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Plant-Bee Interaction Network in an Atlantic Forest Fragment of a Neotropical Metropolis

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Abstract

Urbanization is a major driver of biodiversity loss and profoundly alters the structure of species interaction networks. Nevertheless, urban forest remnants may still sustain structurally and functionally diverse pollinator networks. Here, we characterize the structural and functional organization of a plant-bee interaction network within a large Atlantic Forest fragment embedded in a tropical metropolis in northeastern Brazil. We quantified 4,700 plant-bee interactions involving 19 plant and 80 bee species and evaluated network connectance, nestedness, modularity, specialization, and species-level functional roles. The network was relatively sparse, exhibited low nestedness, moderate modularity, and high specialization. Most plant and bee species occupied peripheral positions, whereas a small subset of abundant eusocial stingless bees, particularly *Trigona spinipes* (Fabricius) and *Scaptotrigona tubiba* (Smith), functioned as connectors linking interaction modules. No species acted as a true network hub, indicating limited integration among modules. Together, these patterns reveal a network dominated by a few generalists and many low-degree species, consistent with functional filtering in urban landscapes. Despite this, the remnant supported ecologically important interactions involving both generalist and specialized pollinator guilds. Our findings highlight the ecological value of large, heterogeneous urban forest patches, such as Pituaçu Metropolitan Park, and their role in maintaining pollination network structure and function, with important implications for the planning and conservation of urban green areas in tropical cities.

Introduction

Accelerating urban expansion is one of the most pervasive forms of land-use change worldwide, reshaping ecosystems and threatening biodiversity at multiple scales (Fahrig, 2003; McKinney, 2006). By 2050, nearly two-thirds of the global population will inhabit cities (United Nations, 2019). Despite this rapid expansion, urban green spaces may harbor considerable biodiversity and act as refuges for species capable of adapting to anthropogenic environments (Hall et al., 2017; Normandin et al., 2017). Within this urbanized context, forest fragments embedded in cities can function as key biodiversity refuges, maintaining habitat heterogeneity and sustaining ecological interactions (Aronson et al., 2017). However, the transformation of natural habitats into anthropogenically modified landscapes nevertheless has profound ecological consequences, including habitat fragmentation, loss of native vegetation, altered microclimatic conditions, and disruption of species interactions (Haddad et al., 2015; Theodorou, 2022). In general, urbanization alters local microclimates, reduces vegetation cover, and homogenizes biotic communities, leading to marked declines in species richness and interaction patterns (Shochat et al., 2010; Kowarik, 2011; Theodorou, 2022).

Among the taxa most affected by urban-driven changes are bees (Anthophila), the dominant pollinators of flowering plants and key providers of ecosystem services (Ollerton et al., 2011). Bees rely heavily on floral resources and nesting substrates that are often scarce in cities (Cane, 2005; Zanette et al., 2005), making them highly sensitive to habitat loss and landscape simplification. Their decline has been reported across diverse regions, frequently accompanied by the disappearance of rare or specialized species (Potts et al., 2010). In long-term surveys in Brazilian urban areas, for instance, Martins et al. (2013) recorded nearly a 50% reduction in bee richness over four decades, alongside increases in social and cavity-nesting species. Such shifts reveal a process of functional filtering in which resilient, generalist groups dominate urban communities, while solitary and specialized taxa are progressively excluded (Banaszak-Cibicka & Żmihorski, 2012; Fortel et al., 2014; Graf et al., 2022).

Moreover, urbanization profoundly reshapes the structure of mutualistic networks linking bees and plants, as species loss and altered interactions alter network topology and reduce functional redundancy (Pereira et al., 2022; Herrmann et al., 2023; Pardee et al., 2023). Empirical evidence shows that pollination networks in urban landscapes tend to be more specialized and modular, but less nested, reflecting restricted resource sharing among species (Baldock et al., 2015; Tavares-Brancher et al., 2024; Graf et al., 2025). These structural changes are closely related to landscape attributes, such as vegetation cover and environmental heterogeneity, which determine the availability of floral and nesting resources and, in turn, the diversity and organization of local pollinator communities and their interactions (Geslin et al., 2013; Moreira et al., 2015; Boscolo et al., 2017).

