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# Plant-hummingbird interaction networks in urban areas: Generalization and the importance of trees with specialized flowers as a nectar resource for pollinator conservation

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## ABSTRACT

Cities harbour considerable biodiversity and there has been an increased concern about the conservation of pollinators in urban environments. Here, we evaluated how urbanization affects plant-hummingbird interactions at two spatial scales. First, in a medium-sized city from southeastern Brazil (> 600,000 inhabitants), we contrasted interaction networks from urban and natural areas, and used artificial nectar feeder stations to evaluate changes in the composition of hummingbird assemblages across an urbanization gradient. Second, we compiled data on six urban plant-hummingbird interaction networks from south and southeastern Brazil to identify the characteristics associated with the most important plants. Locally, urbanization affected hummingbird communities by promoting higher generalization and dominance by more aggressive hummingbirds. Notably, specialized long-billed hermits were absent both in the urban interaction network and at feeder stations from more urbanized areas. Across networks, trees were more important for hummingbirds than shrubs/herbs as were specialized ornithophilous flowers in relation to non-ornithophilous flowers. Plant origin (native or exotic) did not matter. Our results indicate that urban plant-hummingbird communities are organized differently than their counterparts from natural areas, which usually feature key hermits and few trees. Since hermits provide important pollination services, especially for specialized ornithophilous plants, initiatives such as green corridors and preference for native plants with specialized hummingbird-pollinated flowers in urban landscaping may contribute to community restoration and ecosystem functioning.

## 1. Introduction

Cities, large and small, are part of our modern world and should be considered as an integrative part of conservation practice (Sanderson and Huron, 2011). Urban areas may harbour considerable biodiversity, with evidence that urban green spaces, including remnants of native vegetation as well as artificial habitats such as parks and gardens, have

an important role in the conservation of animals and plants (Aronson et al., 2017). In spite of this, there is still much to know about how biodiversity persists and can be promoted in urban areas. For instance, urbanization may lead to increased biotic homogenization and favour generalist species, with negative consequences for the functioning of ecosystem processes in urban areas (Aronson et al., 2014; Chace and Walsh, 2006; Coetzee et al., 2018; Pauw and Louw, 2012). In this

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context, there has been a recent and increased concern over conservation of pollinators in urban environments, with the notion that pollination is one of the major ecosystem services provided by nature (Hall et al., 2017; Knight et al., 2018). Studies on urban biodiversity, however, are still largely lacking in tropical regions when compared to temperate Europe and North America (Aronson et al., 2014; Kowarik, 2011), even though some interactions such as those involving plants and pollinators are more prevalent in tropical than temperate areas (Ollerton et al., 2011). Moreover, tropical plant-pollinator communities often include pollinator groups not commonly found in temperate regions, such as vertebrates (Vizentin-Bugoni et al., 2018). Calls for conservation and valuation of pollinators in urban areas, however, have been mostly centred on insect pollinators (e.g., Baldock et al., 2015; Hall et al., 2017). Considering the importance of vertebrate pollinators for many plant species (Ratto et al., 2018), to understand how they persist in relation to urbanization would contribute to pollinator conservation efforts globally (Dicks et al., 2016).

Birds that visit flowers to feed on nectar are the most speciose vertebrate pollinators in the world (Cronk and Ojeda, 2008; Fleming and Muchhala, 2008), with hummingbirds distributed throughout the Americas constituting the most diverse and specialized group of avian pollinators (Fleming and Muchhala, 2008; Zanata et al., 2017). Despite their observed morphological and feeding specialization, hummingbirds show great flexibility in resource use, as evident from their frequent use of artificial nectar feeders and plants showing adaptations to other pollinators (Arizmendi et al., 2007; Maruyama et al., 2013; Sonne et al., 2016; Waser et al., 2018). This flexibility may contribute to their persistence in urban environments, although resource use adjustment has been shown to be species-specific in natural areas (Tinoco et al., 2017). Currently, knowledge on how avian pollinators persist in urban areas remains scarce (but see e.g., Coetzee et al., 2018), including for hummingbirds. Studies indicate that urbanization has drastic effects on the ecology of hummingbirds, for instance by promoting range expansion and changes in migration dynamics for Northern hemisphere species (Greig et al., 2017). Few other studies consider their interaction with nectar plants at the community scale, mostly in remnants of native vegetation surrounded by an urban matrix (Matias et al., 2016; Mendonça and Anjos, 2005; Rodrigues and Araujo, 2011). Thus, we lack more comprehensive studies investigating the community structure of hummingbirds in urban areas, contrasting their organization between urban and natural areas, and considering distinct communities simultaneously.

