



RESEARCH ARTICLE - BEES

A Picky Generalist: Nesting Females of *Pseudaugochlora graminea* (Halictidae) are Highly Specialized in an Urban Area

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Abstract

Urban areas act as important shelters to support bee populations, but some guilds, such as generalist species, benefit more than others. We aimed to investigate if the floral preferences of a polylectic species would change throughout the years and if gardening practices such as mowing could affect the females' floral preferences and, thus, the bee-plant interaction networks in an urban area within a medium-sized city in Brazil. Nesting females of *Pseudaugochlora graminea* (Fabricius) (Halictidae) were collected and had the pollen grains attached to their scopae removed, acetolyzed, and identified in two different periods: March 2019 and March 2022. Only five plant species were identified in samples from 2019, while 13 species were detected in 2022 despite mowing and plant replacements throughout three years. Among the floral sources observed, both exotic and native species were visited by females for pollen and nectar collection. Despite being a generalist species, all interaction networks between *P. graminea* females and plant species were highly specialized. Females concentrated their pollen gathering on a few plant species, represented by less than ten individuals in the study area. Mowing led to the destruction of the third most important pollen source in 2019. However, plant replacements may have favored females by some nectar sources seedlings. Our findings demonstrate that gardening practices impacted the floral choices of females of a generalist bee species, whose females established highly specialized interaction networks with plants in an urban area.

Introduction

Urbanization is a human land-use change steadily growing worldwide that represents one of the major threats to biodiversity (Czech et al., 2000). On a global scale, most of the population (55%) live in urban areas, with the highest proportions (more than 70%) of urbanized regions located, respectively, in North America, Latin America and the Caribbean, Europe, and Oceania (United Nations, 2018). The increase in urban areas is worrisome since it leads to habitat fragmentation, degradation, and biodiversity loss (McDonald et al., 2008; Zambrano et al., 2019). Nevertheless, several taxa can benefit from the heterogeneity of urban areas and

reach high diversity in such zones, especially in areas with moderate levels of urbanization (McKinney, 2008). Bees (Anthophila), for instance, can profit from the speciose flora composed of native and exotic species found in cities (McKinney, 2008; Roulston & Goodell, 2011; Martins et al., 2017). Additionally, urban areas are a mosaic of heterogeneous habitats that can favor the establishment of different bee species populations compared to more homogeneous rural lands (Senapathi et al., 2015; Banaszak-Cibicka et al., 2018). Moreover, differently from cities, agricultural landscapes may threaten bees due to the use of pesticides, such as neonicotinoids, which reduce the density and nesting of wild species (Rundlöf et al., 2015).



Although several studies have demonstrated that urban areas are essential shelters for bees (Lowenstein et al., 2014; Baldock et al., 2015; Hall et al., 2017; Banaszak-Cibicka et al., 2018; Dylewski et al., 2019; Theodorou et al., 2020), it is noteworthy that some bee guilds are more negatively affected by urbanization than others (Cane et al., 2006; Banaszak-Cibicka & Żmihorski, 2012; Threlfall et al., 2015; Guimarães-Alves & Gaglianone, 2021). Eusocial species such as *Apis mellifera* L., stingless bees (Meliponini), and *Bombus* spp. (Apidae), with their perennial nests, have been shown to thrive in cities with higher reproductive output, nest densities, and diversity (Zanette et al., 2005; Osborne et al., 2008; Samuelson et al., 2018; Guimarães-Alves & Gaglianone, 2021). Cavity-nesting bees also tend to be highly abundant and speciose in urban areas since human constructions and man-made structures can act as essential substrates for nesting females (Cane et al., 2006; Fortel et al., 2014; Guimarães-Alves & Gaglianone, 2021). Polylectic bees with a broad diet and foraging preferences are also favored in cities (Banaszak-Cibicka & Żmihorski, 2012; Lanner et al., 2020; Guimarães-Alves & Gaglianone, 2021), which is expected considering the combination of exotic and native species in urban areas (McKinney, 2008). Indeed, the bee-plant networks of polylectic species such as bumble bees exhibited a generalized foraging behavior (measured by the degree of specialization) along an urbanization gradient in Germany (Hülsmann et al., 2015). Similar results were observed in Canada, where bees interacted with more plant species in residential gardens compared to semi-natural habitats, which was driven by more exotic plant species (Martins et al., 2017).