Simplified and homogeneous urban environments often favor resilient, social, and polylectic species that act as network hubs, such as *Trigona spinipes* (Fabricius) and *Apis mellifera* L., maintaining the network cohesion under environmental stress (Theodorou et al., 2017; Graf et al., 2022). In contrast, solitary and oligolectic bees lose interaction partners in fragmented habitats, reinforcing network compartmentalization and reducing pollination stability (Aizen et al., 2012; Valiente-Banuet et al., 2015). Urbanization also reshapes the functional roles within networks: as specialists disappear, a small subset of robust generalists persists as connectors or hubs, disproportionately supporting the remaining structure (García-Algarra et al., 2017; Suni et al., 2022; Marcacci et al., 2023). This functional simplification reduces complementarity and increases dependence on dominant species, ultimately lowering network robustness to environmental disturbances (Hagen et al., 2012; Simmons et al., 2019).

In this study, we characterize the structural and functional organization of a plant-bee interaction network within a large Atlantic Forest fragment embedded in a tropical metropolis. Specifically, we address two questions: (i) What is the overall topological structure (i.e., connectance, nestedness, modularity, and specialization) of a plant-bee network in an urban Atlantic Forest remnant? and (ii) How are bee species functionally positioned within the network, and which taxa act as peripherals, connectors, or hubs? Through this integrative approach, we aim to understand how urban forest remnants contribute to maintaining pollination interactions and to provide ecological insights relevant to the planning and conservation of green spaces in tropical cities.

Material and Methods

Study area

The study was conducted in the Pituaçu Metropolitan Park (PMP), located in the city of Salvador, Bahia, northeastern Brazil (12°59′52.7″ S, 38°27′05.4″ W). The park is a state-managed urban protected area, officially established in 1973, administered by the Instituto do Meio Ambiente e Recursos Hídricos (INEMA) of Bahia state, covering approximately 392 ha and representing one of the largest urban remnants of the Atlantic Forest in the Salvador Metropolitan Region (INEMA, 2025). The park allows controlled public access and recreational activities, while maintaining remnant Atlantic Forest vegetation and freshwater ecosystems. The local climate is tropical humid (Af) according to Köppen's classification (Alvares et al., 2013), with mean annual precipitation exceeding 1,500 mm. The rainy season extends from April to July, accounting for about 60% of the annual rainfall, while the dry season occurs from September to March. Mean temperatures remain above 18 °C in the coldest months and 25 °C in the warmest months.

Landscape characterization

Within a 2.5-km radius buffer centered on the focal point, the area was predominantly covered by urbanized zones (~43%), followed by forest formations (~24%) and mosaics of uses (~19%), interspersed with aquatic environments (~12%) (Fig 1). We quantified the landscape composition surrounding the sampling point using the MapBiomas Collection 7 land-use and land-cover dataset for 1998 (MapBiomas, 2023), the sampling year. The spatial inspection was conducted in R v.4.5.1 (R Core Team, 2025).

The vegetation of PMP is classified as Dense Ombrophilous Forest, with vegetation at different stages of secondary succession due to a long history of anthropogenic disturbance. The landscape forms a heterogeneous mosaic of low secondary forest, open shrubby formations, and aquatic habitats surrounding the Pituaçu reservoir. The local flora includes elements typical of coastal restinga vegetation, such as *Syagrus coronata* (Mart.) Becc. (Arecaceae), *Tapirira guianensis* Aubl. and *Schinus terebinthifolia* Raddi (Anacardiaceae), interspersed with woody species characteristic of the original Atlantic Forest, including *Bowdichia virgilioides* Kunth and *Andira fraxinifolia* Benth., *Stryphnodendron pulcherrimum* (Willd.) Hochr. (Fabaceae), *Byrsonima sericea* DC. (Malpighiaceae), and *Eschweilera ovata* (Cambess.) Mart. ex Miers (Lecythidaceae) (CONDER, 1992; ECOA, 2013; Ramalho et al., 2014; Silva et al., 2015).