One promising way to assess the health and functioning of plant-pollinator interactions in urban areas lies in the use of interaction networks (Baldock et al., 2015; Kaiser-Bunbury and Blüthgen, 2015). Considering the assemblage of plant and pollinators interacting at the community level as a network of interactions allows a better understanding of the structure and dynamics of these systems (Bascompte and Jordano, 2007; Knight et al., 2018; Vizentin-Bugoni et al., 2014), and could contribute to conservation efforts (Kaiser-Bunbury and Blüthgen, 2015; Ramírez-Burbano et al., 2017). To provide insights on the structure, functioning and potential conservation and management strategies of avian pollinators in urban areas, we evaluated how urbanization affects plant-hummingbird interactions at two spatial scales in Brazil. First, in a medium-sized city (> 600 thousand inhabitants), we evaluated changes in the structure between two plant-hummingbird interaction networks, one from urban and another from preserved natural areas. Also, in the same city, we evaluated changes in hummingbird assemblages across an urbanization gradient using feeder stations as standardized sources of artificial nectar. Second, considering a broader regional scale, we gathered information on urban plant-hummingbird interaction networks in six distinct localities from the southeast and south of Brazil, to identify the most important nectar plants for hummingbirds within the urban communities. Here, we ask which characteristics of the nectar plants are associated with their importance across the networks of interactions with hummingbirds.

For the focal city, we expected higher generalization of the plant-hummingbird network in the urban area and a marked difference in the composition of hummingbird assemblages, due to the tendency of habitat and diet specialists to disappear from urban areas (Coetzee et al., 2018; Devictor et al., 2007). As for the regional cross-network analyses, we expected alien plants, frequently found in urban landscapes (Aronson et al., 2014; Kowarik, 2011; Moro and Castro, 2015), to be more important, because generalist hummingbirds that persist in urban areas show a higher probability of including alien plants in their interactions (Maruyama et al., 2016). Whether a plant showed floral traits characteristic of bird pollination syndrome, i.e., ornithophily, was expected to be unimportant because hummingbirds are flexible in nectar resource use (Maruyama et al., 2013; Waser et al., 2018). Finding which of these characteristics make an “important hummingbird supporting plant” will constitute the first step in the conservation and management of these pollinators in urban areas.

## 2. Material and methods

### 2.1. Gradient of urbanization and plant-hummingbird interactions

The first part of the study was carried out at the city of Uberlândia, state of Minas Gerais in Brazil (18°55'23"S, 48°17'19"W). The city had a population of around 660,000 residents as of 2015 in an area of 4115 km<sup>2</sup>, of which 219 km<sup>2</sup> is urbanized ([www.cidades.ibge.gov.br](http://www.cidades.ibge.gov.br)). The natural vegetation in the region is *Cerrado*, the Neotropical savannah ecosystem in Central Brazil characterized by patchy distribution of forests and other vegetation types embedded in typical shrubby savanna areas (Silva and Bates, 2002). Climate is seasonal, characterized by a warm rainy season from October to March and a cooler dry season from April to September. Mean monthly temperature is 22.8 °C and mean annual precipitation is 1482 mm (Cardoso et al., 2009).

We recorded hummingbird visits to plants in the Umuarama campus of the Federal University of Uberlândia (18°53'04"S, 48°15'36"W, Fig. S1), which is surrounded by a residential neighbourhood. We recorded hummingbird visitation frequency on plants producing nectar through focal plant observations, in 2–31 plant individuals per species according to their abundance in the study area, from September 2007 to August 2008. Observations were carried out from 05:30 h to 18:00 h during daylight, in days with good weather conditions, totalling 126.2 h. Each visit was defined from the moment the hummingbird started probing the flowers, until it left the plant individual. During each visit, we identified and characterized hummingbird behaviour, whether it visited the flower legitimately or acted as a floral larcenist, i.e. robber or thief (Maruyama et al., 2015). We built a network considering all visits as well as another network considering only the legitimate interactions, to facilitate the comparison with a natural area network (see below). While the former relates to an energetic perspective for the birds, the latter indicates a potential of pollination for plants.

We built quantitative interaction networks considering the number of visits as a measure of the strength of the interactions. Because the number of flowers varies among individuals and species, we considered a visit every time a hummingbird approached an individual plant and fed on at least one flower, and left. We then calculated several complementary network metrics that characterize distinct aspects of the network structure: Nestedness quantifies the degree to which interactions of specialized species are subsets of interactions of the more generalist species in the networks and was calculated as the Nestedness metric based on Overlap and Decreasing Fill - NODF index and its quantitative variation weighted NODF, i.e., wNODF (Almeida-Neto et al., 2008; Almeida-Neto and Ulrich, 2011). Connectance is calculated as the proportion of the possible links in the network that are actually realized (Jordano, 1987). Complementary specialization,  $H_2'$ , is an index designed to measure network-wide specialization for quantitative interaction matrices and describes how species restrict their interactions from those randomly expected based on partner availability

(Blüthgen et al., 2006). Lastly, modularity quantifies the prevalence of interactions within modules in relation to interactions between modules, and it was calculated using the DIRTLPAwb+ algorithm (Beckett, 2016). The organization of interactions into modules provides information on how the interactions are partitioned in the community (Maruyama et al., 2014, 2015). We estimated the modularity with the function *computeModules()* in *bipartite* package (Dormann et al., 2008) setting the number of steps to  $10^7$  and default options.

