Few plants and one dominant fly shape a unique pollination network in a Neotropical mangrove

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ABSTRACT

Mangroves are unique ecosystems supported by very small plant assemblages. Those few plants tend to be insect-pollinated and make generalized interactions, which leads to competition for pollinators. Mangroves are poorly studied in terms of pollination ecology, and we still do not know how those interactions scale up to form networks. We described the pollination network of a Neotropical mangrove to understand how plant species share pollinators and to gain insight into network assembly in a species-poor ecosystem. We assessed year-round pollination interactions in a mangrove in north-eastern Brazil comprising three entomophilous plant species and described the topology of the resulting network in terms of nestedness, specialization, and modularity. We also assessed the relative importance and niche breadth of different pollinator groups using centrality metrics. The network had highly imbalanced node classes, comprising three zoophilous plant species and 29 insect species from the orders Diptera, Hymenoptera, and Lepidoptera. Pollinator species were mostly peripheral and rarely interacted with all plants, while plant species formed a generalized core. A single dominant fly species, *Palpada albifrons*, visited all plants and made most interactions, softening the separation between modules. The network was nonetheless moderately specialized due to several exclusive interactions with a taxonomic signal. These taxon-specific interaction patterns point to idiosyncrasies in mangrove pollination systems instead of the expected generalized interactions with non-selective insects. However, the mangrove's reproductive dynamics seems to be dominated by a single pollinator species, and its network topology is heavily influenced by the low plant richness resultant from strong environmental filters.

1. Introduction

Thriving across tropical and subtropical intertidal zones all around the world, mangroves are unique ecosystems in terms of biological diversity and biogeographic distribution (Duke, 2017). In the intersection between estuarine and marine waters, the evolutionary history of mangroves is shaped by a saline environment and by tide dynamics, hence the species that occupy this habitat need to pass through strong environmental filters (Duke, 1992). As a result, mangroves are marked by a low diversity of plants, which are physiologically adapted to osmotic and anoxic stress (Ricklefs and Latham, 1993; Ellison et al., 1999). In the Atlantic and Eastern Pacific region (sensu Duke et al., 1998), ca.

15 species from eight plant genera are recognized as mangrove species (Duke et al., 1998; Lo et al., 2014). Local mangrove communities in this region represent only a subset of this pool.

Such low plant diversity may result in peculiar patterns of pollination interactions, such as a high dependence of the pollinators on zoophilous plants, especially when mangrove species share similar pollination systems that are mainly composed of accessible and unspecialized flowers (Nadia et al., 2012, 2013; Nadia and Machado, 2014a). For instance, entomophilous Brazilian mangrove species that occur in sympatry, forming a small three-species assemblage with similarly small and accessible flowers, have shown segregated flowering peaks at different times of the year (Nadia et al., 2012; Nadia and Machado,

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2014a). Non-overlapping phenologies could be interpreted as a strategy to minimize competition for pollinators and reduce mixed pollen loads (Oleques et al., 2017). However, to make such an assertion, we must first understand to what extent those plant species rely on the same pollinators.

Unfortunately, mangroves have been poorly studied from a pollination biology perspective (Hermansen et al., 2014), and only a few studies, carried out mostly in the Paleotropics, have addressed plant-pollinator interactions in those ecosystems at the community level (e.g., Akter et al., 2020; Chakraborti et al., 2019; Panda et al., 2019). Although we know that most mangrove species so far studied are entomophilous and pollinated mainly by bees, flies, and butterflies (Sánchez-Núñez and Mancera-Pineda, 2012; Hermansen et al., 2014), it is still unclear, for instance, how plant-pollination interactions in these species-poor ecosystems scale up to form networks and to what extent species share and compete for pollinators. Therefore, mangroves offer the opportunity to study how small plant assemblages, which generate an undiversified pool of floral resources, affect higher-level interaction patterns.

We aimed at filling this gap in knowledge by describing the structure of a plant-pollinator interaction network from a mangrove in Brazil. Our objective was to advance knowledge on mangrove pollination at the community level by (i) describing the structure of the local network in the light of current knowledge about mutualistic networks, and (ii) comparing pollinator importance across taxonomic groups. Because of the very low plant diversity, and considering the plants' unspecialized, accessible flowers, we expected to find an unbalanced network in which pollinators have little selectivity, leading to a generalized, non-modular network without a taxonomic signal in the interactions.

