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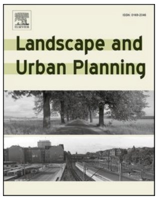

Research Paper

One for all, all for one? Pollinator groups differ in diversity and specialization of interactions across urban green spaces

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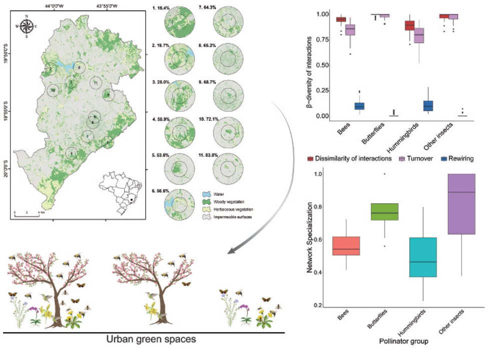
HIGHLIGHTS

- Distinct pollinator groups respond to urbanization differently.
- Plant composition and plant-pollinator co-occurrence explain these dissimilarities.
- Urban green spaces with unique interactions vary across pollinator groups.
- Pollinator groups show varying levels of interaction specialization.
- Considering such differences helps build effective urban conservation strategies.

GRAPHICAL ABSTRACT



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ABSTRACT

Urbanization poses significant threats to pollinators, but they may respond differently to habitat modification according to their nesting and foraging requirements. Despite the diversity of pollinator groups and species found in urban areas, research often focus on bees, neglecting other groups. Whether bee response to urbanization suffice in representing the wider pollinator spectrum, however, is poorly understood. Here, we examined how urbanization impacts the interaction networks between plants and different pollinator groups and evaluated the dissimilarities of urban green spaces at both local and regional scales within a Neotropical metropolis. Recording 1,404 interactions between 262 plant and 220 pollinator species, we found that network specialization varied among pollinator groups but was not affected by urban impervious surface cover. Such lack of difference may happen owing to the prevalence of generalist species across urban environments. Importantly, urban green spaces showed high dissimilarities in species and interactions, emphasizing the heterogeneity found across the urban landscape. Plant composition also varied between urban green spaces and was strongly correlated with interaction dissimilarities, indicating that floral resources contribute to unique interactions found in different areas. Our results suggest that although important, bees alone do not represent the wider response of pollinators

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to urbanization. Furthermore, the high dissimilarities influenced by site specific plant-pollinator co-occurrence underscore that multiple and connected green spaces are required to safeguard plant-pollinator interaction diversity and its vital ecosystem function in cities.

1. Introduction

Urbanization significantly impacts biodiversity, including pollinators and their ecosystem function, mainly by converting natural vegetation to impermeable surfaces (Bennett et al., 2020; Teixido et al., 2022). Despite the negative impact associated with urbanization, urban green spaces have the potential to maintain a diversity of pollinators if adequate resources, including food and nesting sites, are available (Aronson et al., 2017; Hall et al., 2017; Silva et al., 2023). In this context, contemporary conservation strategies have recognized the pivotal role of urban green spaces in supporting biodiversity (Baldock, 2020; Beninde et al., 2015; Lepczyk et al., 2017; Vega and Küffer, 2021). Although most pollinator species found in urban areas are considered generalist flower visitors (Geslin et al., 2013; Maruyama et al., 2024; Youngsteadt and Keighron, 2023), pollinators comprise a diverse group of animals, including both insects and vertebrates, which may respond to the unique conditions imposed by urbanization and interact with flowers in different ways (Nascimento et al., 2020; Silva et al., 2023).

Urbanization also affects the diversity, distribution, phenology, and fitness of plants that are resources for pollinators (Neil and Wu, 2006; Ruas et al., 2022; Youngsteadt and Keighron, 2023). Previous studies showed that urbanization exerts an overall negative impact on the diversity and the distribution of native plants, attributing this decline primarily to shifts in land use, biotic invasion and predominance of a few species used in urban landscaping (Gomes et al., 2023; Hou et al., 2023; Ruas et al., 2022, but see Kühn et al., 2004). These trends result in the biotic homogenization of plant communities, which in turn can affect pollinators and their interactions in the urban landscape (Deguines et al., 2016; Dylewski et al., 2023; Ganuza et al., 2022; Lokatis and Jeschke, 2022). In this context, despite recognizing the critical role of floral resources and urban green spaces for pollinator conservation (Baldock, 2020), information such as the required amount of urban green spaces necessary for sustaining pollinator diversity and fostering their vital ecological interactions remains scarce.

Although a diversity of pollinators is found in urban settings (Fenoglio et al., 2020; Liang et al., 2023; Silva et al. 2023; Tsujimoto et al., 2023), most research focuses on only one or two groups of pollinators, particularly bees. However, even among insects there are important differences (Guenat et al., 2019; Theodorou et al., 2020; Liang et al., 2023). While bees are the most important group of pollinators, as they pollinate most of flowering plants (Ollerton, 2017), taking these insects to represent the effect of urbanization on the wider spectrum of pollinators (e.g., Marcacci et al., 2023; Tavares-Brancher et al., 2024a) and generalizations must be approached carefully. Pollinators are extremely diverse, encompassing variations in foraging behavior and morphological characteristics directly linked to resource acquisition (Geslin et al., 2013; Kawahara et al., 2023; Maruyama et al., 2019; Raguso, 2020), leading to varied responses to urbanization. Consequently, the few existing pollinator-friendly urban planning practices based on such studies may overlook other pollinator groups which are important in specific regions and known to use distinct set of flowers when compared to bees (Danieli-Silva et al., 2012; Machatschek, 2022; Majewska and Altizer, 2020; Nascimento et al., 2020; Orford et al., 2015; Ratto et al., 2018; Smitley et al., 2016; Ssymank et al., 2008). Recognizing the diversity of pollinator groups, and the overall lack of data from some of the most biodiverse tropical regions of the world (Silva et al., 2023; Wenzel et al., 2020), is critical for a better understanding of urbanization effects on pollinators across diverse geographic and ecological contexts.

Understanding the contribution of different pollinator groups goes beyond simply assessing species diversity. Evaluating interaction diversity is essential, as it serves as a key metric for assessing ecosystem health and predicting species loss, thereby offering insights into the functionality, resistance, and resilience of ecosystems (Schleuning et al., 2015; Valiente-Banuet et al., 2015). In this context, the use of network approaches represents an efficient tool to evaluate changes in the interactions between plants and different groups of pollinators according to urbanization (Geslin et al., 2013; Suni et al., 2022; Theodorou et al., 2017; Udy et al., 2020). Network approaches allow the calculation of indices that provide information about the distribution and complexity of interactions in a community, going beyond species diversity indices that provide information about the number and diversity of assemblages (Blüthgen et al., 2006; Landi et al., 2018; Peet, 1974). Therefore, they allow the understanding of how interactions vary in space according to different environmental gradients (Tylianakis and Morris, 2017).