The significance of these network-level metrics was assessed by comparing the observed values to those generated by null models. For NODF, we used the *r1* algorithm from *vegan* package (Oksanen et al., 2018), which uses the row and column marginal frequencies as probabilities to distribute the presence of interactions. For quantitative indices, we used the Patefield algorithm (Patefield, 1981) to generate simulated matrices with the same marginal totals as the original network, so that species interacting with highest frequency (or least) in the observed matrices were the same in the simulated ones. We estimated the 95% Confidence Interval (CI) for each metric from the simulated values, and a metric value was considered significant if it was higher than the CI. All network analyses were conducted with the *bipartite* package (Dormann et al., 2008). The urban network was compared to another network previously described for a natural reserve in the municipality, the Panga Ecological Station (hereafter 'Panga'; 19°10'27"S, 48°23'51"W, Fig. S1, 222 observation hours), which represents the natural setting of plant-hummingbird interactions in the original vegetation from the study region. The Panga network considered only the legitimate interactions (see Maruyama et al., 2014 for details) and was subjected to the same network analysis as the urban network.

Besides comparing the networks at the two extremes of the urbanization gradient, we characterized the hummingbird assemblages across 12 sampling points (Fig. S1 and Table S1) with distinct levels of urbanization and vegetation characteristics. The sampling points were distributed in three city squares, two urban parks and three natural reserves. Each set of three sampling points correspond to one of the four habitat categories with increasing vegetation density: (1) city squares; (2) urban parks; (3) natural savannah; and (4) forest areas. While (1) and (2) correspond to urban settings, (3) and (4) represent the natural vegetation types from the study region. All sampling points were at least 1 km distant from each other and data collection was carried out in 2010. City squares are paved areas, with scattered ornamental plants. Urban parks in contrast have some remnant of natural vegetation, embedded in paved and managed lawn areas. Natural reserves sampled are distant 8.4 (F1), 9.3 (SA1, SA2) and 30.8 km (SA3, FO2, FO3) from the city centre. We considered the sequence from city squares to urban parks and then natural reserves to represent an urbanization gradient.

We used artificial nectar feeder stations with no restriction to hummingbird access to attract and characterize the hummingbird assemblage in each area. In each sampling point, we installed a feeding station with four nectar feeders (Fig. S2). The sugar water in the feeders had 20% (g/g) concentration, checked with a pocket refractometer, and had the same volume in each feeder (ca. 300 ml). We installed the feeding station at each sampling point 42 h. Before the beginning of the observations and recording of hummingbird species, so that birds could find the resource and get used to it. The amount of sugar water in the feeders was sufficient to last until the beginning of the observations. Just before our observations started, we replaced the feeders in each station with clean ones, containing the same amount of water and sugar concentration. The feeding station was removed from the sampling point at the end of each sampling. We used feeders in order to offer a large amount of resource in one spot to attract all the potentially occurring hummingbird species at a specific site, as well as to standardize the amount of resource offered during each sampling for comparisons across the gradient of urbanization. Artificial feeders are known to attract a diverse number of hummingbirds, and at the same time, by placing them in each site during a short period of time, we avoid attracting species that do not usually occur at the study area (Sonne et al.,

2016).