2. Methods

2.1. Study site

Fieldwork and data collection were carried out in an estuarine area of approximately 300 ha at the Itapessoca River, northern coast of Pernambuco, north-eastern Brazil (7°40′39.8″S, 34°50′21.8″W), from 2002 to 2008. The site is located within the Atlantic Forest biome and has an average annual rainfall of 2,053 mm and an average temperature of 23.9 °C, with marked dry and rainy seasons occurring from September to January and from February to August, respectively. The study site is surrounded by highly populated urban areas. The *restinga* (sandy coastal vegetation) associated with the mangrove has been intensively fragmented by civil construction. Consequently, several holiday homes, as well as a helipad, are in close contact with the mangrove. In addition, Itapessoca Island, on the other side of the river (illustrated in Fig. 1), harbours a cement industry. Due to the highly degraded condition of the vegetation surrounding the mangrove and considering our objective of describing the network formed by typical mangrove species, we did not sample the neighbouring *restinga*.

The sampled mangrove forest harbours four woody plant species: *Rhizophora mangle* (Rhizophoraceae), *Avicennia schaueriana* (Acanthaceae), *Conocarpus erectus*, and *Laguncularia racemosa* (Combretaceae). These species delimit four conspicuous vegetation zones (Fig. 1). The *Rhizophora* zone spans from the riverbank up to 300 m towards the interior of the mangrove and is dominated by *R. mangle*, with a few individuals of *A. schuaeriana* and *L. racemosa*. The intermediate zone follows, spanning from 300 m to 400 m away from the river, where *R. mangle*, *A. schaueriana,* and *L. racemosa* occur in equal proportions. The *Laguncularia* zone, from 400 m to 500 m away from the river, is characterized by a dominance of *L. racemosa* and a few individuals of *A. schaueriana* and *R. mangle*. Finally, the transition zone between the mangrove and the coastal *restinga* vegetation, where *C. erectus* starts to appear, and all four species are found in smaller, but similar proportions. We sampled interactions within the *Laguncularia* and in transition zones (Fig. 1), where all entomophilous species could be observed. We excluded the anemophilous *R. mangle* from the study, as it does not interact with flower visitors. Entomophilous epiphytes, such as those from the Orchidaceae or Bromeliaceae families, did not occur at the study site.

2.2. Study species

All three studied entomophilous species have pale flowers and generalist pollination systems involving small insects, especially Diptera, Hymenoptera, and Lepidoptera (Nadia et al., 2013; Nadia and Machado, 2014a). In addition, the three species show segregated flowering peaks (Nadia et al., 2012). *Avicennia schaueriana* blooms in the dry season, from September to February, peaking in November. *Conocarpus erectus* blooms from the mid rainy season until the dry season (from May to September), peaking in August. *Laguncularia racemosa* has an irregular flowering throughout both seasons, and peaks in May (Nadia et al., 2012).

2.3. Sampling of interactions

We recorded the floral visitors of the three plant species monthly through direct observation of focal individuals, for a total of 48 months (Jun. 2002 to May 2006), which represents a plant-centred approach (Vizentin-Bugoni et al., 2018). Floral visitors were recorded for 4 h between the beginning and end of the active flowering period (from 0700 to 1500 h) on each sampling day. These observations totalled 576 h and were qualitative, hence interaction frequencies were not quantified. Between 2007 and 2008, an additional 10 h of observation was performed for each species during their respective flowering peaks to quantify pollinator visitation frequencies, resulting in 30 h of quantitative observation.

Floral visitors had their visiting behaviour carefully observed and were considered pollinators only if they touched both reproductive organs of a flower during the visit (anthers and stigma). Nectar robbers, i.
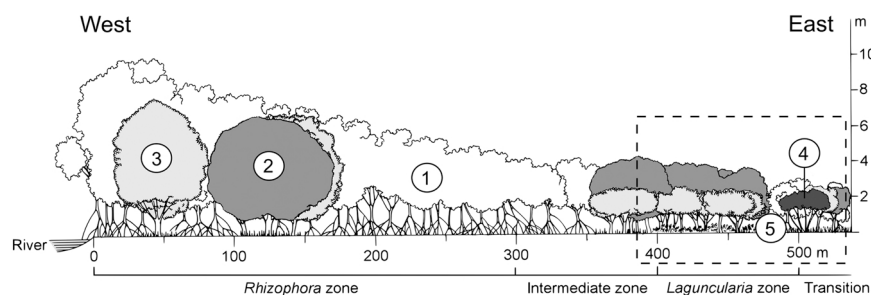

Fig. 1. The species gradient of the studied mangrove area. The woody plant species are represented by different shades of gray: 1 – *Rizophora mangle*; 2 – *Avicennia schaueriana*; 3 – *Laguncularia racemosa*; 4 – *Conocarpus erectus*; 5 – Herbaceous species associated with coastal vegetation. The dashed rectangle marks the zones where our study was conducted.

e., floral visitors that visited or damaged flowers without pollinating them, were excluded. On many occasions, several individuals of multiple pollinator species visited a plant simultaneously, which precluded us from isolating the visits made by an individual pollinator. Therefore, interaction frequencies between a plant species *j* and a pollinator species *i* were calculated as the number of visits made by the pollinator species *i* to the flowers of plant species *j* during the entire observation period. Hence, the frequencies reported here do not correspond necessarily to the interactions between plants and individual pollinators, but rather to the intensity of the foraging activity of pollinator species on the plants. All insects were classified as unique species or morphotypes except for Halictidae bees, which are difficult to distinguish via observation and were thus grouped into a single node that may contain up to three species recorded in the area (Nadia and Machado, 2014a).