With this in mind, we studied how interaction networks vary between distinct pollinator groups—bees, butterflies, flies, wasps, and hummingbirds—in a tropical metropolis using a comprehensive sampling design. We analyzed whether these pollinator groups present different interactions with flowers and whether their interactions exhibit similar responses to urbanization. Furthermore, we estimated how the increasing number of urban green spaces sampled changed the recorded diversity of plant-pollinator interactions across the city. We addressed the following research questions: 1) Do different levels of urbanization affect the interaction specialization of different pollinator groups? 2) Do the plant-pollinator interaction networks of different pollinator groups exhibit differences in network specialization? 3) Do urban green spaces exhibit consistent patterns of interactions across the city? 4) How many urban green spaces are necessary to represent the diversity of the plant-pollinator interactions across the entire city? By addressing these questions, we aim to deepen our understanding of how urbanization influences pollinator communities and their interactions within urban green spaces.

We hypothesized that with increasing urbanization, a decline in the specialization of pollinator groups would be observed due to biotic homogenization and reduced availability of floral resources in urban green spaces. However, the extent of this decline would vary across pollinator groups due to differences in floral and pollinator traits, resource availability for specific groups and responses to urbanization (Concepción et al., 2015; Graf et al., 2022; Maruyama et al., 2019; Ramírez-Restrepo and MacGregor-Fors, 2017; Winfree et al., 2011). Previous studies have shown that neotropical urban areas can provide diverse floral resources, especially for bees and hummingbirds in contrast to other groups such as butterflies, wasps, and flies (Beaujour and Cézilly, 2022; Nascimento et al., 2020; Maruyama et al. 2024). A higher availability of diverse floral resources represents a greater opportunity to develop more specialized interactions (Fontaine et al., 2005; Ghazoul, 2006). Hence, we also predicted that the former groups of pollinators would show higher interaction specialization than the latter. Regarding the similarity of interactions across the city, we expected that urban green spaces would exhibit high interaction similarity owed to biotic homogenization across the cityscape (Fournier et al., 2020; White et al., 2022). Finally, due to the resulting high interaction similarity, we expected that urban green spaces are to a certain degree redundant in terms of species and interactions composition. In answering these questions, we will show how various pollinator groups navigate the challenges posed by urban environments, thereby contributing to a more holistic understanding of their responses to urbanization and how to promote the conservation of different functional groups of pollinators in cities.

2. Materials and methods

2.1. Study area

The study was conducted in Belo Horizonte, Minas Gerais, Southeastern Brazil (Fig. S1), a city located in the transition zone between two very different ecosystems: Cerrado (savanna dominated) and Atlantic Forest (humid tropical forest) (Duarte 2009). The estimated human population in the city is around 2,530,000 inhabitants (IBGE, 2021). It is one of the first planned cities in Brazil, designed with the concept of a "garden city" and it was known after its foundation for the high density of gardens, public squares and street trees (Duarte 2009). However, in the 1960 s, after facing an explosive growth of its population, the city suffered intense landscape changes that led to reduced the number and diversity of street trees and gardens for the expansion of the urban infrastructure (Duarte 2009). The regional climate shows marked seasonality with cold and dry winters (April – September) and hot and rainy summers (October – March) (Alvares et al., 2013). The mean annual temperature in the city is 19.1 °C, while the annual precipitation is 1546 mm (Alvares et al., 2013).

To record interactions between plants and pollinators, we used an urbanization gradient composed of eleven urban green spaces with varying percentages of impervious surfaces. These points ranged from 16.38 % (less urbanized) to 83.80 % (most urbanized) in impervious surface coverage (Fig. S1, Table S1). This gradient, was defined based on a land cover map of Belo Horizonte from Bhakti et al. (2024), which used a supervised classification (Maximum Likelihood algorithm) of *PlanetScope* satellite imagery (3 m resolution, four spectral bands) from 2020 (see Bhakti et al., 2024 to more details). . Then, five buffers of different sizes (ranging from 1000 m to 2000 m) for each of the urban green spaces were used to estimated impervious surface proportions, to assess whether the levels of urbanization and the relative positioning of the urban green spaces within the urban gradient were influenced by the buffer size. After finding out that it did not vary with buffer size, we used the impervious surface data specifically from the 1000 m buffer to match the 1 km observation transect. The eleven study areas encompassed diverse urban landscapes such as parks, squares, and streets. While we initially aimed for random selection of urban green spaces throughout the city, final selection prioritized collector safety and striving for an evenly distributed gradient of urbanization.

2.2. Plant-pollinator species and interaction sampling

For insects, interaction sampling was carried out between September 2021 and August 2022, in both dry and rainy seasons and performed four times in each season, totaling eight days of sampling at each point. Samplings were carried out whenever possible on sunny days, avoiding cloudy or rainy days because of the reduced pollinator activity. At each urban green space, we covered a one kilometer transect, observing the interactions between insects and flowers for 10 min in each flowering plant. In general, the sampling spanned the morning period since it always started at 7:30 am and ended when reaching one kilometer of route. All insects, including honeybees (*Apis mellifera*), that interacted with flowers were either captured for identification with entomological nets or only recorded if a known species was observed by two collectors. For hummingbirds, procedures were similar, but plant focal observation along the transects lasted from 20 to 30 min to improve interaction recording. During observations, interactions between hummingbirds and flowers were recorded, and hummingbirds were identified in the field. For both insects and hummingbirds, we only considered legitimate visits, where floral visitors made direct contact with the reproductive structures of the flower.

Identification of species followed specific sources. For bees, we followed the classification of Melo and Gonçalves (2005). Genera were identified using Silveira et al. (2002), and the species considering specific taxonomic revisions (see a summary in the Moure's Catalog for Neotropical Bee Species (2012)). For the other insects, we used the following sources: for Lepidoptera (Haroldo Palo Jr., 2017; Warren et al., 2023), Diptera (Grisales et al., 2016; Nihei and De Carvalho, 2009; Wolff and Kosmann, 2016), and Vespidae (Goulet and Huber, 1993; Prezoto et al., 2021). Hummingbirds were identified through field observations and, when necessary, by experts who examined photographs taken in the field. Plants were identified to the lowest possible taxonomic level and classified according to their origin (native or non-native) and life form (shrub, tree and other) following the Flora and Funga of Brazil (reflora.jbrj.gov.br).