Pseudaugochlora graminea (Fabricius) (Halictidae) is a small, slender, ground-nesting, solitary, multivoltine bee species that presents the broadest distributional range within the genus, occurring from Texas (United States) to Argentina (Michener & Kerfoot, 1967; Almeida, 2008). Data on literature from surveys conducted in different ecosystems and biomes, from altered areas to preserved habitats, indicate that this species is polylectic (Steiner et al., 2010; Imperatriz-Fonseca et al., 2011; Bonet-Ferrer & Vergara, 2019). In this study, we aimed to investigate if the floral preferences of *P. graminea* in an urban area would change within three years. Our goal was also to evaluate if different gardening practices, such as mowing and plant replacements, could influence the females' choice of the flora in the study area. Considering that the campus and its 600-m radius surroundings bear a highly rich plant species richness (Rocha-Filho et al., 2018), we hypothesized that *P. graminea* nesting females would present a polylectic diet regardless of the sampling period over three years and that low values of specialization would characterize their interaction networks with plants.

Material and Methods

Study site

The study was conducted at the university campus Santa Mônica (18°55'6"S, 48°15'29" W) of the Federal University

of Uberlândia in the Uberlândia municipality, Minas Gerais state, Brazil. The city has a population of 7 713.224, estimated in 2022, and an urbanized area of 172.85 km² and 95.2% of afforestation of public roads (IBGE, 2024). The campus Santa Mônica is located in the east part of Uberlândia, in one of the largest neighborhoods, and encompasses a total area of 280.119 m², which is composed of buildings, sidewalks, streets, parking lots, gardens, and lawns. The flora in the area consists of native plant species from different Brazilian biomes but mostly from the Cerrado, as well as numerous alien species used mainly as ornamental plants in gardens (Rocha-Filho et al., 2018). The climate of the Uberlândia region is classified as mega thermal Aw according to the Köppen system, with a hot/rainy season from October to March and a cold/dry season from April to September (Nimer & Brandão, 1989).

The nest aggregation of *P. graminea* was found in February 2019 at the campus, right beside the stairs of an educational building, in a slightly sloping bank (Fig. S1), occupying an area of 5.90 m x 1.61 m. Most of the nests were built among the exposed roots of a large mango tree, *Mangifera indica* L. (Anacardiaceae), where the soil was more compacted, which provided more protection to these nests against mowing and other gardening activities (Fig S1). According to the University landscaping department, mowing occurs 10 to 15 times to control the grasses on the campus, especially during the rainiest months (from December to March). Mowing was performed with trimming machines and a riding lawn mower, used on the large lawn areas within the campus. These gardening practices affect the flora composition for at least some months since several herbs, prostrate vines, weeds, and small shrubs are permanently eliminated or may sprout after some weeks. Regarding tree species, the plant compensation occurred mainly to replace dead trees or to form a green belt in large lawns. All tree seedlings used are donations from the municipal garden. The plantings were performed only during the rainy season. Among the tree species donated were native species: *Pleroma granulosum* (Desr.) D. Don (Melastomataceae), *Cenostigma pluviosum* (DC.) Gagnon & G.P. Lewis (Fabaceae), *Handroanthus chrysotrichus* (Mart. ex DC.) Mattos, *Tabebuia roseoalba* (Ridl.) Sandwith (Bignoniaceae), and exotic trees such as *Callistemon viminalis* (Sol. ex Gaertn.) G. Don (Myrtaceae), *Bauhinia variegata* L. (Fabaceae), and *Tecoma stans* (L.) Juss. ex Kunth (Bignoniaceae).

Floral sources

The analyses of floral sources used by *P. graminea* females were conducted through two different methodologies: (I) pollen analyses of the grains adhered to the females' scopae and (II) focal observations of flowers.

The collection of pollen adhered to the females' scopae was obtained in two different periods, March 2019 and March 2022, i.e., at the end of the hot/rainy season in the region. The pollen loads attached to females' scopae were removed

nonlethally. After their foraging trips, females carrying pollen loads and returning to their nests were captured with entomological nets and placed individually in vials inserted into a cooler containing ice for approximately two minutes. The vials were removed from the cooler, and the females inside were slowly retrieving their movements and removing their pollen loads against the vials' walls. After recovering from being kept on ice, females left the vials and flew again. All females collected were released after the end of collections in both sampling periods; thus, the pollen content removed from females' scopae belonged to different females. In total, 20 females were collected in March 2019 and 25 in March 2022.