Specimens of each pollinator species were collected, identified to the finest possible taxonomic level with the aid of specialists (see *Acknowledgements*), and deposited as vouchers in the entomological collection of the Floral and Reproductive Biology Laboratory, Federal University of Pernambuco, Brazil. We assessed the completeness of our sampling by estimating the asymptotic species richness of pollinators recorded using the nonparametric Chao1 estimator (Chao et al., 2009), employing an individual-based approach (Colwell et al., 2012).

2.4. Network metrics and significance

Observations of pollinator visits were used to build a weighted bipartite adjacency matrix. Each cell in this matrix was filled with the interaction frequency Y_{ij} corresponding to the number of times a plant species *j* was visited by a pollinator species *i* (see details on the measurement of frequencies in the section above). This matrix was used to calculate the following network-level metrics used to describe topology.

First, the H_2' index was used to measure complementary specialization, or how unique are the sets of interactions made by different species in the network. This index considers interaction weights and is corrected by network size (Blüthgen, 2010). It varies from 0 (perfectly overlapping interactions) to 1 (perfectly complementary interactions).

Second, modularity (Q_w) was used to assess whether the network contains subgroups of species that are more densely connected with one another than with other species outside their subgroup (Olesen et al., 2007). It varies from 0 (non-modular network) to 1 (perfectly modular network). We used the weighted DIRTLPAw+ algorithm from Beckett (2016) to make the calculations. This algorithm underwent 100 iterations, and the module configuration that yielded the highest Q_w value was selected.

Finally, we used nestedness, calculated with the WNODF index (Almeida-Neto and Ulrich, 2011), the weighted version of the widely-used NODF index, to measure whether, and to what extent, the interactions of nodes with lower degrees represent subsets of the interactions of nodes with higher degrees. It varies from 0 (non-nested network) to 1 (perfectly nested network).

We used null model analysis to estimate the significance of the topological metrics (H_2', Q_w, and WNODF). One thousand randomized matrices based on the original network were generated using the *vaznull* model (Vázquez et al., 2007), which constrains the number of species and connectance to be equal to the original matrix while marginal totals are allowed to vary proportionally to the marginal sums of the matrix. Then the metrics were calculated for these randomized matrices. The significance of each metric was estimated as the proportion of randomized values that were equal to or higher than the observed value of each matrix. An observed metric was considered significant when $p \leq 0.05$.

2.5. Species-level metrics

We also calculated three node-level indices for all pollinator species in the network to describe their structural roles within the network,

specifically their relative importance and specialization, to test whether these attributes vary between insect groups.

First, we calculated (i) closeness centrality (*CC*), which measures the proportion of shortest paths that cross the species of interest and varies from 0 to 1 (Martín-González et al., 2010). Central species (*CC* → 1) make a set of interactions that bring them closer to all other species in the network, and so are deemed more relevant in shaping the network.

Next, (ii) interaction push-pull (*IPP*) is a species-level index of interaction asymmetry and measures the net balance of interaction dependencies of a species based on the interaction frequencies with its partners (Vázquez et al., 2007). The index is standardized to vary from −1 to 1, where "pullers" (*IPP* < 0) depend, on average, more on their interacting partners in the other node classes of the network than their partners depend on them, while pushers (*IPP* > 0) provide more for their partners than the reciprocal (Novella-Fernandez et al., 2019). Strong pushers (*IPP* → 1) interact with several species that tend to have high dependencies on them, while strong pullers (*IPP* → −1) are peripheral and interact with prolific species that have diffuse dependencies.

Finally, the (iii) weighted *d'* index (Blüthgen, 2010) measures how unique are the interactions made by a given species and is used as a proxy for species-level specialization. It varies from 0 to 1, where values closer to 1 indicate a narrow niche breadth and thus a specialized species.

To quantify the relative importance of taxonomically and functionally different pollinators, each metric was compared between four groups: flies (Diptera), bees (Hymenoptera), wasps (Hymenoptera), and butterflies and moths (Lepidoptera). Moths were grouped with butterflies because they are functionally very similar, both in terms of feeding behaviour and body size.

We fitted generalized linear models (GLMs) for each metric, in which groups were set as explanatory variables and index values as response variables. For *d'* and *CC*, which are proportional values, the models were fitted with a quasibinomial error distribution and *logit* link function. For *IPP*, which is continuous, the model was fitted with a Gaussian error distribution and an identity link function. All models were checked for overdispersion. Model significance was assessed through comparison with an empty null model using a chi-squared test. Differences between groups were tested by re-running each model successively while switching the intercept group.