2.3. Data analysis

All the data analyses were conducted using R version 4.3.1 (R Core Team, 2023).

We separated pollinators into four groups: *bees*, *butterflies*, *other insects* (which included wasps and flies) and *hummingbirds*. We decided to combine wasps and flies due to the fewer interactions recorded than for other pollinator taxa, precluding the construction of interaction networks separately for each area. After that, we built 43 interaction networks, one for each functional group in each study area. The number is lower than the possible 44 networks because in one area there were no sufficient species/interactions recorded for *other insects* to build the network (at least 2 species of plants and pollinators each). We calculated the sampling completeness for these 43 interaction networks, using the *iNEXT* package (Table S2) (Chao et al., 2016). Sampling completeness is measured as the percentage of observed interaction richness in relation to the expected richness estimated with the Chao 1 richness estimator (Chacoff et al., 2012; Vizentin-Bugoni et al., 2016).

To assess whether the specialization of interactions for the different pollinator groups is affected by urbanization, we calculated the network level specialization H_2' for each interaction network. For this, we used the *networklevel* function of the *bipartite* package (Blüthgen et al., 2006). The network specialization H_2' ranges between 0 indicating low specialization and 1 indicating complete specialization (Blüthgen et al., 2006). To assess the deviation from a random expectation of the calculated H_2' values, we generated 1000 randomized networks and then compared the observed values with the values calculated for each of these randomized networks. We used the *r2dtable* function to generate the randomized networks, in which network size and marginal totals are constrained in the randomizations (Dormann et al., 2008).

We investigated the impact of urbanization on the network specialization H_2' of the interaction networks from the different pollinator groups with Generalized Linear Mixed Models (GLMMs) using the *lme4* package (Bates et al., 2015). We took the network specialization H_2' as the response variable, and pollinator groups, urbanization, and the interaction between these two variables as the explanatory variables and used a Gaussian distribution with appropriate model validations. We checked the model assumptions using the *simulateResiduals*, *testOverdispersion* and *testZeroInflation* functions from *DHARMa* package (Hartig, 2022). We included sampling completeness as a random factor in our models, because it was weakly but significantly correlated with network specialization H_2' (Pearson correlation $r = -0.26$, $p = 0.003$).

To evaluate whether different pollinator groups exhibit distinct specialization of interactions H_2', we employed an *analysis of variance* (ANOVA) utilizing the *aov* function from the *stats* package and the pollinator groups as the independent variable (R Core Team, 2023). Subsequently, to identify which of the pollinator groups were significantly different, pairwise comparisons were performed using the *glht* function from the *multcomp* package (Hothorn et al., 2008). Next, we evaluated if network specialization H_2' of the different pollinator groups showed an association across sampled areas using Pearson correlation tests with the *cor* function from the *stats* package (R Core Team, 2023).

To explore the dissimilarity of interactions along our urbanization gradient and how this changed according to pollinator groups, we computed the β-diversity of interactions following the approach proposed by (Poisot et al., 2012). Our analysis involved two data grouping strategies. First, for each pollinator group, we computed pairwise β-diversity measures among the 11 different urban green spaces, to represent the local scale. Because for "*other insects*" group, we had no sufficient recorded interactions in one urban green space (I10), we ended up with a total of 45 β-diversity estimates. Next, for the 11 local networks (L net) per pollinator group (total of 43), we constructed 11 metanetworks (M net), which represent the regional scale. A metanetwork is defined as a network lumping together all the local interaction networks, to represent a "regional" network, and here we constructed for each local network L_i a corresponding metanetwork M_{-i} in which the only network not included is the local network L_i. Thus, we compared interactions of local networks against all the other networks to assess whether a specific locality displayed a high or low number of distinct interactions in relation to all the remaining networks across the urban landscape.

We used *betalinkr_multi* function from the *bipartite* package to calculate total interaction β-diversity (βWN), and its components turnover of interactions (βST), and rewiring of interactions (βOS) for the networks (Dormann et al., 2008; Poisot et al., 2012; Souza et al., 2021). Given differences in network richness, we applied the recommended additive partitioning method with the *commondenom* argument. This method, originally proposed by (Novotny, 2009), includes a secondary dissimilarity partitioning (βWN and βOS) and yields 'true' components (βWNrepl, βOSrepl) without the dissimilarity caused by richness differences between networks. β-diversity values range from 0 to 1, with higher values suggest greater dissimilarity. After that, we performed Pearson correlation tests between the β-diversity of interactions (βWN) of the different pollinator groups to investigate whether areas demonstrating increased dissimilarity, i.e. featuring a greater number of unique interactions, for one pollinator group also exhibited a similar trend for other pollinator groups.

We also investigated whether urban green spaces exhibited differences in plant and pollinator compositions and whether these differences correlated with the β-diversity of interactions. To achieve this, we constructed distance matrices between urban green spaces using the *vegdist* function from the *vegan* package (Oksanen et al., 2019). We used the *Bray-Curtis* index considering the floral abundance of each plant species. Subsequently, we conducted Pearson correlation tests between plant and interaction β-diversity to assess potential associations. We log-transformed these datasets before conducting the correlation tests.

To assess the representativeness of urban green areas in relation to the overall plant-pollinator interactions across the entire urban landscape, we constructed plant-pollinator interaction networks for each of the 11 sampled areas grouping interactions across all pollinator groups, as well as separated by the four pollinator groups. Subsequently, these interaction networks were randomly combined to generate various combinations, modifying the number of combined areas. Therefore, the first combination included a single randomly chosen area ($n = 11$ different networks), followed by combinations of two areas ($n = 55$), three areas ($n = 165$), four areas ($n = 330$), five areas ($n = 462$), six areas ($n = 462$), seven areas ($n = 330$), eight areas ($n = 165$), nine areas ($n = 55$), ten areas ($n = 11$), and the final combination with eleven areas ($n = 1$). Following this, we computed the mean number of plants, pollinators, and interactions for each of these combinations to determine whether, as the number of combined areas increased, the number of plants, pollinators, and interactions stabilized.

Finally, to elucidate the underlying factors driving the differences in species and interaction patterns, we constructed a matrix expressing the frequency of co-occurrence for each plant-pollinator pair across the urban green spaces. Initially, we created presence-absence matrices for both pollinators and plants to determine their occurrence across different areas. By combining these matrices, we identified the number of areas where each plant-pollinator pair co-occurred, with frequencies ranging from 0 (no co-occurrence) to 11 (co-occurrence in all areas). Using our overall interaction matrix, we then calculated the presence, absence, and frequency of interactions between each species pair. Then, we applied a Mantel test to examine the association between the co-occurrence matrix and the matrices of interaction presence/absence and interaction frequency. By comparing these two matrices, we could investigate whether the observed interaction patterns were influenced primarily by the inherent characteristics of each urban green space, such as plant species composition, or whether they were simply a result of the likelihood of plant and pollinator pairs co-occurring in the same spaces, without a direct effect of urbanization.