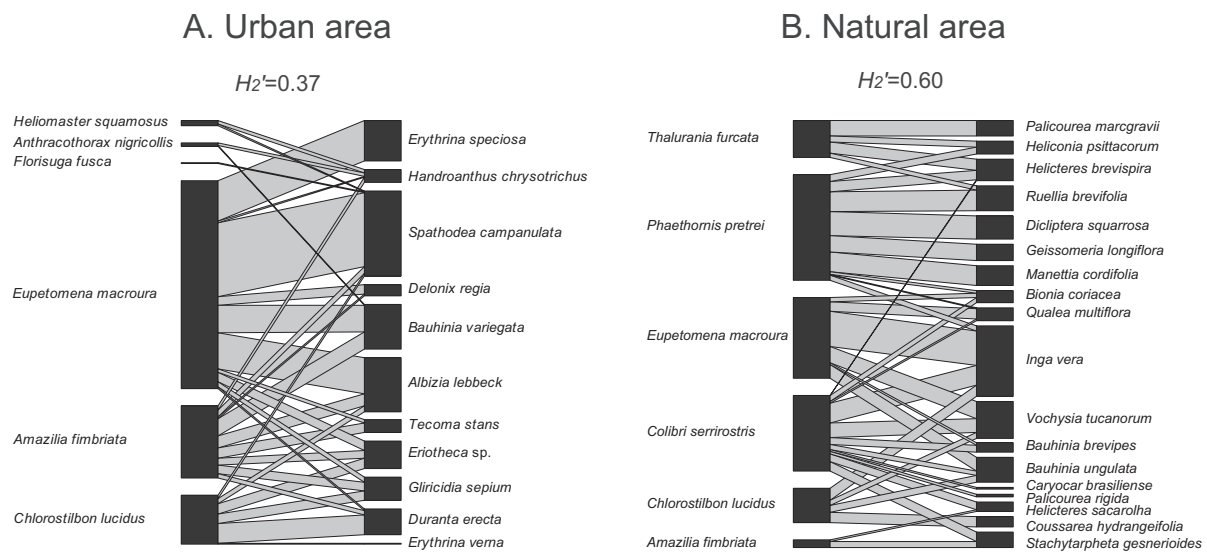
At each sampling point we recorded hummingbirds at the feeding stations from 07:00 h to 12:00 h, five times during the rainy season (January to April) and five times during the dry season (June to September). We sampled points in random sequence, always in days with good weather conditions, with a minimum interval of one week before the same point was sampled again. In total, each point was sampled for 50 h, totalling 600 observation hours. Observations were conducted with use of binoculars and we recorded the hummingbird species at the feeding stations, counting the number of visits defined from the moment a hummingbird entered the observer's field of view until it left, but only recorded the visit if it probed at the artificial nectar feeders. We also recorded any instance of agonistic interactions among hummingbirds. Although agonistic interactions were common, the structure of the feeding station with feeders positioned at each point of the cross kept any particular hummingbird from dominating the nectar source and preventing other hummingbirds from visiting.

We used the hummingbird species and their frequency of visits to feeding stations to contrast the community composition across the gradient of urbanizations with a non-Metric Multidimensional Scaling (nMDS), using the frequency of visits as reflecting their activity in the area. We first standardized the data to zero mean and unit variance then computed Bray–Curtis dissimilarity indices among communities associated to each locality. The resulting dissimilarity matrix was used for nMDS with function *metaMDSiter()* in *vegan* package (Oksanen et al., 2018). Most common species were also projected in the ordination plot by computing their weighted average scores to evaluate their association with localities (rare species with < 100 records were omitted for better visualization). We conducted a permutation test ( $n = 999$ ) to assess the differences in species composition among habitat types, using the function *factorfit()* in *vegan* (Oksanen et al., 2018). We additionally computed an Analysis of Similarities (ANOSIM) and Principal Coordinate Analysis (PCoA) in the same dissimilarity matrix, but results were similar and are only reported in the Supplements (Fig. S3).

## 2.2. Identifying key plant species in urban plant-hummingbird networks

For the second part of the study, we compiled data on six plant-hummingbird assemblages from urban areas in the south and south-eastern Brazil to identify what characterizes an important plant resource for hummingbirds. Besides the aforementioned urban network from Uberlândia, we gathered data on five other localities, which sampled other university campuses and urban neighbourhood areas such as pavement and gardens (Marcon, 2016; Mendonça and Anjos, 2005; Fig. S1 and Table S2). For all areas, except one, we built quantitative interaction matrices based on focal observation of hummingbird visitation to plant individuals, in which the frequency of interaction represents the visit of a specific hummingbird species to a plant species. For one network from Londrina, state of Paraná, the frequency of interaction depicts the number of days a particular hummingbird species was recorded visiting a particular plant species within the sampling transect (Mendonça and Anjos, 2005). While this difference in the sampling occurs, all species level metrics were standardized for plants and hummingbirds separately within the networks by subtracting the mean value and dividing it by the standard deviation, i.e., z-score, before subsequent use in the analysis, so that all metrics reflects the role of one species in relation to other species within a network (e.g., Maruyama et al., 2016; Vidal et al., 2014). We considered all hummingbird visitations, including illegitimate nectar consumption (Maruyama et al., 2015), because we were interested in the role of the plants as nectar source for these birds. For all networks, we also estimated the sampling completeness of the interactions, contrasting the observed number of specific plant-hummingbird combinations, i.e., interaction richness, with the one estimated through Chao 1 estimator (Chacoff et al., 2012; Ramírez-Burbano et al., 2017; Vizentin-Bugoni et al., 2016).





**Fig. 1.** Plant-hummingbird interaction networks from urban (A) and natural (B) areas in Uberlândia, Minas Gerais, southeastern Brazil. The urban area network shows less interaction partitioning and, thus, it is less specialized than the observed in natural Cerrado area in the region. See also Table 1.