2.6. Software

All network and statistical analyses were performed in R 4.0.2 (R Development Core Team, 2019). Network and null model analyses were made using the package *bipartite* for R (Dormann et al., 2019). Boxplots were drawn using the package *ggplot2* for R (Wickham, 2016). The network graph was drawn in Gephi 0.9.2 (Bastian et al., 2009).

3. Results

3.1. Plant-pollinator interactions

We recorded 38 pollinator species of the orders Hymenoptera (42.1%), Diptera (31.6%), and Lepidoptera (26.3%) (Fig. 2). A complete list of floral visitors is provided in the Supplementary Material (Table S1) and Fig. 3 depicts some common floral visitors recorded. Here, we use the term "species" to refer to each unique insect morphotype. The plant species that interacted with the largest number of pollinator species was *C. erectus* (*n* = 30), followed by *A. schaueriana* (*n* = 19), and lastly *L. racemosa* (*n* = 14). Out of the 38 insect species recorded, 29 had their visitation frequency quantified for all three plant species and were thus included in the network analysis.

From these 29 pollinator species, we recorded 3052 legitimate visits: 1233 (40.4%) to *A. schaueriana*, 1060 (34.7%) to *C. erectus*, and 759 (24.9%) to *L. racemosa*. Most visits were made by the fly *Palpada albifrons* (58.7%), followed by wasps (Hymenoptera) (16.7%), other Diptera
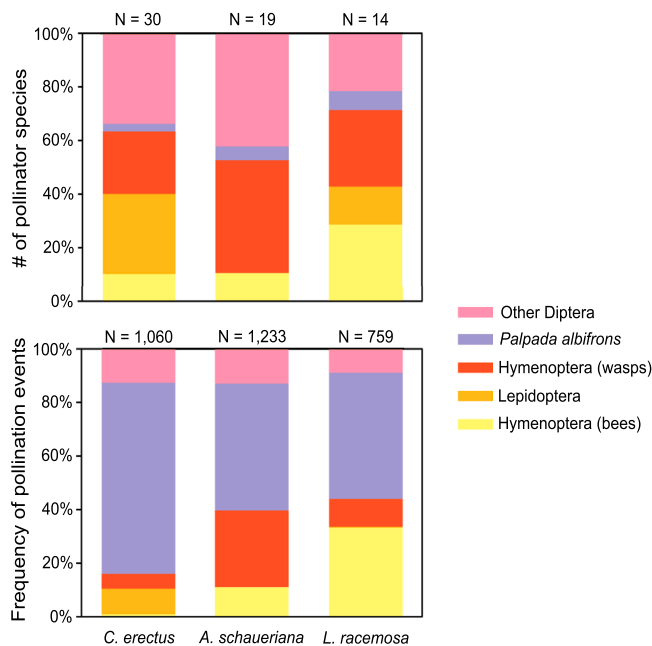
Fig. 2. Visitation data of the three entomophilous plant species in a northeastern Brazilian mangrove. The proportions of pollinator species (top) and their visitation frequencies (bottom) of each studied mangrove tree species. The fly *Palpada albifrons* was separated from the other Diptera species to highlight its disproportional contribution to visitation frequencies.

(12%), bees (Hymenoptera) (9%), and Lepidoptera (3.5%) (Fig. 2). An asymptotic richness of 35.00 ± 7.29 pollinator species was estimated to occur in the community, thus leading to a mean sampling completeness of 82.9%.

3.2. Network structure

The network had highly imbalanced node classes, with 29 pollinator species interacting with only three plant species (Fig. 4). Its topology was moderately specialized ($H'_2 = 0.46$, $Z = 15.35$, $p = 0.00$), little nested (WNODF $= 0.32$, $Z = -4.27$, $p = 0.99$), and little modular (Qw $= 0.26$, $Z = 18.18$, $p = 0.00$).

Three overlapping modules were identified, each associated with a different plant species. The fly *P. albifrons*, although belonging to the *C. erectus* module, interacted very frequently with all three plant species, thus reducing module segregation (Fig. 4). All modules contained at least one species from each insect group, except for the *A. schaueriana* module, which did not include Lepidoptera.

Nevertheless, there seems to be a weak taxonomic signal in the interactions. All but one Lepidoptera were placed in the *C. erectus* module, interacting weakly but almost exclusively with it (98.2% of interactions from Lepidoptera were with *C. erectus*). Meanwhile, wasps interacted mostly with *A. schaueriana* (77.8% of wasp interactions), and while each of the three bee nodes occupied a different module, most of their interactions (91.3%) were made with *L. racemosa* due to the specialized Halictidae node. Flies did now show any clear preference and visited all plants similarly.