3. Results

3.1. Overall results

We recorded a total of 1404 interactions involving 262 plant and 220 pollinator species. *Bees* showed the highest number of interactions (937, involving 205 plant and 97 pollinator species), with *Apis mellifera*, the only non-native pollinator species, interacting with 106 different plant species and being the most frequent pollinator in urban green spaces, present in all 11 of them (see Table S3 for more information on pollinator species occurrence). *Hummingbirds* were involved in 217 interactions (with 57 plant and 7 pollinator species), while *butterflies* accounted for 157 interactions (with 63 plant and 76 pollinator species). The group classified as "*other insects*" recorded 93 interactions (75 plant-fly and 18 plant-wasp), involving 52 plant and 40 pollinator species (29 flies and 11 wasps) (Table S4). Regarding plant families, Asteraceae was the most common (14.12 % of species), followed by Fabaceae (11.45 %), Acanthaceae (5.73 %), and Bignoniaceae (4.58 %). Native species comprised 57.63 % of the total, while 38.55 % were non-native (see Table S5 for further information on plant origin and occurrence in urban green spaces).

3.2. Network specialization across urban green spaces

Urbanization did not significantly influence network specialization H_2' of pollinator groups, which remained relatively constant across the urbanization gradient ($F = 0.230$; $DF = 1$; $p = 0.6345$). Still, pollinator groups differed in network specialization, with *bees* and *hummingbirds* exhibiting lower specialization compared to *butterflies* and *other insects* ($F = 7.489$; $DF = 3$; $p < 0.001$; Fig. 1). At the same time, pollinator groups did not show correlation on network specialization across the urban landscape (Fig. 2), with network specialization varying independently among groups across areas. The only exception was a negative and marginally significant correlation between *hummingbirds* and *other insects* ($r = -0.6991$, $p = 0.0536$, Fig. 2).

3.3. The dissimilarity of plant-pollinator interactions

All sampled areas exhibited highly dissimilar interactions from each other (β-diversity of interactions > 0.70, Fig. 3a). The primary factor contributing to this dissimilarity was species composition, i.e. interaction turnover (Fig. 3a). Nevertheless, areas with more dissimilar interactions for one group were not the same for others in most cases (Table S6, Fig. 4a). Specifically, *bees* and *hummingbirds* exhibited a moderate correlation ($r = 0.57$) in the dissimilarity of interactions (Fig. 4a). In contrast, for *butterflies* and *hummingbirds*, *bees* and *other insects*, the correlations were low and non-significant ($r < 0.25$). Finally, no correlation was observed between the interaction dissimilarities of *bees* and *butterflies*, as well as between *butterflies* and *other insects*, suggesting that the dissimilarity of interactions vary independently for these groups (Fig. 4a).

In terms of unique interactions for each area in relation to the overall urban landscape, all local interaction networks exhibited highly dissimilar interactions (β-diversity of interactions > 0.70) with the metanetworks (Table S7, Fig. 3b). Again, the primary driver of this dissimilarity was interaction turnover (Fig. 3b). Importantly, the areas

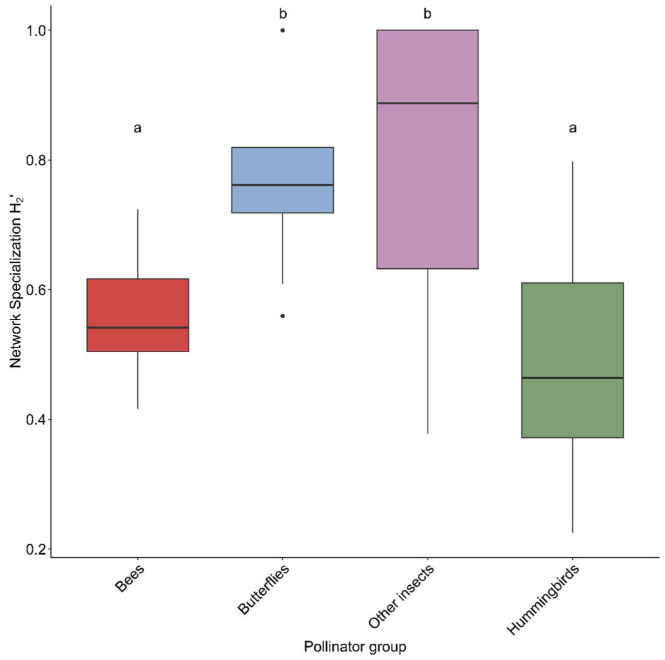

Fig. 1. Network specialization (H_2') of urban pollinator groups. Different letters assigned to the groups denote significant differences in network specialization. Confidence intervals are displayed in the boxplots to provide a visual representation of the variability within each group.

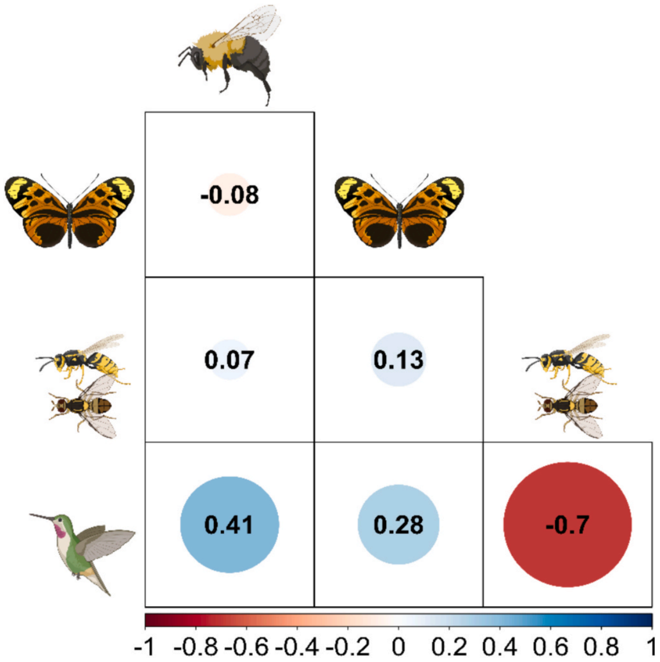

Fig. 2. Correlation results between the network specialization H_2' among pollinator groups. The size of the circles in the panel reflects the strength of the correlation between the network specialization of different pollinator groups, with larger circles representing stronger correlations. Furthermore, the colour of the circles indicates the nature of the correlation, with red representing a negative and blue representing a positive correlation. None of these correlations were significant ($p < 0.05$).

demonstrating high dissimilarity in interactions varied across different pollinator groups (see Table S7, Fig. 4b). Specifically, *butterflies* and *hummingbirds* exhibited the highest positive correlation ($r = 0.64$), while *bees* and *other insects* displayed the highest negative correlation ($r = -0.65$, Fig. 4b), but values were only moderate. In other words, areas with more unique butterfly interactions also tend to moderately have more unique hummingbird interactions, but areas with more unique bee interactions tend to have fewer unique interactions for the *other insects* group. Besides these associations, there were no significant correlations between other pollinator group combinations (Fig. 4b).