Focal observations of floral sources used by *P. graminea* specimens were performed only in 2022 on four sunny days by walking through the area for 30 minutes, observing all flowering plants located in transects of 10m, totaling 21 hours of observations. Each flowering plant was observed for five minutes. The specimens observed on flowers were recorded and photographed when possible. At the nest aggregation, observations started around 6h30 am.

Pollen analyses

The pollen inside the vials received 2 ml of 70% ethanol and was kept in the laboratory at room temperature for at least 24 hours. Subsequently, the ethanol in the samples was discarded, and the pollen samples received 4 ml of absolute acetic acid for 24 hours before being acetolyzed according to the protocol described by Erdtman (1960). After the acetolysis, a small cube of glycerin gelatin was inserted into each pollen sample and placed on microscopic slides, totaling three slides per pollen sample. The slides were examined under a light microscope, and the first 400 pollen grains observed randomly in each slide were counted and identified (1200 pollen grains per pollen sample) (Vergeron, 1964). We calculated the relative frequency (RF) of each pollen type identified in the samples using the following formula: the total number of grains identified in a sample multiplied by 100 and divided by the total number of grains counted in the sample. The identification of pollen grains was performed based on the palynological reference collection of Laboratório de Ecologia e Evolução de Abelhas e Vespas of Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto, University of São Paulo. All plant names of the species identified in the samples, as well as their origin, follow the Flora e Funga do Brasil online database (<https://floradobrasil.jbrj.gov.br/reflora/PrincipalUC/PrincipalUC.do>).

After identifying the floral sources visited by *P. graminea* females, we calculated how distant the plant specimens of the species identified in the samples located within the campus area were from the nest aggregation. All plant individuals of the species used by the bees and plant specimens belonging to the same genera of these plant species identified in the samples were counted and assigned their geographical coordinates with the app MAPinr. All coordinates of the

plant individuals were marked, and the *P. graminea* nest aggregation coordinates were plotted on a map generated with the software QGIS 2.18.7 (<https://qgis.org/en/site/>).

Bee-plant interaction networks

Networks were constructed using the package *bipartite* for R Studio (Dormann, 2011; Dormann et al., 2008; 2009) in R ver. 4.2.2 (www.r-project.org) to describe the bee-plant interactions in the urban area in the two studied periods. Only the data regarding pollen analysis from the pollen grains attached to the females' bodies was used to build the bee-plant networks. We used the following indices to characterize the interaction networks: degree, specialization, and connectance. Degree (D) determines the number of *P. graminea* females that interact with each plant species or the number of each plant species that interact with each *P. graminea* female. The specialization in diet (H_2') describes the resource partitioning between two groups in the entire network (Blüthgen et al., 2006). This index reduces with higher specialization and ranges from 0 (maximum generalization) to 1 (maximum specialization). Lastly, connectance (C) is the proportion of realized interactions to all possible interactions in the network. This index is calculated as follows: $C = I/(r \cdot c)$, where I is the total number of nonzero elements in the matrix, r is the number of rows, and c is the number of columns (Blüthgen et al., 2006).

Results

Floral sources

A total of 24 plant species were recorded as pollen or nectar sources to *P. graminea* females; one pollen type was not identified (Table 1, Fig S2). Samples from March 2019 had only five pollen types, while 13 types were identified in samples from March 2022, with only two species, *P. granulosum* and *Solanum palinacanthum* Dunal (Solanaceae), recorded in samples from both studied years (Table 1). Additionally, the proportion of pollen types collected by females in 2019 was markedly characterized by the dominance of *P. granulosum*, with 73.19% of the pollen grains counted, followed by *Solanum sisymbriifolium* Lam. (Solanaceae) (15.03%), *S. palinacanthum* (6.8%), and *B. variegata* (3.48%). In 2022, the percentages of the four species more visited by females were less uneven, with *Senna spectabilis* (DC.) H.S. Irwin & Barneby (Fabaceae) (33.21%) as the primary pollen source, followed by *P. granulosum* (25.16%), *S. palinacanthum* (13.47%), and *Chamaecrista rotundifolia* (Pers.) Greene (Fabaceae) (11.93%).