3.3. Species roles

Pollinator taxonomic groups did not differ significantly from one another in terms of centrality ($\chi^2 = 2.57$, d.f. $= 25$, $p = 0.24$) and were, on average, peripheral (pooled groups: $CC = 0.04 \pm 0.1$) when compared to plants ($CC = 0.51 \pm 0.15$), except for the fly *Palpada albifrons* ($CC = 0.50$, Fig. 5A). Pollinator groups also behaved similarly in terms of specialization ($\chi^2 = 2.08$, d.f. $= 25$, $p = 0.1$) and were overall

unspecialized ($d' = 0.14 \pm 0.11$), with highlights to the specialized Halictidae node ($d' = 0.51$), which interacted almost exclusively with *L. racemosa*, and the least specialized fly species *P. albifrons* ($d' = 0.03$, Fig. 5B).

However, pollinators differed significantly from one another in terms of interaction asymmetry ($\chi^2 = 0.91$, d.f. $= 25$, $p = 0.04$) and acted almost entirely as pullers (IPP < 0), again except for *P. albifrons* (IPP $= 0.25$). Lepidopterans were the strongest pullers (IPP $= -0.94 \pm 0.15$) due their numerous weak interactions mostly with *C. erectus* and differed from the weaker pullers from the fly (IPP $= -0.59 \pm 0.39$, estimate $= 0.20$, $t = 2.4$, $p = 0.02$) and wasp (IPP $= -0.50 \pm 0.27$, estimate $= 0.23$, $t = 2.3$, $p = 0.03$) groups (Fig. 5C). The small bee group encompassed two strong pullers and a weak one (Halictidae node) and thus did not differ significantly from any other pollinator group ($p > 0.5$ for all comparisons).

4. Discussion

4.1. A unique topology

We described for the first time a mangrove pollination network and found an atypically simple core-periphery topology explained by a very low plant richness and generalized pollination systems. These factors resulted in highly imbalanced node classes: a core formed by a few generalist plants associated with several peripheral pollinators, except for one central fly species. This topology, which resembles a core-periphery mesoscale structure (Elliott et al., 2020), deviates from all four most common topological archetypes observed in interaction networks: gradient, nested, compartmented (modular), and compound (Lewinsohn et al., 2006; Pinheiro et al., 2019).

The observed topology also differs from previous evidence suggesting that nestedness is common among pollination networks (Bascompte et al., 2003; Bastolla et al., 2009; Joppa et al., 2010), especially in smaller single-taxon systems (Bezerra et al., 2009). It also differs from more recent studies, which propose that interaction networks that comprise higher taxonomic diversity tend to have either modular (Olesen et al., 2007; Mello et al., 2011) or compound (Mello et al., 2019; Pinheiro et al., 2019; Queiroz et al., 2020) topologies. The studied network, however, deviated from all expectations and showed moderate specialization. The key to understanding this unusual topology is the disproportionally central fly species *P. albifrons*. Although the three plant species were visited by somewhat different pollinator groups, *P. albifrons* strongly reduced module segregation. The pollination systems of those plants also shed some light on the interaction patterns observed.

4.2. Exploring generalist pollination systems

Fly pollination is frequently associated with unspecialized flowers that are visited by several other insects (Endress, 1994; Nadia and Machado, 2014b), but many plant species predicted to be ecological generalists based on floral phenotype may, in reality, be mostly or exclusively pollinated by flies, as suggested by Pombal and Morellato (1995). *Palpada albifrons* may serve as an example of this contradiction. Its prominent role, which could be regarded as that of a keystone species (Martín-González et al., 2010; Mello et al., 2015) when compared to all other peripheral pollinators, may lead the plants to compete for its services, thus increasing phenological displacement in the community. The higher visitation frequencies of *P. albifrons*, however, may not necessarily translate into a higher contribution to plant fitness if this species is not effective in removing or depositing pollen or promoting cross-pollination (Santiago-Hernández et al., 2019). Therefore, we must be cautious when interpreting the high visitation frequencies of *P. albifrons*, and the role of other less central pollinators should not be disregarded.