Besides dissimilarity in interactions, sampled areas also showed high plant species dissimilarity, with mean β-diversity = 0.87 ± 0.11. The number of plant species in urban green spaces ranged from 28 to 73 (Table S8). Most sampled areas had a higher number of native plants compared to non-native ones (Table S8). Specifically, seven areas presented more native than non-native species, while four showed the opposite pattern (Table S8). The number of unique plant species per urban green space varied from 4 (9.52 %) to 28 (56.00 %). Notably, the site with the highest total number of plant species also had the greatest number of unique species (Tables S3 and S8). Additionally, the number of species shared per urban green space ranged from 21 (61.76 %) to 48 (65.75 %), highlighting the variation in the composition of plants in these spaces. Finally, the dissimilarity of interactions exhibited a high positive correlation with the dissimilarity for plants ($r = 0.71$; $p < 0.0001$).

3.4. *The representativeness of individual urban green spaces*

As expected, the diversity of interactions increased with the number of urban green spaces when considering all pollinator groups together, but our data showed no indication of saturation of the curve in the recorded interactions (Fig. 5a). For the richness of plants and pollinators, though, there are some tendencies for stabilization. When considering each pollinator group separately, we more or less observed similar patterns (Fig. 5b-e), except for *butterflies* that showed higher richness for pollinators than plants, and together with *other insects*, did not show a pattern of stabilization for species recorded (Fig. 5 c and d).

Finally, the co-occurrence of plants and pollinators was positively and moderately associated with the presence ($r = 0.53$; $p = 0.001$) and frequency of interactions ($r = 0.48$; $p = 0.001$). This indicates that the more frequently plants and pollinators co-occurred, the higher the likelihood of interactions occurring. Seven pollinator species (four bee species and three hummingbird species) were present in all urban green spaces, while most pollinator species were found in only one of the areas ($n = 124$, 56.36 %) (Table S9). For plants, *Sphagneticola trilobata* was the only species that occurred in all areas, followed by *Callistemon viminalis* ($n = 10$ urban green spaces), *Rhododendron indicum* ($n = 9$), and *Justicia brandegeeana* ($n = 8$), which occurred in many areas but not all (Table S9). Most observed interactions were between species that co-occurred only once ($n = 540$; 51.48 % of interactions; Table S9). Only interactions between *Sphagneticola trilobata* and the bee species, *Apis mellifera*, *Trigona spinipes*, *Meliponini* spp. (which included the species *Paratrigona lineata*, *Nannotrigona testaceicor* and *Plebeia* sp.), and *Tetragonisca angustula*, were recorded in all urban green spaces (Table S9). The three hummingbird species occurring in all urban green spaces interacted with different plants in some areas because the plants most visited by them were not present in all sampled areas (Table S9).

4. Discussion

Here, we investigated whether distinct groups of pollinators – *bees*, *butterflies*, *flies, wasps,* and *hummingbirds* – exhibit similar interaction patterns across urban green spaces with different amounts of impervious surface in a tropical metropole. Our results showed that pollinator groups differed in network specialization and importantly showed no similarity on its variation across the study sites. Moreover, urban green spaces were highly dissimilar from each other at the local and regional scales, with the interaction dissimilarity mostly explained by interaction turnover. This high dissimilarity in interactions mostly resulted from area-specific co-occurrences of plants and pollinators suggesting that

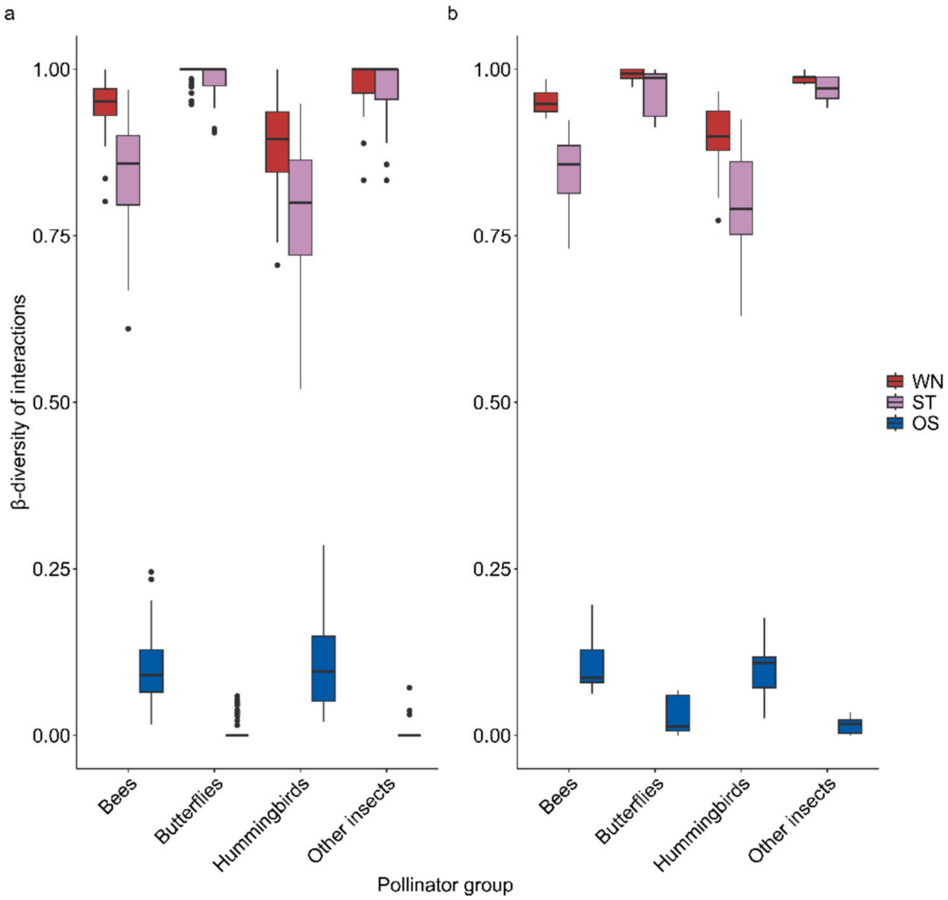

Fig. 3. β-diversity of interactions according to the pollinator groups. A- β-diversity of interactions based in the pairwise comparisons of the urban green spaces: B- β-diversity of interactions based in the pairwise comparisons of the local $I_{1:11}$ and metanetworks $I_{1:11-x}$. WN represents the total dissimilarity of interactions, with OS representing the rewiring, and ST representing the turnover components. Box plots show the median (horizontal line), the lower and upper bounds of each box plot denote the first and third quartiles, and the whiskers above and below the box plot show 1.5 times the interquartile range. The points located outside of the whiskers of the box plot represent the outliers.