We calculated indices that reflect distinct aspects of the importance of a plant species within the interaction networks: degree ( $k$ ) expressing the number of hummingbird partners in the network; species strength ( $s$ ) as the sum of the proportions of interactions performed by a given plant species across all its interacting hummingbirds; betweenness centrality ( $bc$ ) quantifying to what extent a species lies on the shortest path among other pairs of species, thus indicating the importance of a plant species as a network connector; closeness centrality ( $cc$ ), which quantifies the proximity of a species to all other species in the network; and species-level specialization ( $d'$ ), which quantifies how exclusive the interactions of a species are in relation to the availability of partners. All species-level indices were quantified by the function *specieslevel()* in *bipartite* (Dormann et al., 2008). While  $k$  is based only on the binary information of the interactions,  $s$  and  $d'$  are based on the interaction frequency. For centrality measures  $bc$  and  $cc$ , we calculated the quantitative extensions available in *bipartite* (Dormann et al., 2008). Although reflecting distinct aspects of the role of species, all indices, except  $d'$ , were correlated (Pearson's  $r > 0.78 \pm 0.14$ , mean  $\pm$  sd). Hence, we performed a Principal Component Analysis (PCA) on the four correlated indices to generate a new index which synthesizes the overall importance of a species in the network (Sazima et al., 2010; Vidal et al., 2014). The first PC axis explained 72.6% of the overall variation in plants, and was then used as an index for species importance in the network (Sazima et al., 2010; Vidal et al., 2014).

We used this index of species importance (PC1) and  $d'$  as a response variable in Linear Mixed Models using the *lme4* package (Bates et al., 2015). As fixed factors, we included for plants: (1) Status, as native or alien species, defined according to the Brazilian Flora ([reflora.jbrj.gov.br](http://reflora.jbrj.gov.br)). Since this database also provides information on distribution of plants according to states and biomes, plants that were found outside their natural areas of occurrence, even if Brazilian natives, were classified as aliens (Brazilian Exotics in Table S3). The same was done for species for which no matching record could be found in the Brazilian Flora, even though regarded as a valid species in a wider database (Kew Gardens The Plant List - [www.theplantlist.org/](http://www.theplantlist.org/)), as well as known ornamental hybrids (see Table S3); (2) Plant growth form/habit, specifically contrasting trees, shrubs and other smaller forms such as herbs and climbers (the latter two grouped); and (3) Whether presenting flowers conforming to the traditional concept of specialization to bird pollination, i.e. ornithophily (Cronk and Ojeda, 2008; Ferreira et al., 2016). Although we standardized the species-level indices within the community before pooling the data, some plants were found repeatedly

across distinct networks, so we included the plant species identity as a random factor in the analysis. To attain a probability for each categorical fixed factor, we compared the model with and without each factor using the function *Anova()* in the *car* package (Fox and Weisberg, 2011). For plant habit, after finding a significant difference, we also conducted a post hoc Tukey test for multiple comparisons using the function *glht()* in the package *multcomp* (Hothorn et al., 2008). All analyses described were conducted in R (R Core Team, 2016).

### 3. Results

#### 3.1. Gradient of urbanization and plant-hummingbird interactions

Considering all visits to plants, 501 interactions among six hummingbird species and 11 plant species were recorded in the urban network from Uberlândia (Table S4, Fig. 1). Removing the illegitimate interactions from the matrix did not change the matrix size (i.e. species richness), but the number of interactions decreased to 438 (Table S4). Overall, removing illegitimate interactions did not change network metrics or the significance of the parameters (Table 1). However, when compared to a network describing the typical community of plants and hummingbirds from the natural area of the region, the urban network was considerably less specialized and modular, indicating less niche partitioning among hummingbirds visiting flowers (Table 1, Fig. 1).

For the analysis across urban to natural gradient with artificial feeders, 10 hummingbird species were recorded, with a total of 3100 visits (Table S5). Visits were more frequent in urban parks (958 visits, 8 species), followed by savannah (845 visits, 8 species), city squares (708 visits, 3 species) and forests (589 visits, 4 species). The optimal nMDS ordination with two dimensions (Fig. 2A) resulted in a solution with stress of 4.03% ( $r^2 = 0.99$ ). Most frequent hummingbird species were, in order, *Eupetomena macroura* (Fig. 2B), *Thalurania furcata*, *Amazilia fimbriata*, *Chlorostilbon lucidus* and *Phaethornis pretrei* (Fig. 2B; Table S5). The distribution of localities in the ordination showed that city squares were characterized by the presence of *E. macroura*, and these communities were more similar to natural open savannah areas. Urban parks that contained patches of natural forest were more similar to forest communities, except for one park where *C. lucidus* was very frequent (Urban Park #1; Table S5). A permutation test indicated that habitat type influenced species composition (goodness of fit,  $R^2 = 0.79$   $p = 0.002$ ). We observed a total of 759 agonistic interactions at the feeder stations, the aggressions being more frequent in open areas in