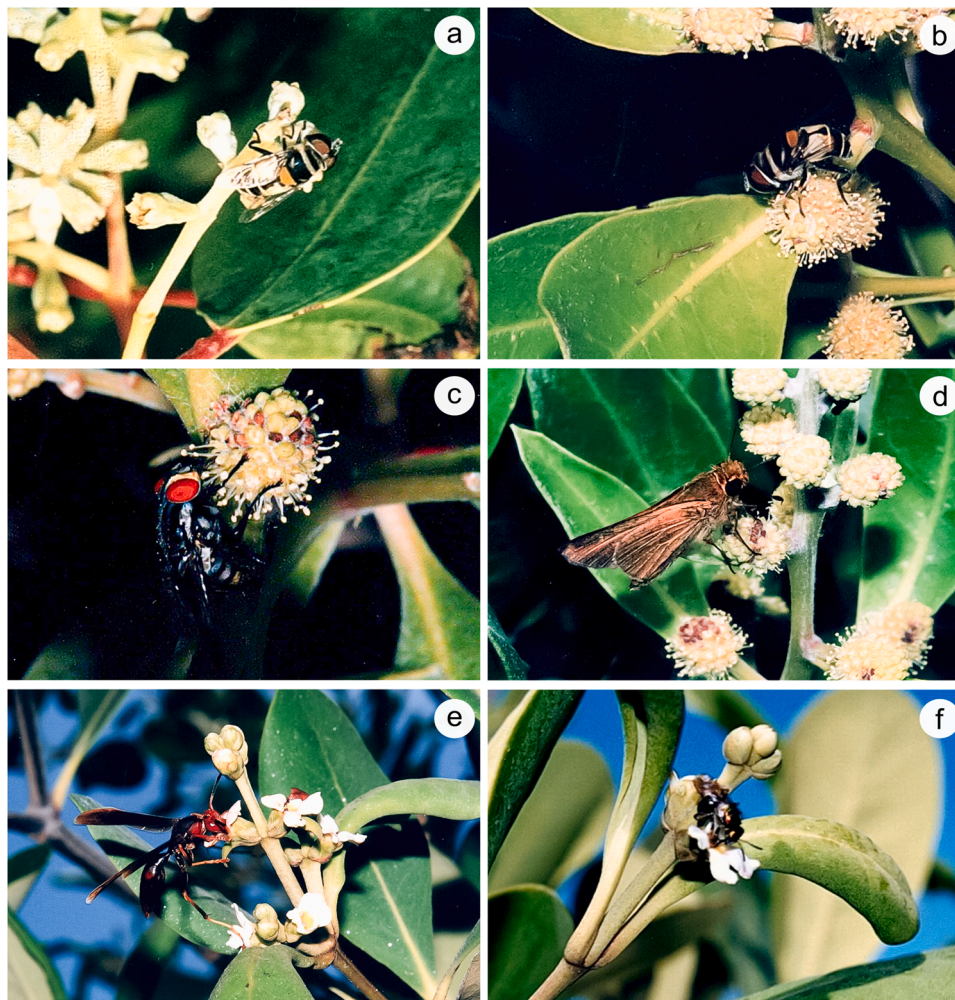Interestingly, *P. albifrons* does not present such high visitation rates

Fig. 3. Interactions between the main pollinators and plant species in a northeastern Brazilian mangrove. The dominant fly *Palpada albifrons* visiting *Languncularia racemosa* (a) and *Conocarpus erectus* (b); *C. erectus* also visited by a Sarcophagidae fly (c) and a Noctuid moth (d); *Avicennia schaueriana* visited by the wasp *Polistes lanio* (e) and by a Halictidae bee (f).
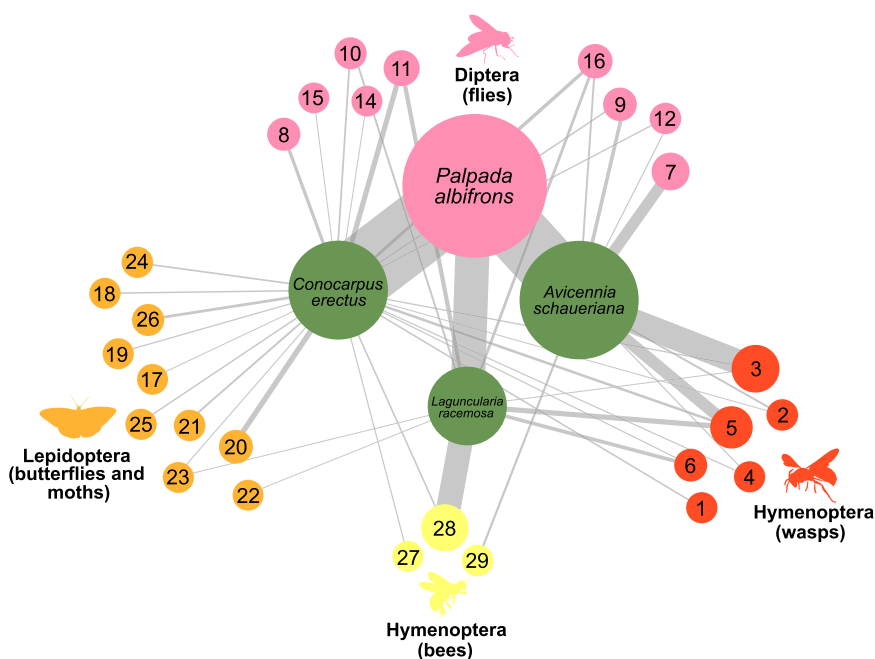