few urban areas were insufficient to support a high proportion of plant and pollinator species, and that the full set of green spaces is required to maintain the overall diversity of interactions. This finding underscores the critical importance of conserving a broad spectrum of habitats to safeguard pollinator diversity.

Urbanization, measured as the proportion of impervious surface, did not affect the network specialization for any of the pollinator groups, corroborating previous research showing relative stability of interaction specialization across urban landscapes (Bosenbecker et al. 2024; Fisogni et al., 2022; Geslin et al., 2013; Schneiberg et al., 2020; Tavares-Brancher et al., 2024b; Wenzel et al., 2020). Such lack of difference may happen owing to the prevalence of generalist species across the urban environments (Maruyama et al., 2024; Wenzel et al., 2020). Factors such as diminished overall vegetation cover, increased percentage of impervious surface, the low diversity and fragmented distribution of floral resources, often dominated by non-native plant species, negatively affect specialist pollinators, while pollinators with a broad diet are favored in urban settings (Geslin et al., 2013; Maruyama et al., 2019; Wenzel et al., 2020). Although not affected by urbanization, pollinator groups showed unconcerted variation across urban green spaces. Although bees were the most diverse and responsible for most interactions in the urban landscape, diverse urban pollinator communities comprise more than this group (Liang et al., 2023; Silva et al., 2023), and differences we found for interaction networks indicate that bees alone do not necessarily represent the broader pollinator fauna.

Bees and hummingbirds showed more generalized interactions than butterflies and other insects. This trend is likely influenced by a combination of diverse foraging behaviors, versatile access to floral resources, unique morphological traits inherent to each pollinator group, and the dominance of some species from both groups in urban areas (Geslin et al., 2013; Maruyama et al., 2019; Tavares-Brancher et al., 2024b). For instance, the prevalence of generalist bees, such as *Apis, Trigona,* and *Tetragonisca* genera, underscores their adaptability and resilience in urban environments (Antonini et al., 2013; Muller, 1996; Silva et al., 2023; Twerd and Banaszak-Cibicka, 2019). Similarly, hummingbirds, known for their importance as pollinators in the Neotropics, exhibit widespread occurrence and generalist tendencies in urban areas (Bosenbecker et al. 2024, Maruyama et al. 2024).

In contrast, butterflies, wasps, and flies often engage in interactions with specific plant species, driven by factors such as feeding preferences, morphology, and behavior (Lebeau et al., 2017; Raguso, 2020; Ramírez-Restrepo and MacGregor-Fors, 2017). Butterflies, for example, acquire nectar utilizing elongated proboscises from narrow-tubed flowers (Kawahara et al., 2023). This trait may contribute to the development of more specialized networks even in highly urbanized areas, as not all plants used in urban landscaping meet the specific requirements of this pollinator group. Similarly, flies and wasps can exhibit specific food preferences based on plant characteristics, including nectar type, odor, color, and resource availability (Raguso, 2020). These differences were also reflected in the varying levels of specialization networks presented by the groups in urban green spaces. A notable contrast is observed between hummingbirds and other insects, which exhibit a negative correlation in network specialization. This likely results from the types of plants favored by each group. Hummingbirds are particularly

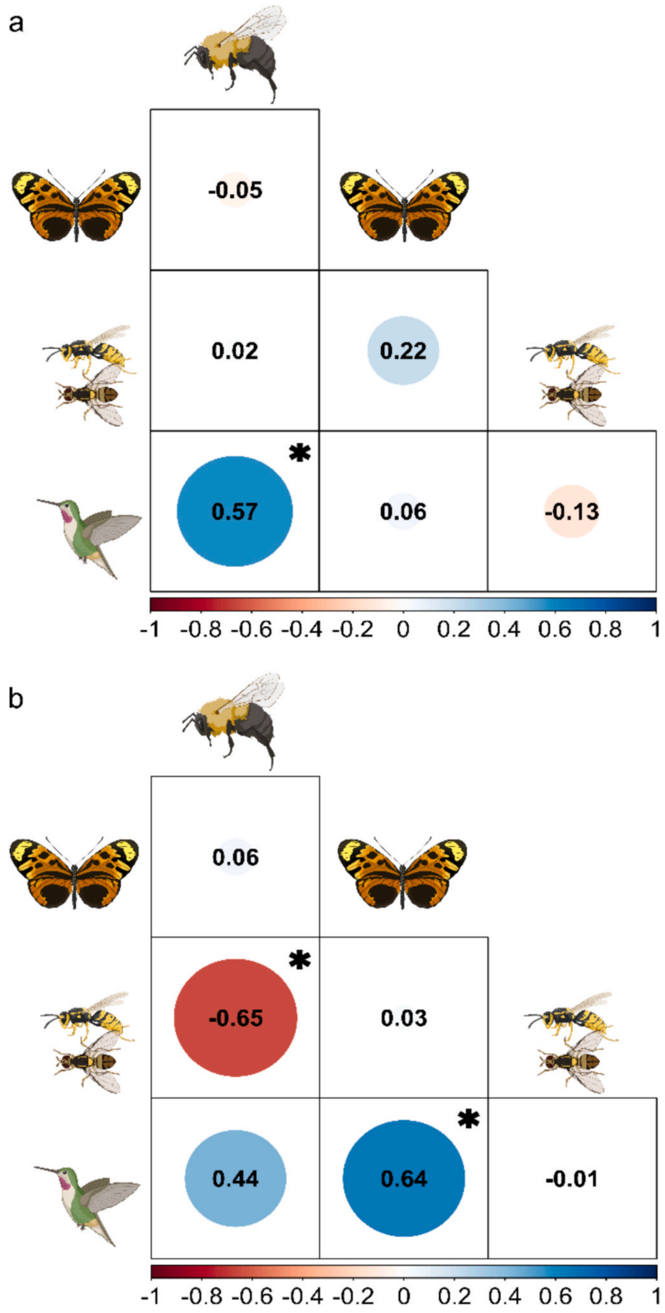

Fig. 4. Correlation of dissimilarity of interactions (WN) between the different pollinator groups. A- Correlation values of the dissimilarity of interactions (WN) between the pollinator groups, based in the pairwise comparisons of the urban green spaces. B- Correlation values of the dissimilarity of interactions (WN) between the pollinator groups, based on the comparison between meta and local networks. The size of the circles in both panels correspond to the strength of correlation between pollinator groups, with larger circles indicating stronger correlations. Additionally, the color of the circles denotes the nature of the correlation, with red indicating a negative and blue indicating positive correlations. Boxes with * represent significant correlations ($p < 0.05$).