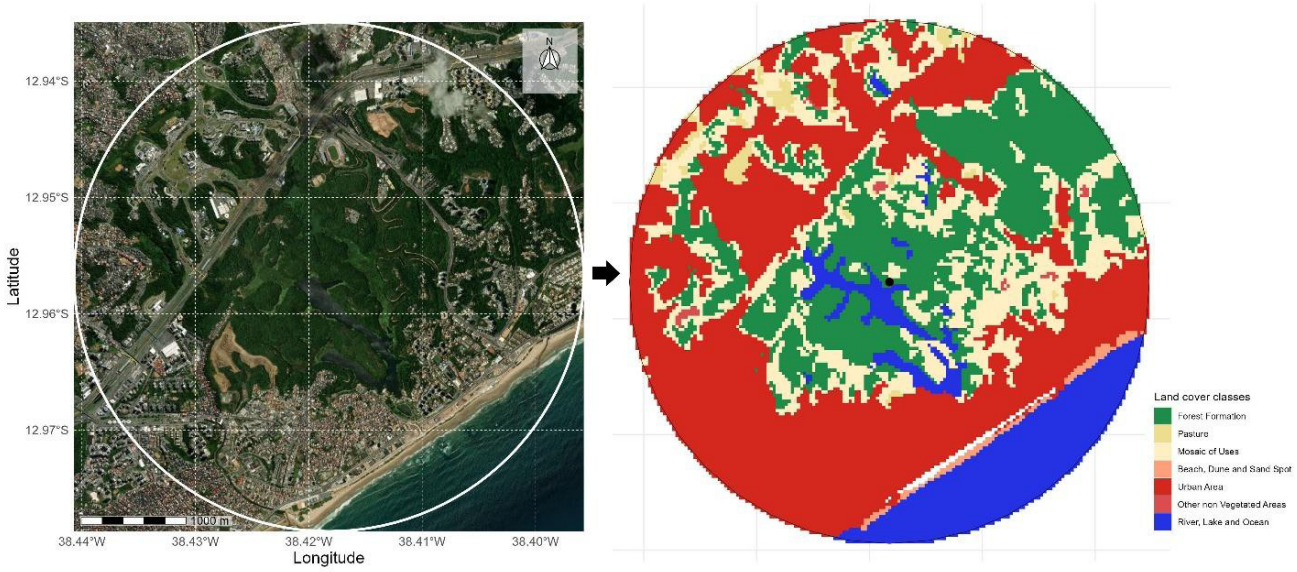

Fig 1. Satellite-based imagery overlaid with a 2.5-km radius buffer and geographic graticule, illustrating the spatial context of the study site (Source: Esri World Imagery) and land-cover classification within the same buffer derived from MapBiomas Collection 7 (year 1998), showing the distribution of habitat types in the Pituaçu Metropolitan Park (PMP) and surroundings, Salvador, Bahia, northeastern Brazil.

Historically, dominated by dense Atlantic Rainforest, the region was gradually converted to agriculture and pasture, leaving a regenerating forest fragment within heavily urbanized surroundings (CONDER, 1992; Santos, 2018). Despite its ecological importance and legal protection, the PMP still experiences intense human pressures from recreation, fishing, waste disposal, and urban expansion (Santos, 2018).

Sampling design

We conducted bee-plant interactions during weekly sampling from October 1997 to December 1998. Collections followed a standardized active-flower sampling protocol (Sakagami et al., 1967), along a 2.5 km preexisting trail that crossed different vegetation types within the park. Sampling was conducted between 08:00 and 17:00 h under favorable weather conditions, avoiding rainy or overcast days. To minimize temporal bias, the starting point of the trail was alternated among sampling days, ensuring that plants were surveyed during both morning and afternoon periods. The collector continuously walked the trail, inspecting all flowering plants and capturing visiting bees with an entomological net. In this study, an interaction was defined as a direct floral visitation event in which an individual bee was observed actively foraging on the reproductive structures of a flowering plant species.

Sampling effort differed among vegetation strata. Tree species (>4 m in height) were observed for approximately 30 minutes each, while shrub (1–3 m) and herbaceous (<1 m) plants were observed for 15 minutes each. The total sampling effort was estimated from the cumulative observation time across vegetation strata, resulting in approximately 240 hours of effective sampling over 60 sampling days (Silva et al., 2015).

Species identification

Sampled bees were transferred to labeled vials. In the laboratory, specimens were pinned, dried, and later identified to the lowest possible taxonomic level, usually to species, using identification keys (Michener, 2007) and reference collections. When necessary, selected specimens were sent to taxonomic specialists for confirmation or detailed identification. Subsequent revisions and bees' nomenclature were standardized according to Moure's Bee Catalog (Moure & Melo, 2025). Vouchers were deposited in the Hymenoptera Collection of the Zoology Museum of the Federal University of Bahia (MZUFBA) and in the Alexandre Leal Costa Herbarium (ALCB) for long-term preservation.