Fig. 4. The interaction network between plants and pollinators in a northeastern Brazilian mangrove. Only pollinators that had their interaction frequencies measured were included. Plants are displayed in green at the center of the network, and pollinators are represented in different colors for each taxon. Node size is proportional to the total sum of the interaction frequencies made by each species, and link width corresponds to the interaction frequency recorded for each pair of species. Node codes: **1** – Wasp 1; **2** – *Sceliphron* sp.; **3** – *Polistes lanio*; **4** – *Lesticia* sp.; **5** – Crabronidae; **6** – *Brachygastra lecheguana*; **7** – *Tabanus obsoletus*; **8** – Syrphidae 1; **9** – Sarcophagidae 1; **10** – Sarcophagidae 2; **11** – Sarcophagidae 3; **12** – Sarcophagidae 4; **14** – Diptera 1; **15** – Diptera 2; **16** – Caliphoridae 1; **17** – Riodinidae 1; **18** – *Junonia evarete*; **19** – Hesperiidae; **20** – Moth 1; **21** – Moth 2; **22** – Moth 3; **23** – Butterfly 1; **24** - Butterfly 2; **25** – Butterfly 3; **26** – Butterfly 4; **27** – *Xylocopa* sp.; **28** – Halictidae spp.; **29** – *Augochlora* sp.
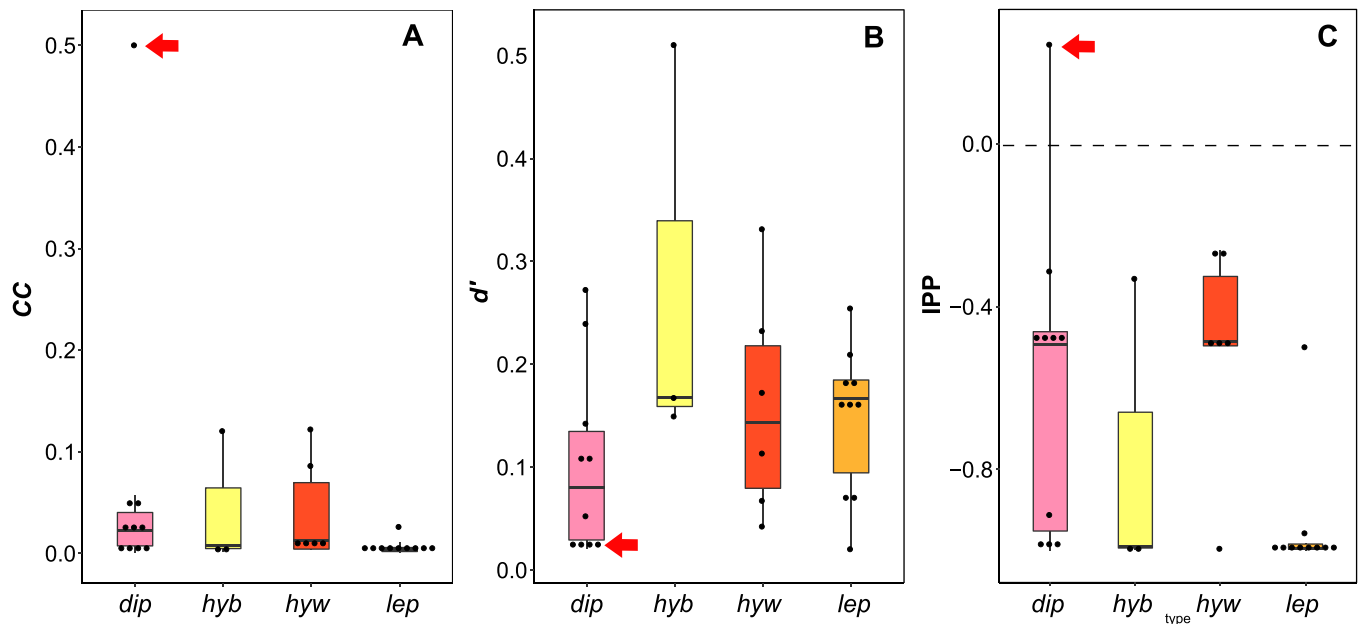
Fig. 5. Species-level metrics of the pollinators in the mangrove network. weighted closeness centrality (**A**), specialization (**B**), and interaction push-pull (**C**). Horizontal lines inside boxes represent median values, and whiskers represent standard deviations. The red arrow highlights the fly *Palpada albifrons* in all plots: ***dip***: Diptera; ***hyb***: Hymenoptera (bees); ***hyw***: Hymenoptera (wasps); ***lep***: Lepidoptera.

in North American mangrove communities with similar species assemblages, when compared to native bees or the invasive honeybee *Apis mellifera* (Landry and Rathcke, 2012; Landry, 2013). Its predominance in the studied community might be associated with an increased abundance resulting from local factors, such as the availability of dead wood associated with water that serves nesting sites for this group (Landry, 2013; Maier, 1982). Furthermore, *P. albifrons* could be more resistant to disturbances such as habitat fragmentation, as some mangrove-residing pollinators tend to occur in high abundance close to disturbed and urbanized areas (Akter et al., 2020). The disturbed and fragmented state of the surrounding *restinga*, the relative isolation of the studied mangrove, and its small area could in fact have driven the patterns observed in the network, by suppressing populations of less resistant floral visitors while benefiting others. However, the biology of *P. albifrons* has not been studied in detail despite its large range across tropical Americas (Thompson, 1981; Pascarella et al., 2001), and delving into possible explanations for its dominance is out of the scope of our study.