attracted to tubular flowers, while wasps and flies are more commonly associated with open flowers (Kodric-Brown, Brown, Byers, & Gori, 1984; McCall & Primack, 1992). Consequently, in urban green spaces where tubular plants are more prevalent, hummingbirds are more likely to engage in specialized interactions, whereas wasps and flies tend to exhibit less specialized behavior. These differences show that the diversity of flowering plants in an environment influence the foraging behavior of different pollinator groups in many ways. In urban environments, a larger pool of floral resources may be available to bees but not for other pollinator groups (Gomes et al., 2023). This may encourage more generalist behavior in terms of foraging for bees. Nevertheless, it is crucial to emphasize the necessity for other multitaxa studies including various pollinator groups, vertebrates and invertebrates, as such studies have been rare (Guenat et al., 2019; Maruyama et al., 2022; Theodorou et al., 2020).

Similarly, features of each urban green space seem to be important also for the dissimilarity of interactions. Previous studies showed that areas that are spatially closer or have similar environmental characteristics will present a low dissimilarity of species and interactions due to biotic homogenization (White et al., 2022). However, contrary to our expectations, all sampled areas were highly dissimilar regarding interactions. These dissimilarities were primarily driven by interaction turnover and may be attributed to either spatial distance or environmental dissimilarity (Trøjelsgaard et al., 2015; White et al., 2022). In our case, as we did not find a direct effect of urbanization, quantified as amount of impervious surface, on interactions, thus local biotic characteristics, such as the composition of floral resources used by pollinators, may modulate the occurrence of pollinators and their interactions (Marcacci et al., 2023; White et al., 2022). In accordance, we found that the urban green spaces were highly dissimilar in plant species composition, with a high correlation between plant composition and the dissimilarity of interactions. Characteristics such as the presence and the proportion of native and non-native plant species, the balance between herbaceous and woody plants, and the diversity of floral and nesting resources represent some local attributes that may vary with the urban green spaces and that are important for pollinators (Bosenbecker et al. 2024; Hou et al., 2023; Maruyama et al. 2019; Nascimento et al., 2020; Tavares-Brancher et al., 2024b). Consequently, these variations can affect the turnover of interactions (Marcacci et al., 2023; White et al., 2022). Additionally, the predominance of native species in the urban green spaces and the location of Belo Horizonte in the transition zone between Cerrado and Atlantic Forest can indicate that the original distribution of the plants still remains. As a result, each urban green space harbors distinct vegetation types. Even in the regional analyses, where there is a discrepancy in richness between local networks and metanetworks, we consistently found turnover as the primary force driving dissimilarities when teasing apart the effect of richness differences.

The correlation analyses for dissimilarity showed that urban green spaces with high interaction dissimilarity for bees also tend to exhibit a high dissimilarity of hummingbird interactions. This likely reflects the foraging characteristics of these groups and the plants they use. Both bees and hummingbirds tend to be generalists in urban areas and utilize a wide variety of plants (Banaszak-Cibicka & Żmihorski, 2012; Silva et al., 2023; Maruyama et al., 2024; Tavares-Brancher et al., 2024b). Hummingbirds prefer tubular and nectar-rich flowers, which are also highly attractive to bees, particularly long-tongued species capable of accessing resources from elongated floral tubes (Kodric-Brown et al., 1984; Mayfield et al., 2001). When considering the specific urban green spaces with high interaction dissimilarity when compared to the entire city (the regional metanetwork), the negative correlation between bees and the group of other pollinators combining flies and wasps, and the positive correlation between hummingbirds and butterflies are likely results of the uneven distribution of floral resources in the study area and the resource preferences of each pollinator group (Gomes et al., 2023; Nascimento et al. 2020). The observed spatial heterogeneity of plant resources in urban environments may create microhabitats that favor certain pollinator assemblages in specific urban green spaces (Dylewski et al., 2019), underscoring the importance of maintain many different urban green spaces to conserve more diverse pollinator assemblages in urban landscapes.

We also found considerable increase in the diversity of recorded interactions with the number of urban green spaces, while plant and pollinator richness saturated more quickly. While the turnover component was the most important factor behind interaction dissimilarity