Network analysis

Plant-bee interactions were organized into a quantitative bipartite interaction matrix, in which rows and columns represented bee and plant species in each partition. The cells of the matrix contained the interaction frequency, measured as the number of individual bee visits recorded for each specific plant-bee pair across the entire sampling period. To describe the structural organization of the plant-bee assemblage in the PMP, we calculated four complementary metrics that capture distinct aspects of network structure: (i) Connectance (C) – the proportion of realized interactions relative to all possible links in the network, expressed as $C = L / (I \times J)$, where L is the number of observed links and I and J are the number of plant and bee species, respectively. This metric ranges from 0 to 1, with higher values indicating more densely connected webs (Jordano, 1987); (ii) Nestedness – Weighted Nestedness metric based on Overlap and Decreasing Fill (wNODF) that

quantifies the extent to which the interactions of specialist species form subsets of those of more generalist species, considering interaction frequencies (Almeida-Neto et al., 2008; Almeida-Neto & Ulrich, 2011). Values range from 0 (non-nested) to 100 (perfect nestedness); (iii) Modularity (Q) – estimated using the Beckett algorithm (Dormann & Strauss, 2014), which detects groups of species (modules) that interact more frequently among themselves than with other network members. Modularity values range from 0 (no modular structure) to 1 (highly compartmentalized); and (iv) Network-level specialization (H2') – a standardized metric describing the overall level of niche partitioning in the network, calculated from the relative abundance of interactions between species while considering both the number and strength of their links (Blüthgen et al., 2006). H2' values range from 0 (complete generalization) to 1 (complete specialization). All network analyses were performed using the 'bipartite' package (Dormann et al., 2009).

To evaluate whether the observed network structure differed from random expectations, we compared each empirical metric (i.e., Weighted NODF, modularity (Q), and H2') with values generated under a null model implemented using the Patefield algorithm (Patefield, 1981), which randomizes the interaction matrix while maintaining the total number of interactions per plant and pollinator species (Ulrich & Gotelli, 2010). For each network, 999 randomized matrices were generated, and the metrics were recalculated for each iteration to produce null distributions. All analyses were conducted using the packages 'bipartite' (Dormann et al., 2009) and 'vegan' (Oksanen et al., 2001) in R v.4.5.1 (R Core Team, 2025).

Species roles in the network

To identify the functional roles of each species within the network, we used the module topology approach proposed by Guimerà & Amaral (2005) and adapted to ecological networks by Olesen et al. (2007). After detecting network modules using the Beckett algorithm (Dormann & Strauss, 2014), we calculated for each species two complementary topological descriptors: (i) the within-module degree (z), which measures how well a species is connected to other species within its own module, and (ii) the among-module connectivity (c), which quantifies the extent to which a species connects different modules within the network.

Based on their position in the z–c space, species were classified into four topological roles following standard thresholds: peripherals ($z \leq 2.5$, $c \leq 0.62$), which have few links and interact mainly within a single module; connectors ($z \leq 2.5$, $c > 0.62$), which link different modules and contribute to network coherence; module hubs ($z > 2.5$, $c \leq 0.62$), which are highly connected within their own module; and network hubs ($z > 2.5$, $c > 0.62$), which are highly connected both within and among modules (Olesen et al., 2007). This analysis was performed using the 'bipartite' package (Dormann et al., 2009) in R v.4.5.1 (R Core Team, 2025).