**Table 1**

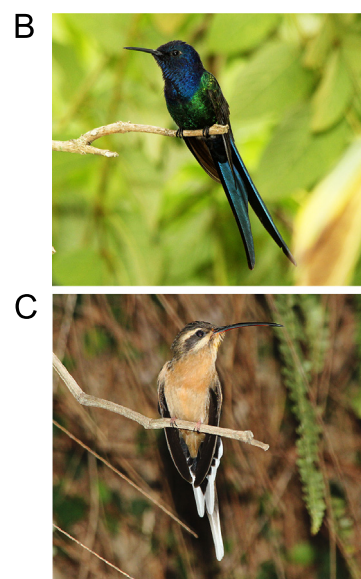
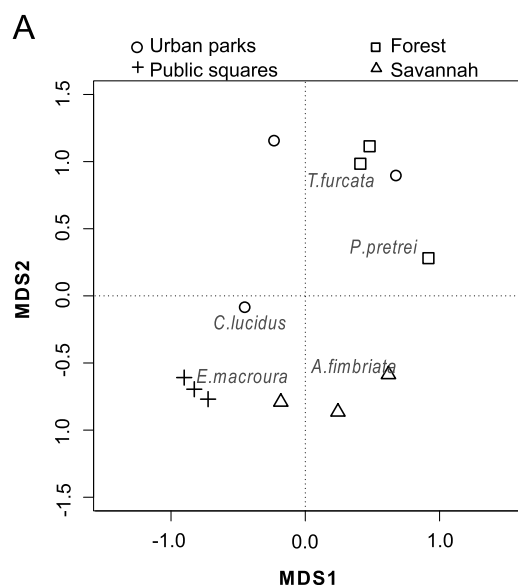
Comparison of network parameters and metrics among urban and natural area networks from Uberlândia, Minas Gerais, southeastern Brazil. For the urban area, we show values for both the network built considering all interactions (visitation) as well as the one considering only the legitimate interactions in which hummingbirds touched the reproductive structures of the flowers, thus characterizing potential pollination as in the natural area (pollination). Asterisks indicate network metrics that were significant in comparison to null models.

	Urban area		Natural area
	Visitation	Pollination	
Hummingbird richness	6	6	6
Plant richness	11	11	18
Interactions	501	438	554
Nestedness			
<i>NODF</i>	68.9	68.9	41.0
<i>wNODF</i>	38.4	36.7	18.9
Connectance	0.45	0.45	0.33
Specialization			
<i>H<sub>2</sub>'</i>	0.37*	0.33*	0.60*
Hummingbird < <i>d'</i> >	0.32*	0.28*	0.58*
Modularity ( <i>Q</i> )	0.27*	0.27*	0.49*
Sampling completeness	93.0%	87.0%	98.6%

relation to the forest habitat (Table S6). *Eupetomena macroura* was by far the most aggressive species around the stations, with 65.1% of the attacks initiated (Table S6).

### 3.2. Identifying key plant species in urban plant-hummingbird networks

We recorded 94 plant species (Table S3) used as nectar source by 14 hummingbird species (Table S7) across six urban plant-hummingbird interaction networks from the south and southeastern Brazil. These networks varied in their sampling completeness (Table S2), stressing the importance of standardization of the species indices values before the analysis. Analysing species-level contribution of plants to networks (Fig. 3), we found that while alien and native plants did not differ in their importance ( $\chi^2 = 0.01$ ,  $p = 0.91$ ), ornithophilous plants were more important than non-ornithophilous ones ( $\chi^2 = 7.38$ ,  $p = 0.006$ ). Plants differed in their importance according to habit ( $\chi^2 = 17.34$ ,  $p < 0.001$ ). Specifically, trees were more important than shrubs as well as other growth forms, while the latter two were equally less important (Tukey *post-hoc* comparisons,  $p < 0.05$ , Fig. 3C). In contrast,



**Fig. 2.** A. nMDS ordination plot with data from hummingbirds attracted to artificial feeding stations. The solution with two dimension had stress value of 4.03% and permutation test indicated that habitat distinct species composition (goodness of fit,  $R^2 = 0.7904$   $p = 0.002$ ). Different points indicate distinct habitats, and we also show the most commonly recorded species, with  $n > 100$ , showing their habitat affinity; B. Swallow-tailed Hummingbird, *Eupetomena macroura*; C. Planalto Hermit, *Phaethornis pretrei* (Photographs by Ivan Sazima; Colour online).

