate interactions. The visitation network was modular ($Q_w = 0.36$) and with a "high" z-score (r2dtable: 10.76; vaznull: 41.00). However, modularity increased in the mutualistic subnetwork ($Q_w = 0.46$), with a higher z-score (r2dtable: 22.91; vaznull: 934.05). Note that the number of modules and their compositions varies among the networks

The submodules in the mutualistic network (Figure 4, blue squares) revealed which plant species had a set of more related legitimate visitors (Figure 4). However, the number of legitimate visitors in these sets varied among plant species. Three plant species had only one legitimate visitor species each in their submodules (*C. debilis*, *M. albicans* and *L. imbricata*). Three other species had two to four legitimate visitor species in their modules (*C. stenodon*, *P. alpestris* and *T. guianensis*). Chamaecrista desvauxii, *M. radula* and *O. floribunda* had five or more legitimate visitor species.

3.3 | Species level

Most bee species in the visitation network (83%) had low withinmodule (z) and among-module (c) connectivity values, meaning that they showed preference to distinct poricidal species with few links, mostly within their module (peripheral roles). Only nine of the 55 bee species were generalist species (interactions with many plants with poricidal anthers), with either high z- or c-values (Figure 5). Most generalists were connector species (low z, high c) that link modules but which belong to none. None of the non-buzzing bees was a connector (Figure 5). Augochloropsis sp. 4 was identified as a module hub species, with many links within-modules (high z) and few among-modules (high c). Trigona sp. 1 and M. quinquefasciata were visitation network hubs (high c and z). Trigona sp. 1, an illegitimate visitor, damaging anthers without contacting the stigma, interacted with most plant species (8 spp.) and was responsible for the majority of interactions with flowers of the different plant species in the visitation network (Figure 2).

The mutualistic network did not show network hubs, but the proportion of specialist bee species was similar to the visitation network (85%). Five species were generalists, and the two *Bombus* species showed single anther buzzing in other plant species. Two species were module hubs (*Bombus morio*, *Centris fuscata*) and three were connectors (*B. pauloensis*, *C. tarsata*, *Euglossa melanotricha*; Figure 5).

Bombus spp., M. quinquefasciata, Augochloropsis sp. 4 and P. pandora had varied roles in flowers. Their buzzing behaviour and legitimacy of interactions differed in different plant species. The bees were flower buzzing in certain plant species but anther-buzzing in others. Bombus brevivillus, B. morio and B. pauloensis were flower buzzing in most plant species, except C. desvauxii, L. imbricata and T. guianensis. However, the species of Bombus touched the stigma of all plant species in most visits (legitimate visitors). Bees of M. quinquefasciata showed anther buzzing in flowers of almost all species, but flower buzzing only in the flowers of O. floribunda. However, M. quinquefasciata touched the stigma in most visits, except in T. guianensis. Bees of Augochloropsis sp. 4 showed flower buzzing and were legitimate flower visitors only in M. albicans. In most plants, Augochloropsis sp. 4 was an anther-buzzing bee. P. pandora visited mainly C. desvauxii but was a legitimate visitor only in flowers of O. floribunda (See Figure 1; Supporting Information Table S1).

4 | DISCUSSION

Although the poricidal co-occurring and co-flowering plant species require a common specialized mechanism of pollen extraction, their pollinators were highly dissimilar and formed compartments of interacting species. As expected, the specialization of the subset of mutualistic interactions was higher than the overall visitation network and constrained pollinators to one or a few per plant species. Flower-buzzing bees made up most of the mutualistic partners of poricidal plants. These bees had many more legitimate visits than anther-buzzing and non-buzzing bees, and were more faithful to a subset of plant species, and thus more likely to promote cross-pollination.

4.1 | Subsets of interacting species

Because plants with poricidal anthers require a common mechanism to extract pollen, we supposed that these plants would share pollinators. However, our results show that the pollinators of these plant species are dissimilar and overlap only partially. Our network was characterized by modular interactions. Modules exist because some species do not interact or interact less with certain species in the community (Dormann & Strauss, 2014). The modules of the mutualistic subnetwork include a range of shared pollinators among few poricidal plants. Besides, each plant species is in a different submodule, with its own core of pollinators. Thus, only a subset of all possible buzzing bees interacts with certain plant species. Other co-flowering species, like those of the genera Acacia, Avicennia, Laguncularia, Ipomoea, Ophrys and Vigna, also avoid pollinator sharing (Gögler et al., 2015; Landry, 2012; Matsumoto et al., 2015; Queiroz, Quirino, & Machado, 2015; Souza, Snak, & Varassin, 2017; Stone, Willmer, & Rowe, 1998). Pollination efficiency should decrease when flowers of different plant species are visited by the same pollinator species in the same period, leading to a reduction in flower visitation rates for each plant species (Fishbein & Venable, 1996; Waser & Fugate, 1986; Waser, 1978a, 1978b) and to heterospecific pollen flow (Ashton, Givnish, & Appanah, 1988). Thus, the vibration requisite is not the ultimate specialization barrier of poricidal plants. Additional interspecific features of the flowers, such as differences in the amount of pollen, floral colour, position, size or shape, and/or morphological/ behavioural characteristics of the bees such as differences in buzzing characteristics (frequency, amplitude, duration), flower handling time or bee size, may mediate the interactions and segregate pollinators among the co-flowering species with poricidal anthers.