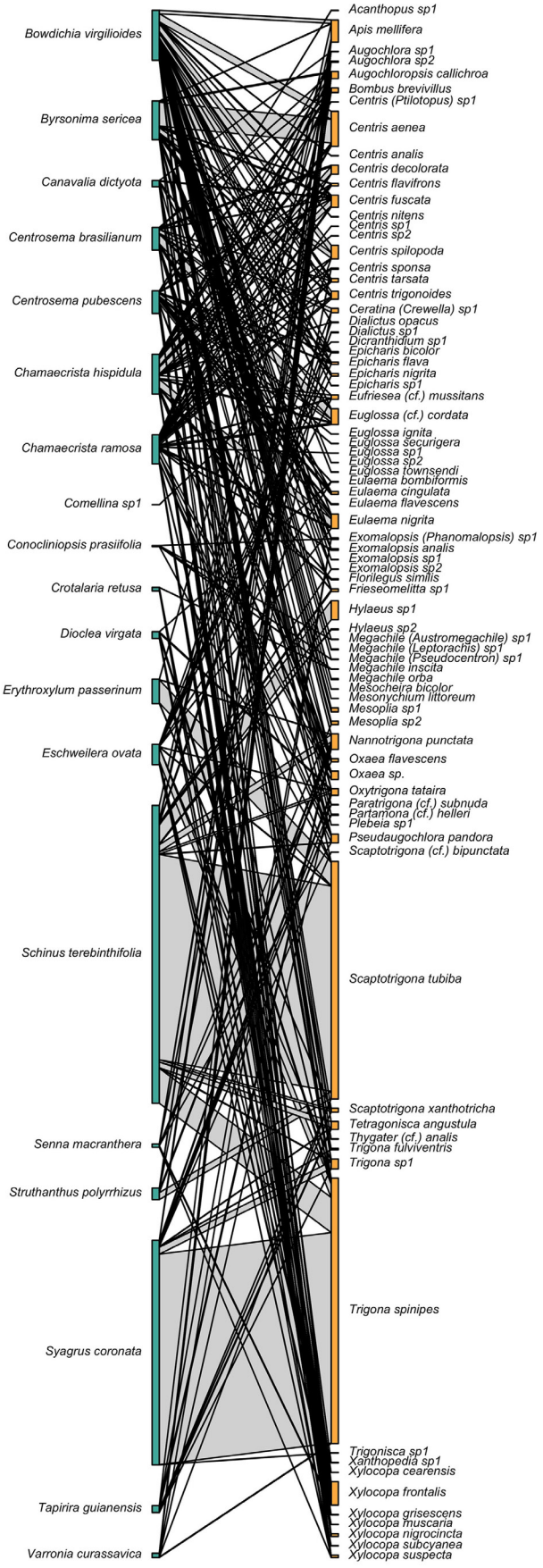

Fig 2. Plant-bee interaction network recorded in the urban Atlantic Forest fragment. Orange bars represent bee species, and green bars represent plant species. The width of each bar is proportional to the number of interaction partners, and links indicate observed frequency between plants and pollinator visits.

Results

Eusocial bees were the most species-rich group (n = 14 species) and had the highest overall abundance, totaling 3,190 recorded interactions with 15 plant species. *T. spinipes* (n = 1,532 individuals) and *Scaptotrigona tubiba* (n = 1,370 individuals) were the most abundant and highly connected species, each interacting with nine plant species. Among plants, *B. virgilioides* and *S. coronata* exhibited the greatest number of eusocial bee visitors, interacting with 11 and 10 species, respectively.

A total of 18 oil-collecting bee species from the tribes Centridini and Tapinotaspidini were recorded in this plant-bee interaction network (Supplementary Material 1). Among them, *Centris fuscata* Lepeletier exhibited the highest number of plant partners (n = 7), whereas most oil-collecting bee species interacted with up to three plant species. These oil-collecting bees visited nine plant species. *B. virgilioides*, *B. sericea*, *Chamaecrista hispidula* (Vahl) H. S. Irwin & Barneby, and *Chamaecrista ramosa* (Vogel) H. S. Irwin & Barneby were the main host plants supporting a greater diversity of oil-collecting bees.

The plant-bee interaction network in the Atlantic Forest urban fragment comprised 19 plant species and 80 bee species (Fig 2; Supplementary Material 1). On average, each plant interacted with 16.42 (± 12.03) bee species. In contrast, each bee species interacted with 3.90 (± 2.53) plant species. Most plant and bee species interacted with only a few partners. On average, each plant species was visited by a few bee species (median degree = 3), whereas a few highly generalist species formed the structural core of the network, *B. virgilioides* showed the highest number of partners (n = 46 bee species), followed by *C. hispidula* and *C. ramosa* (n = 26 bee species each). Among pollinators, *S. tubiba*, *Augochloropsis callichroa* (Cockerell), and *T. spinipes* visited the highest number of plant species (9 each).