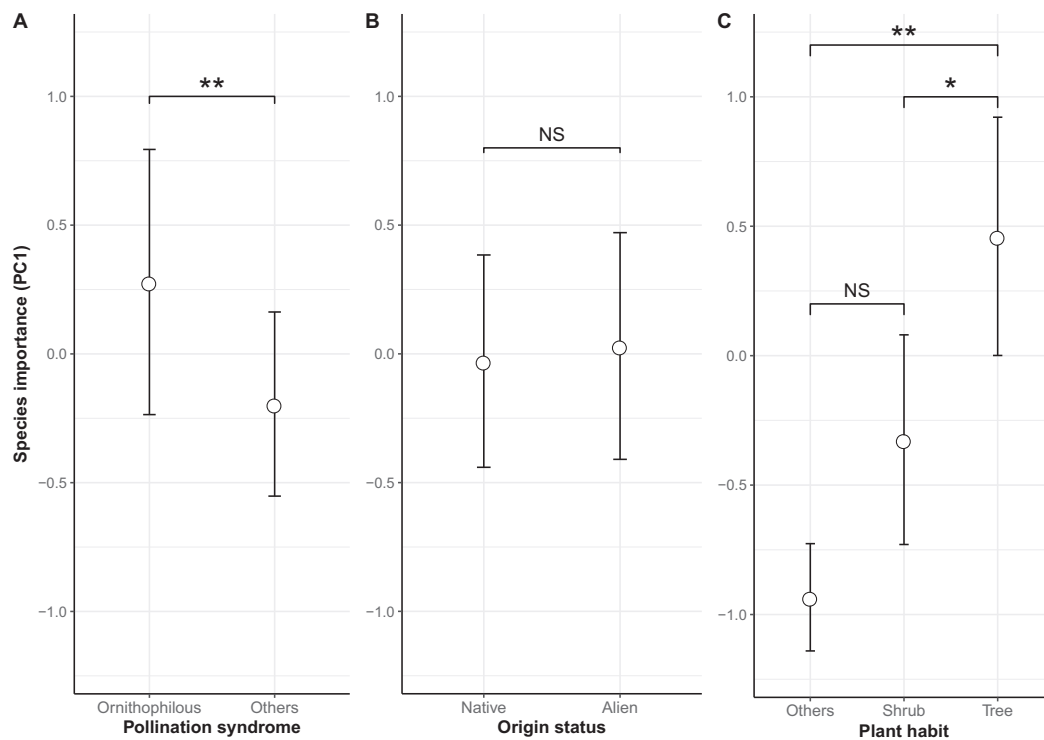
when analysing species-level specialization  $d'$ , none of the fixed factors were significant ( $p > 0.05$ ). There was no significant interaction among the predictors.

## 4. Discussion

Although there is a consensus that urbanization has drastic effects on biodiversity, we still lack knowledge on how it affects species interactions and many of the ecological processes at some of the most biodiverse regions in the world. We here show that urbanization led to more generalized hummingbird-plant interactions and assemblages in urbanized areas when compared to original natural habitats. Moreover, cross-networks analysis indicated that some plant traits are related to the importance of species within the networks, namely highly-rewarding trees and plants that show specialized adaptations to bird pollination (ornithophily).

When comparing the plant-hummingbird interaction networks from natural and urban areas, we found that the urban area network was considerably more generalized than the natural area network, with lower specialization and modularity. This is likely related to the absence of the functionally specialized hermit hummingbird, *Phaethornis pretrei*, in the urban area. The absence of the most specialized hummingbird implies hummingbird communities with lower functional diversity, as previously observed across gradients of deforestation in semi-natural landscapes (Hadley et al., 2018). Because hummingbird trait diversity is a strong predictor of interaction partitioning within plant-hummingbird communities (Maruyama et al., 2018), the absence of functionally specialized key species, those with longer bills, also implies more generalized interaction networks (Maglianesi et al., 2015; Maruyama et al., 2014). As for other nectarivore birds (e.g., Coetzee et al., 2018; Pauw and Louw, 2012), we show that urbanization has stronger effects on specialized hummingbirds, leading to functionally less diverse communities and consequently more generalized interaction networks.

Hummingbird community composition varied among habitats, both between and within natural and urban sites. A division was apparent between more open savannahs and public squares in relation to forests and urban parks, the latter two with higher tree cover. Hummingbird communities in natural areas of the region are organized according to species preferences for open savannah or forest habitats (Maruyama et al., 2014), and our results show that this preference extends to urban areas. Even within forest dwellers, while morphologically more generalized *Thalurania furcata* was common in urban parks, the more



**Fig. 3.** The importance of plants in plant-hummingbird network across five urban areas in Brazil. We contrast plant species importance, indicated as the first Principal Component of a PCA combining four correlated species level indices, according to three distinct parameters: A. adaptation to bird pollination; B. whether the plant is native or exotic to the place recorded; and C. habit, contrasting trees, shrubs and other life forms including herbs and climbers, grouped as "others". Categories were compared with likelihood ratio test results, contrasting linear mixed effect models with and without the fixed factor under evaluation. Circles represent the mean value, and error bars the 95% Confidence Interval. \*  $p < 0.05$ , \*\* $p < 0.01$ , NS  $p > 0.05$ .