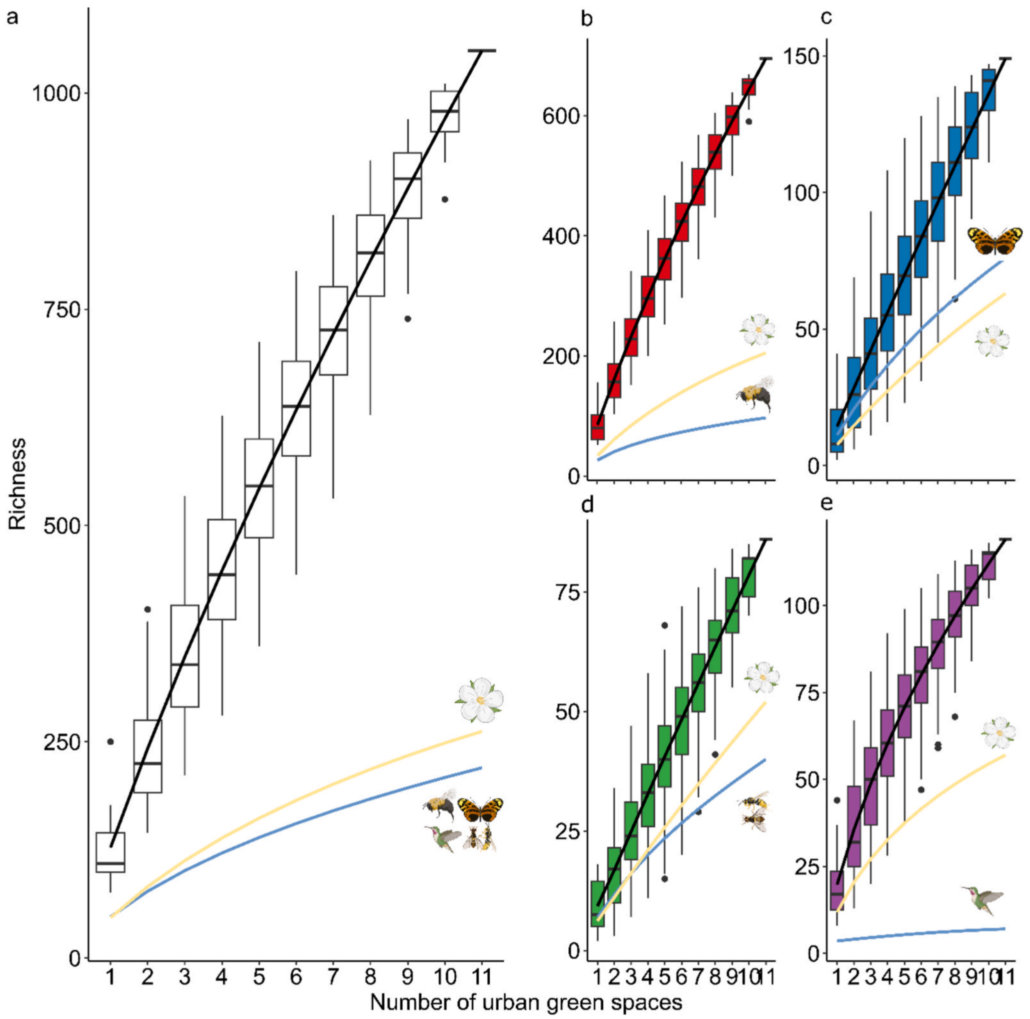

Fig. 5. Richness of interactions, plants, and pollinators across increasing number of urban green spaces. Richness of interactions, plants, and pollinators A- considering all pollinator groups, B- only for *bees*, C- only for *butterflies*, D- only for *other insects* and E- for *hummingbirds*. The yellow lines across the panels represent the mean richness of plants, the blue lines represent the mean richness of pollinators, and the black lines represent the mean richness of interactions. The boxplots represent the data distribution: the horizontal black line inside each box is the median, while the box itself spans from the first quartile (Q1) to the third quartile (Q3), covering 50 % of the data. The lower fence marks the lower limit of the data, calculated as Q1 − 1.5 × IQR (where *lQR* is the interquartile range). The upper fence indicates the upper limit, calculated as Q3 + 1.5 × IQR. The vertical lines (whiskers) indicate the data range without outliers, while points outside the whiskers are outliers, representing extreme values distant from the central pattern.

estimates, we found that species composition per se is not the only driver behind the different patterns for interactions and species. Rather, the co-occurrence of species in each area seems to be relevant, as indicated by the moderate increase of the likelihood of recording an interaction when species co-occur across multiple urban green spaces (Burkle et al., 2013; Peralta et al., 2024).The lower contribution of the rewiring component to interaction dissimilarities also supports this, as co-occurring species did not tend to change their interactions (Poisot et al., 2012) and may be interpretated as species having a limited flexibility in changing interactions. Previous studies have shown that the spatial overlap of plants and pollinators is a major factor in recording interactions (Bartomeus et al., 2016; Peralta et al., 2024). However, here, we found that a few species co-occur in all green spaces and most interactions occurred between species that co-occurred in only one of them. This probably happened due to the varying compositions of plants and pollinators across the cityscape, which reduces the likelihood of these species interacting in multiple areas and increases the number of unique interactions.

Our results highlight important implications for urban management. First, a diversity of urban green spaces is necessary to support a high diversity of pollinators and ecological interactions. Consequently, urban planners should aim for heterogeneous urban landscapes, particularly in terms of plant diversity. In the case of Belo Horizonte, a tropical city with an unequal distribution of urban green spaces and floral resources (Pena et al. 2016; Gomes et al. 2023), there is a need to maintain and increase the number of urban green spaces to capture the heterogeneity of the urban landscape. This heterogeneity can also be achieved while prioritizing the use of native plant species in urban landscaping, which is essential in areas currently dominated by a few dominant non-native species. Second, the promotion of this diversity should encompass different pollinator groups and their specific requirements. Despite being a “garden city,” Belo Horizonte shows an unequal distribution of resources for pollinator groups (Gomes et al. 2023). Therefore, the use of plants known to be used by a wide range of pollinator groups combined with plants that are important for specific groups (e.g. oil flowers for bees) are an interesting strategy to promote different pollinator groups and their interactions. Finally, it is important to emphasize that connectivity and the permeability of the urban matrix remain critical factors for maintaining biodiversity in cities. Therefore, it is necessary not only to promote plant diversity but also species co-occurrence to formulate effective conservation strategies, such as enhancing the connectivity of urban green spaces (Graffigna et al., 2024). For this, establishment of ecological corridors and more permeable urban matrices would allow pollinators to access different habitats, thereby facilitating interactions and enhancing the resilience and functionality of ecosystems (Graffigna et al., 2024).

5. Conclusion

In summary, we showed that while interaction of pollinator groups did not respond to increasing proportion of impervious surface in the landscape, they differed in their interaction specialization overall and in how it varied across the urban landscape. Moreover, urban green spaces harboring the most unique interactions differed between pollinator groups. Such differences may be explained by the diversity and distribution of specific floral resources. Therefore, conservation strategies exclusively targeting one pollinator group may fail to promote the conservation of others. Instead, a more holistic approach that considers the specific needs of each pollinator group and interactions is needed. The unexpectedly high dissimilarity of interactions across the urban landscape also underscores the necessity of having multiple green spaces with different characteristics to maintain pollination functions in urban areas. This means that pollinator-friendly urban planning requires consideration of diversity for both pollinator groups and urban green spaces. We believe that prioritizing these features in urban green spaces will not only enhance the habitat quality for pollinators but also sustain the vital ecosystem function they provide.

CRediT authorship contribution statement

Victor H.D. Silva: Writing – review & editing, Writing – original draft, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Ingrid N. Gomes:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation. **Camila Bosenbecker:** Writing – review & editing, Methodology, Investigation, Funding acquisition, Data curation. **Robert R. Junker:** Writing – review & editing, Writing – original draft, Supervision, Formal analysis, Conceptualization. **Pietro K. Maruyama:** Writing – review & editing, Writing – original draft, Supervision, Formal analysis, Conceptualization.

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. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.landurbplan.2025.105361.

Data availability

Data will be made available on request.

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