The plant-bee interaction network comprised 4,700 individual interactions across 250 unique plant–bee pairs, yielding a connectance of 0.15. Nestedness (WNODF) was relatively low (observed = 20.07; null mean = 53.59; z-score = -14.77; p = 0.001), indicating that the network was significantly less nested than expected by chance. In contrast, the network exhibited strong specialization, with H2' = 0.62 markedly higher than the null expectation (null mean = 0.03; z-score = 298.70; p = 0.001). The network also displayed a moderate but significant modular structure, with Beckett's modularity index (Q = 0.37) exceeding the null expectation (null mean = 0.20; z = 23.55; p = 0.001). Overall, these results indicate that the urban plant-bee network is relatively sparse and weakly nested, yet highly specialized and organized into distinct interaction modules.

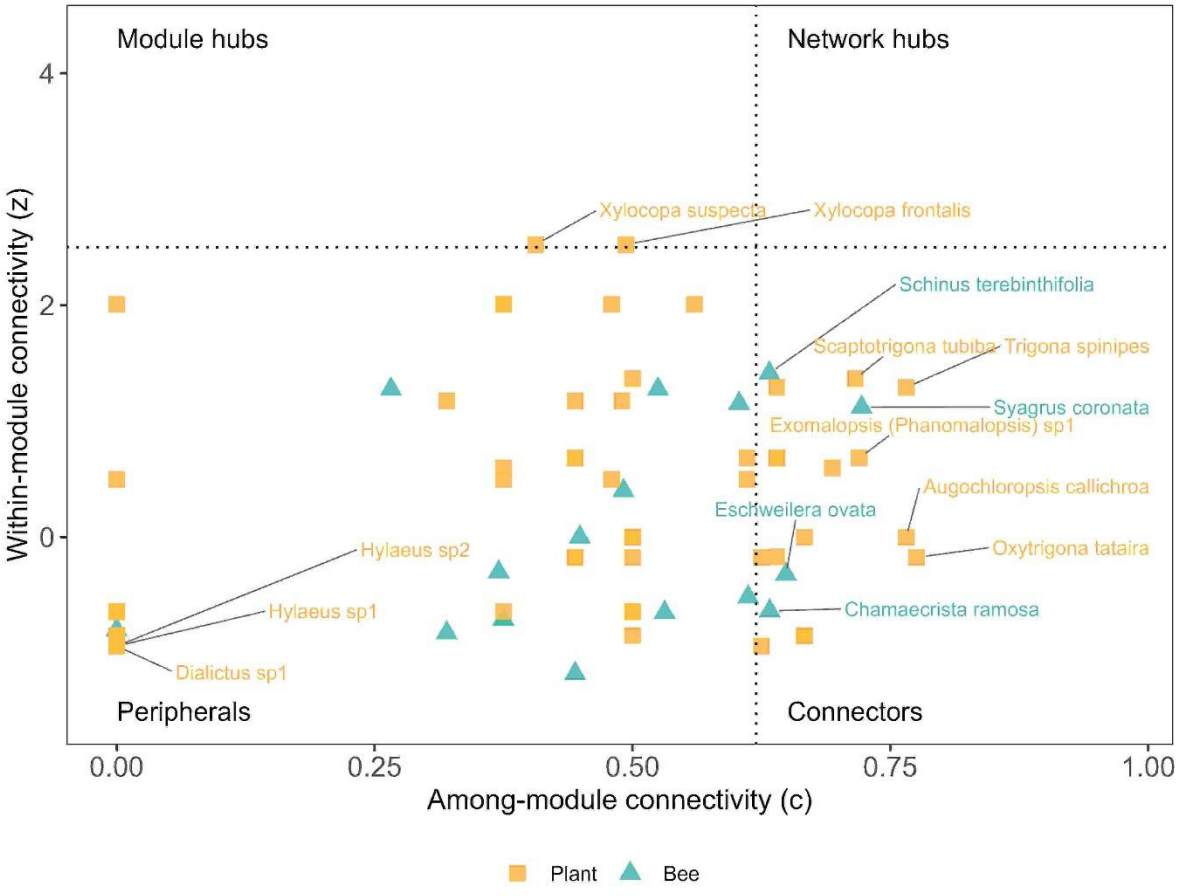

Fig 3. Distribution of plant (green triangles) and bee (orange squares) species according to their values of among-module connectivity (c) and within-module connectivity (z) in the Atlantic Forest urban fragment plant-bee interaction network. The threshold values of z = 2.5 and c = 0.62 followed Guimerà and Amaral (2005), considering four topological roles: peripherals, connectors, module hubs, and network hubs.