specialized *Phaethornis pretrei* (Fig. 1C) was mostly restricted to natural forests, in accordance with observations that *T. fuscata* persists in highly fragmented forest habitats surrounded by urban and agricultural matrices (Matias et al., 2016). At the same time, in public squares with the least vegetation cover, there was a clear dominance by the large-bodied *Eupetomena macroura* (Fig. 1B), usually associated in natural areas with highly-rewarding nectar sources that it defends aggressively (Justino et al., 2012). Because scattered trees with large floral display are common in this kind of highly-managed habitat, they may elicit territorial behaviour and particularly benefit this aggressive hummingbird (see Table S5–S6). Essentially, these results indicate that distinct types of urban green spaces, especially with regard to the amount and structure of vegetation, end up having distinct hummingbird composition, mirroring results previously reported for birds and other organisms in urban areas (Koh and Sodhi, 2004; Pacheco and Vasconcelos, 2007; Sandström et al., 2006).

Ornithophilous plants and also trees were more important than other plants as nectar sources across urban plant-hummingbird networks, while a plant's origin did not matter. These results contrast to what has been found in plant-hummingbird networks in natural areas. First, previous studies have shown that specific adaptations to bird pollination syndromes do not necessarily correlate to a higher importance of plants for hummingbirds in natural areas (Maruyama et al., 2013, 2016; Waser et al., 2018). Some of these floral traits are in fact interpreted as adaptations of the plants to avoid insects (Lunau et al., 2011). If ornithophilous traits act in filtering out other nectar consumers, plants showing such adaptations could act as a "private niche" for avian pollinators, promoting their persistence in urban areas. Second, hummingbirds in natural areas are rarely found as pollinators for trees, and are more commonly associated with herbs and shrubs instead (Buzato et al., 2000; Stiles, 1978). Disregarding the role of hummingbirds as pollinators of the plants in urban networks, for which we do not currently have information, trees supposedly offering high

amounts of nectar are important for maintenance of hummingbirds in the urban setting. Third, alien plants are found to be disproportionately important in plant-hummingbird networks from natural areas across the Americas (Maruyama et al., 2016), a trend not found here despite frequent planting of alien plants in urban environments (Aronson et al., 2014; Kowarik, 2011; Moro and Castro, 2015).

To be able to maintain pollinators in urban environments, we first need a better knowledge about how pollinators persist, so we can adopt practices that can promote their conservation. However, recent focus has been mostly on insect pollinators even though vertebrates are a relevant component of the pollinator fauna, especially in the tropics. We here provide a first evaluation for one of the most speciose and relevant groups of tropical vertebrate pollinators: the hummingbirds. The observed lack of a specialized pollinator and consequent higher generalization in urban areas indicate that not all the components of the interaction network are conserved. Because network structure is thought to have important consequences for ecosystem functioning and biological conservation (Bascompte and Jordano, 2007; Kaiser-Bunbury and Blüthgen, 2015), initiatives that keep or re-establish the specialists modules within the network should be promoted. For instance, although not present in the focal network compared with the natural area, the specialized hermit hummingbird *Phaethornis pretrei* was recorded in other urban networks evaluated for cross-network comparison. Interestingly, even in these areas, the hermit was mostly recorded interacting with specialized ornithophilous plants, often with long tubular flowers (see Mendonça and Anjos, 2005, Tables S3–S4). Moreover, as this species is a traplining forest dweller, patches and corridors of green areas within the city may be able to restore its presence (Kormann et al., 2016). Because native compared to exotic status seemingly does not matter for the plants' role in maintaining hummingbirds, planting of native ornithophilous plants should be promoted, particularly since many Brazilian native plants have potential for ornamental use (Moro and Castro, 2015). In any case, the choice of

species should be done with consideration of their potential effect on native plants and other pollinators naturally persisting in urban environments (Johnson et al., 2017). Urbanization seem to additionally promote dominance by the most aggressive hummingbirds, which may benefit from highly-rewarding trees planted in urban areas and/or at artificial nectar feeders often placed by people (Justino et al., 2012; Sonne et al., 2016). It is possible that these artificial nectar feeders not only affect the distribution of hummingbirds, but also disrupt the reproduction of native plants still persisting in urban areas (Arizmendi et al., 2007), a consequence yet to be evaluated in the Tropics.

In summary, we suggest that it would be opportune to pursue the trends found here more broadly, especially as our results indicate that urban plant-hummingbird communities are organized differently to their counterparts in natural areas. We propose that a more general comparison is needed to better investigate the way in which urban and natural interaction networks differ, and also consider other functional group of pollinators (e.g. bats, hawkmoths) for which assessment is lacking. Moreover, future studies could go further than our somewhat holistic “floral syndrome” approach in identifying important plant species by, for instance, investigating which quantitative floral and plant traits are in fact associated with the importance a plant has for pollinators. In this regard, large-scale comparison of urban vs. natural interaction networks may advance the understanding of the drivers of changes in the structure and dynamics of urban interaction networks and the conservation of ecosystem processes such as pollination.

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