Despite the homogenizing power of *P. albifrons* and the low plant richness found in the studied mangrove, specialization arose from a weak taxonomic signal in the interactions. Lepidopterans interacted almost exclusively with *C. erectus*, wasps preferred *A. schaueriana*, especially *Polistes lanio* with its relatively frequent and exclusive interactions with its flowers, and Halictidae bees visited mostly *L. racemosa*. These patterns suggest at least a certain degree of functional specialization in the plants. A closer look at floral biology, which affects pollinator attraction (Fenster et al., 2004) and network structure (Kantsa et al., 2018), may help to understand these patterns. For example, the small and tubular flowers of *C. erectus* are organized in dense glomerular inflorescences (Nadia and Machado, 2014a), which provide the landing platforms required by butterflies and moths to settle and feed on flowers (Willmer, 2011; Rech et al., 2014). This trait probably leads lepidopterans to seek *C. erectus* to the detriment of other species, whose flowers are solitary and offer smaller to no landing areas (Nadia et al., 2012). Meanwhile, the high sugar concentration in the nectar of *A. schaueriana* (Nadia et al., 2013) could lead wasps, which have strong energy requirements, to seek sources of concentrated sugar (Rech et al., 2014), and so select its flowers more frequently.

However, the strong relationship between Halictidae bees and *L. racemosa* is less clear in terms of floral biology, but this mangrove

species increases in abundance near the edge of the mangrove and closer to fragmented *restinga* and the civil constructions, while it has been shown that Halictidae bees tend to predominate in highly disturbed anthropic environments in Brazil (Pinheiro-Machado et al., 2002; Souza and Campos, 2008; Taura and Laroca, 2001). The spatial intersection between species could be driving this specific interaction, which would suggest that a combination of micro (e.g., floral traits) and macroscale (e.g. spatial distribution of species) factors explain the observed patterns.

We must also address a possible temporal mismatch. The network was formed by compiling data from different flowering peaks, hence many unrealized links and some network patterns such as the moderately modular structure could be a result of a phenological mismatch between plants and animals (Olesen et al., 2011) rather than a morphological mismatch (Maruyama et al., 2014; Vizentin-Bugoni et al., 2014), or innate pollinator preferences (Kantsa et al., 2018). Tropical insect populations fluctuate seasonally in abundance according to several factors, ranging from rainfall to predator activity (Wolda, 1978; Silva et al., 2011; Molleman et al., 2016). Therefore, non-synchronized phenologies between plants and insects may have affected network fill, although previous works with this system that investigated year-round interactions suggest a persisting low overlap in pollinators between *C. erectus* and *L. racemosa* (Nadia and Machado, 2014a) a high usage of wasps by *A. schaueriana* especially during the beginning and peak of flowering, only at the end being replaced by flies (Nadia et al., 2013).

4.3. Conclusions and future directions

Despite a weak taxonomic signal in plant-pollinator interactions, the mangrove's reproductive dynamics and network structure seem to be driven by one fly species. Perhaps this dominance occurs often in mangroves and other species-poor ecosystems, alongside this simple, unbalanced topology. High dependence on a few species has been recorded in isolated communities such as islands, where pollinators become a limiting resource for plants (Schleuning et al., 2014).

Although not perfectly comparable to islands, mangroves may serve as an analogy for a similarly challenging ecosystem, since patches of species-poor mangroves increase competition for both plants and pollinators, especially in the increasingly disturbed, fragmented, urbanized

mangroves of Brazil (Ferreira and Lacerda, 2016). Further large-scale studies in "biogeographic anomalies" are key to understanding network topologies that deviate from the four usual archetypes. Moreover, in-depth, community-wide studies on morphologically unspecialized flowers are key to assessing ecological specialization, and they may reveal other layers of pollinator partitioning and intrinsic preferences in these systems.

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CRediT authorship contribution statement

TLN and ICM conceptualized the study and designed the methodology. TLN collected the data under the supervision of ICM and wrote the first draft of the manuscript with contributions from ICM and MARM. UMD performed data curation and analysis with contributions from TLN, MARM, and ICM. UMD led the writing of the final version of the manuscript. All authors contributed critically to preliminary versions and gave final approval for publication.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.aquabot.2022.103526.

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