Most species acted as peripherals (81.3% of plants and 82.9% of bees), followed by connectors (18.7% of plants and 16.9% of bees) and two module hubs (2.4% of bees; *Xylocopa frontalis* (Olivier) and *Xylocopa suspecta* Moure & Camargo) (Fig 3). No network hubs were detected, indicating that most species concentrated their interactions within their own modules rather than linking distinct ones. Among bees, *X. frontalis* and *X. suspecta* showed high within-module connectivity, acting as local hubs, while *E. ovata*, *S. coronata*, and *S. terebinthifolia* were the main plant connectors. The predominance of peripheral species reveals a network structure characterized by strong modular segregation and limited cross-module generalization, consistent with a specialized, compartmentalized organization.

Discussion

Our study reveals that the plant-bee interaction network of an urban Atlantic Forest fragment is characterized by low nestedness, moderate modularity, and high specialization, indicating that most species interacted with few partners and that interactions were concentrated within distinct modules. Most of both plants and bees acted as peripheral species, while only a small subset, primarily eusocial stingless bees, functioned as connectors linking modules. Altogether, these patterns indicate a diverse, yet structurally fragile network dominated by a few abundant generalists surrounded by many rare or specialized species. These properties are consistent with recent findings showing that urbanization reshapes mutualistic networks by reducing redundancy and promoting functional filtering (Baldock et al., 2015; Theodorou et al., 2017; Graf et al., 2025).

The markedly low nestedness observed in our network contrasts with many natural plant-pollinator networks, where high nestedness buffers communities against species loss and enhances functional redundancy (Bascompte et al., 2003; Fortuna et al., 2010). Urban systems, however, commonly diverge from this pattern. Previous studies show that pollination networks in cities tend to be less nested than their rural or forest counterparts due to the loss of interaction-rich specialists, reduced floral diversity, and the prevalence of disturbance-tolerant species (Baldock et al., 2015; Olsson et al., 2021). Similar decreases in nestedness have been reported for urban forests in Europe (Herrmann et al., 2023) and Brazil (Graf et al., 2025), where reduced habitat heterogeneity and temporal instability of floral resources limit opportunities for niche overlap.

Moderate modularity in the studied network can be interpreted in the context of the spatial and environmental heterogeneity typical of urban landscapes, which are characterized by mosaics of vegetation patches, impervious surfaces, and multiple sources of human disturbance (Banaszak-Cibicka & Żmihorski, 2012; Harrison & Winfree, 2015). However, the effects of human disturbance on network modularity are highly context dependent. In some cases, highly disturbed systems exhibit lower modularity and higher nestedness due to the loss of specialized interactions and the increasing dominance of generalist species (Sebastián-González et al., 2015). In contrast, other studies report higher modularity under specific disturbance regimes, driven by interaction reorganization associated with interaction rewiring and functional plasticity (Sheykhali et al., 2020). Our findings are consistent with this nuanced view. Despite a relatively small plant species pool, the network exhibited a clear modular structure, likely reflecting the combination of flexible foraging behavior in generalist bees (e.g., *T. spinipes* and *S. tubiba*) and spatial constraints on resource availability across the urban landscape.

The strong network-level specialization contrasts with the establishment that urban assemblages are dominated by generalists and therefore more generalized (Suni et al., 2022). However, increased specialization in disturbed or fragmented habitats has also been documented, particularly when species-rich but interaction-poor assemblages arise. In such contexts, reduced resource availability restricts interaction opportunities, leading to higher apparent specialization due to limited interaction opportunities rather than the coevolution process (Ferreira et al., 2020; Philpott et al., 2025). In our case, high specialization can result from the prevalence of numerous rare or low-degree species (most species were peripheral). In the PMP, this pattern is also explained by the close association between oil-collecting bees and oil-producing plants, and by the presence of flowers with more specialized corollas (e.g., the genera *Centrosema*, *Bowdichia,* and *Eschweilera*). Importantly, although the study area is embedded within a highly urbanized matrix, it represents a relatively large and structurally complex forest fragment. Consequently, network patterns observed here may resemble those reported for other forest fragments, where habitat heterogeneity and resource continuity can maintain modular organization despite surrounding anthropogenic pressure (Sebastián-González et al., 2015; Tylianakis et al., 2010; Hagen et al., 2012).