Future studies can search for the floral traits and bee characteristics that may modulate their interactions. Buzzing bees can adjust their foraging behaviour and adopt different strategies to maximize resource extraction in a subgroup of plant species (Burkart et al., 2014; Corbet & Huang, 2014; Russell et al., ; Switzer, Hogendoorn, Ravi, & Combes, 2016). Thus, it is likely that each buzzing bee species chooses the most rewarding flowers, relative to their buzzing range, in order to increase pollen release while reducing buzzing effort (Buchmann & Cane, 1989; Harder, 1990; Russell et al.,). New studies can test if the choice by bees of the most rewarding plants, within their buzzing range, is one of the selective forces generating modules of interacting species and specialization in the network.

4.2 | The role of flower-buzzing bees

Flower-buzzing bees had much more specialized interactions with poricidal flowers, a typical feature of pollination networks,

MESQUITA-NETO ET AL.

particularly those of bees (Danieli-Silva et al., 2012; Fründ, Linsenmair, & Blüthgen, 2010; Renner, 2007). Functionally specialized, the behaviour of flower-buzzing bees on flowers is more likely to promote pollination. While buzzing flowers, these bees contact the stigma in most visits because their body size usually exceeds the gap between anthers and stigma (see Liu & Pemberton, 2009; Solís-Montero & Vallejo-Marín, 2017). Flower-buzzing bees, like those of Bombini, Centridini, Euglossini and Xylocopini effectively adjust pollen-collecting behaviour to quickly extract large amounts of pollen from poricidal anthers (Buchmann, 1983; Buchmann & Hurley, 1978; Burkart et al., 2014: De Luca et al., 2013: Renner, 1983: Russell, Buchmann, & Papaj, 2017). Almost all these bee species were network peripherals and visit flowers of a few plant species. If this is true, the absence of any flower-buzzing bee species may affect the reproductive success of one or of a set of plant species because they might be key pollinators in the system. A direct consequence of the decline of flower-buzzing bee species would be the decrease in cross pollen flow. A short-time consequence might be that the less efficient anther-buzzing and non-buzzing bee species could exploit more intensively these flowers, occupying the empty niches left by missing flower-buzzing bees.

4.3 | Illegitimate interactions add generalization to the network

Anther-buzzing and non-buzzing bees were responsible for most illegitimate interactions, which increased the generalization of our network. Anther-buzzing bees are intermediates; they are less specialized and effective pollinators than flower-buzzing bees, but more efficient pollinators than non-buzzing bees. Anther-buzzing bees spent more time in the flowers to apply vibrations on anthers individually, but contact stigmas more rarely and are not very effective pollinators of plant species with poricidal anthers (also see Luo, Gu, & Zhang, 2009; Liu & Pemberton, 2009; Renner, 1983; Wanigasekara & Karunaratne, 2012).

Antagonistic interactions of the abundant non-buzzing bees added generalization to the network due to their indiscriminate visits to flowers of all species. Non-buzzing bees are opportunistic and better connected; they used virtually all flowers similarly. Flowers were left visually damaged after destructive visits of non-buzzing bees. The destructive visits of non-buzzing Trigona bees compromise pollination of plants with poricidal anthers because they reduce the visual attractiveness of the flowers to effective pollinators (Hargreaves et al., 2009) and can directly cause negative impacts on the reproductive success of their host plants (Rego et al., 2018). Bees of this genus are widespread and frequently cited as destructive flower visitors (Biesmeijer & Slaa, 2006; Gross, 1993; Rego et al., 2018; Renner, 1983; Schlindwein, Westerkamp, Carvalho, & Milet-Pinheiro, 2014). Although these bees extract pollen less efficiently, they are numerous in poricidal flowers and must be important competitors for flower-buzzing bees in flowers with poricidal anthers. In our study, the non-buzzing Trigona bees were even the visitation network hub and most common flower visitors. Thus, the frequency of visits in flowers alone is not a sufficient parameter for



FIGURE 5 Bees visiting poricidal plants categorized according to within-module (*z*-value) and among-module (*c*-value) connectivity: (a) peripheral species: with few links inside its own module and rarely any to other modules; (b) module hubs: important to the coherence of its own module; (c) connectors: important to the coherence of its own module; (d) network hubs: important to the coherence of both the network and its own module. Bee nodes in the visitation graphic (left) are coloured according to bee functional group: (a) flower-buzzing bees: bees buzzing all the anthers in a flower at once; (b) anther-buzzing bees: bees buzzing a single or set of anthers in a flower; (c) non-buzzing bees; (d) Flower/anther-buzzing bees: bees with two roles in different plants species (flower buzzing and anther buzzing). In the mutualistic graphic (right) only flower-buzzing visits are considered

understanding the biological role of *Trigona* in our network and it could instead, lead to misinterpretations.

4.4 | Buzzing bees shifted their roles across flowers

Medium-sized bees of Augochloropsis, Pseudaugochlora, Melipona, and Bombus workers were flower buzzing in plant species were they contacted stigmas and anther buzzing in others where they generally did not contact stigmas. Thus, the same bee species can be mutualist of a certain plant species and make floral larceny in another. However, these bees were never observed cutting anthers or picking up pollen from the flower surface.

The relationship between bee size and the distance between anthers can influence the buzzing behaviour of a bee in a flower, as well as its efficiency as a pollinator (Solís-Montero & Vallejo-Marín, 2017). In actinomorphic Solanum-type flowers (Buchmann, 1983; De Luca & Vallejo-Marín, 2013; Vogel, 1981), stamens are grouped to a cone and anther pores are close to each other. In these flowers, smaller bees can also vibrate all anthers at once, and bees are efficient pollinators when their body size exceeds the gap between anthers and stigma (Solís-Montero & Vallejo-Marín, 2017). In our study, two medium-sized bee species are among the main pollinators of *O. floribunda* that fit the *Solanum*-type flower but are antherbuzzing non-pollinators in the zygomorphic flowers of *Chamaecrista* and Melastomataceae, which have stamens distant from each other.

We are aware that restricting the stigma contact of a bee during a flower visit to access its legitimacy is a simplified measure with limited explanatory power and can lead to misinterpretations. In the field, it is not practicable to verify if a given bee individual has deposited conspecific pollen grains on the stigma without removing the stigma and analysing it under the microscope. In plants with poricidal anthers, pollen deposition on the stigma may eventually occur even without the body contact of the buzzing bee to the stigma, allowing fruit set in self-compatible species. On the other hand, in mass-flowering selfincompatible species, floral visitors may contact many stigmas in the same plant, leading to an increase in geitonogamy and a decrease in fruit set (de Jong, Waser, & Klinkhamer, 1993; Pinto, Oliveira, & Schlindwein, 2008; Schlindwein et al., 2014). However, in community studies with a large set of interactions, like here, stigma contact appears to be a powerful simplified measure to filter legitimate flower visits. In addition, the legitimacy of a bee species was based on a set of independent observations with a given plant species.

We conclude that plant species with poricidal anthers in co-occurrence and co-flowering share pollinators, however, subgroups of plant species have a set of interacting pollinators. Although non-buzzing bees are network hubs, they contribute little or even negatively to pollination of species with poricidal anthers and were responsible for most antagonist interactions. Among the bees that remove pollen by vibration, the flower-buzzing bees are the most specialized and efficient pollinators. Differing from our prediction (Hypothesis 1), co-occurring and co-flowering plant species with poricidal anthers only partially share pollinators and have modules of interacting species instead. As predicted, non-buzzing bees have less specialized interactions with poricidal flowers than buzzing bees (Hypothesis 2). Thus, the distinction of antagonistic flower visitors and mutualistic partners, and other aspects of the evolutionary history of the partners (see Renner, 2007), may have implications for generalization and specialization approaches of plant-pollinator interactions. While the majority of angiosperms appear to be pollinated by a great range of taxa (Ollerton, 1996; Waser, Chittka, Price, Williams, & Ollerton, 1996), this high level of observed generalization may be partially a consequence of the incorporation of antagonistic interactions on the set of mutualistic ones. Since we independently assessed the interaction type for bee-plant species combinations, we were able to include the dynamic functions of each bee species across different flowers. The interaction-level approach taken in our study confers a high specificity to the pollinator network, leading to a more complex and realistic picture of mutualistic webs versus its embedded florivory, which are otherwise confounded in pooled networks across flower visitors.

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AUTHORS' CONTRIBUTIONS

J.N.M.-N. and C.S. conceived the ideas and designed methodology; J.N.M.-N. collected the data; J.N.M.-N. and N.B. analysed the data; J.N.M.-N. and C.S. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA ACCESSIBILITY

All data are publicly available in the Figshare Repository (Mesquita-Neto, Blüthgen, & Schlindwein, 2018; https://doi.org/10.6084/ m9.figshare.6073598).

ORCID

José N. Mesquita-Neto D https://orcid.org/0000-0002-1519-638X Nico Blüthgen D https://orcid.org/0000-0001-6349-4528 Clemens Schlindwein D http://orcid.org/0000-0002-9947-3902

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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