Eusocial stingless bees, particularly *T. spinipes* and *S. tubiba*, accounted for most interaction events and acted as fundamental connectors in the network. Although eusocial species emerged as important connectors in the network, this pattern may reflect their high abundance and foraging flexibility rather than an explicit effect of social behavior, which was not tested in this study. Such species commonly dominate pollination networks in Neotropical cities (Giannini et al., 2015; Campbell et al., 2019) due to their large colony sizes, generalist foraging behavior, and ability to exploit a wide array of urban floral resources (Kaluza et al., 2018). However, extremely abundant generalist species may also suppress visitation by native or specialist bees by acting as nectar thieves, thereby contributing to urban biotic homogenization through their disproportionately high visitation to generalist plant species (McKinney, 2006; Martins et al., 2013).

In our network, no species functioned as true network hubs, suggesting that although generalists are abundant, their interactions remain constrained within modules, possibly reflecting limited floral overlap or competition with solitary species. This pattern has been observed in other tropical urban systems, where stingless bees dominate visitation yet do not fully integrate the network due to spatial foraging constraints (Slaa et al., 2006; Soares et al., 2021).

The observed combination of weak nestedness, strong specialization, and moderate modularity characterizes a network whose structure is often linked to heightened sensitivity to species loss (Rohr et al., 2014). In such compartmentalized systems, the decline of a few abundant connectors or key host plants can destabilize entire modules, amplifying the effects of disturbance. However, urban ecological networks can retain high functional diversity when remnants are sufficiently large, heterogeneous, and plant-rich (Baldock et al., 2015; Hall et al., 2017). Our results underscore the importance of protecting and effectively managing remnant Atlantic Forest in urban green spaces, which can sustain both generalist and specialist pollinator guilds and preserve ecologically unique interactions in an increasingly urbanized landscape.

This study provides a benchmark of plant-pollinator network structure prior to the most recent urban expansion, offering a valuable reference for future temporal comparisons. A comparison between landscape composition at the time of sampling (1998) and current conditions (2024) indicates a marked expansion of urban cover around the study area (2.5 km radius), increasing from ~43% to over 56%, alongside a minimal reduction in forest coverage (-3%). This progressive urbanization suggests that the Pituaçu Metropolitan Park has become increasingly embedded within an impervious urban matrix, potentially affecting pollinator movement, resource availability, and the stability of interaction modules (Harrison & Winfree, 2015; Hermann et al., 2023). These dynamics highlight the importance of reassessing the network under current landscape conditions to evaluate how continued urban expansion may influence pollination interactions and ecosystem functioning.

In summary, we provide a characterization of a plant-bee interaction network within one of the largest Atlantic Forest remnants inside a tropical metropolis. The network exhibited low nestedness, moderate modularity, and high specialization, with most species occupying peripheral roles and a small subset of abundant eusocial bees acting as connectors. These structural properties reaffirm patterns reported for other urban pollination systems, where interaction networks tend to be compartmentalized and increasingly dependent on disturbance-tolerant generalists (Geslin et al., 2013; Fisogni et al., 2022). At the same time, the persistence of specialized interactions likely reflects both the structural complexity of this large urban forest remnant and shifts in pollinator specialization documented in urban environments, where common and disturbance-tolerant species can exhibit increased specialization and dominate interaction patterns (Suni et al., 2022). By establishing a historical structural baseline, this work contributes to urban ecological network research and provides information for future temporal and spatial comparisons. Further studies incorporating urban gradients, functional traits, and long-term monitoring will be necessary to determine how resilient such networks remain under accelerated urbanization.

Authors' Contributions

M.S.: conceptualization, methodology, investigation, writing-original draft, writing - review & editing.
K.C.R.: writing - original draft, writing - review & editing.
C.M.L.A.: writing - original draft, writing - review & editing.
E.L.S.B.: formal analysis, visualization, writing - original draft, writing - review & editing.

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