Females started foraging around 7 a.m. and leaving their nests until at least early afternoon. The focal observations on flowers revealed females collecting pollen or nectar on flowers of 14 plant species within the campus (Table 1, Fig S2). Of the 14 plant species visited by the females, only five species were also identified in the pollen samples removed from females' scopae (Table 1, Fig 1).

Table 1. Plant species, their origin, their codes used in interaction networks, their floral resources collected by females and the relative frequency of their pollen grains counted on the pollen samples removed from *Pseudaugochlora graminea* females' scopae at the Santa Mônica campus in Uberlândia, Brazil in March 2019 and March 2022. The asterisk indicates only plant species that females were observed collecting resources on flowers.

Plant species	Proportion (%)			Codes	Resource(s) collected	Plant origin
	2019	2022	Total			
Acanthaceae						
<i>Asystasia gangetica</i> *	-	-	-	-	nectar	naturalized
Asteraceae						
<i>Centratherum punctatum</i>	-	0.01	0.006	P	nectar	native
Bignoniaceae						
<i>Fridericia platyphylla</i> *	-	-	-	-	nectar	native
<i>Tecoma stans</i> *	-	0.04	0.022	N	nectar	naturalized
Bixaceae						
<i>Bixa orellana</i> *	-	-	-	-	pollen	native
Cucurbitaceae						
<i>Luffa cylindrica</i>	-	0.02	0.011	M	nectar	cultivated
Fabaceae						
<i>Bauhinia variegata</i>	3.48	-	1.54	A	pollen	naturalized
<i>Calliandra brevipes</i> *	-	-	-	-	nectar	native
<i>Cassia fistula</i>	-	4	2.22	G	pollen	cultivated
<i>Cenostigma pluviosum</i>	-	0.19	0.106	L	nectar	native
<i>Chamaecrista rotundifolia</i> *	-	11.93	6.63	H	pollen	native
<i>Mimosa skinneri</i>	-	3.87	2.15	J	pollen	native
<i>Senna spectabilis</i> *	-	33.21	18.45	F	pollen	native
Type 1	1.51	-	0.67	B	pollen	?
Malvaceae						
<i>Apeiba tibourbou</i>	-	3.95	2.194	I	pollen	native
Melastomataceae						
<i>Pleroma granulosum</i> *	73.19	25.16	46.51	E	pollen	native
Myrtaceae						
<i>Psidium guajava</i>	-	4.14	2.3	K	pollen	naturalized
Rubiaceae						
<i>Ixora casei</i> *	-	-	-	-	nectar	cultivated
<i>Mussaenda philippica</i> *	-	-	-	-	nectar	cultivated
Sapindaceae						
<i>Serjania</i> sp.	-	0.01	0.006	O	nectar	?
Solanaceae						
<i>Solanum palinacanthum</i> *	6.8	13.47	10.51	D	pollen	native
<i>Solanum sisymbriifolium</i>	15.03	-	6.68	C	pollen	native
Turneraceae						
<i>Turnera subulata</i> *	-	-	-	-	nectar	native
Verbenaceae						
<i>Duranta erecta</i> *	-	-	-	-	nectar	naturalized
<i>Lantana camara</i> *	-	-	-	-	nectar	naturalized

In general, we observed a strong preference for pollen collection on flowers with poricidal anthers, with eight species belonging to seven genera and five families (*Cassia*, *Chamaecrista*, *Senna*, *Solanum*, *Apeiba*, *Pleroma*, and *Bixa*) (Table 1). From all 12 pollen sources used by *P. graminea* females, only four plant species have no poricidal anthers: *Psidium guajava* L. (Myrtaceae), *Mimosa skinneri* Benth., *B. variegata*, and Type 1 (Fabaceae), and were visited for pollen gathering by only one female each. The most important pollen sources identified in pollen samples, adding data from both studied periods, were *P. granulosum* (46.51%), *S. spectabilis*

(18.45%), and *S. palinacanthum* (10.51%). The achiote, *Bixa orellana* L. (Bixaceae), was the lone pollen source identified only through flower observations.

Considering pollen analysis and focal observations, thirteen nectar sources were recorded for *P. graminea*. Almost all pollen sources consist of native plant species, but *P. guajava*, *B. variegata*, and *Cassia fistula* L. (Fabaceae), while the nectar source species, in turn, are primarily exotic (Table 1). In most of the nectar sources, especially the plants with long-tubed corolla flowers, females robbed nectar by piercing the base of the corolla to collect this flower resource (Fig S1).

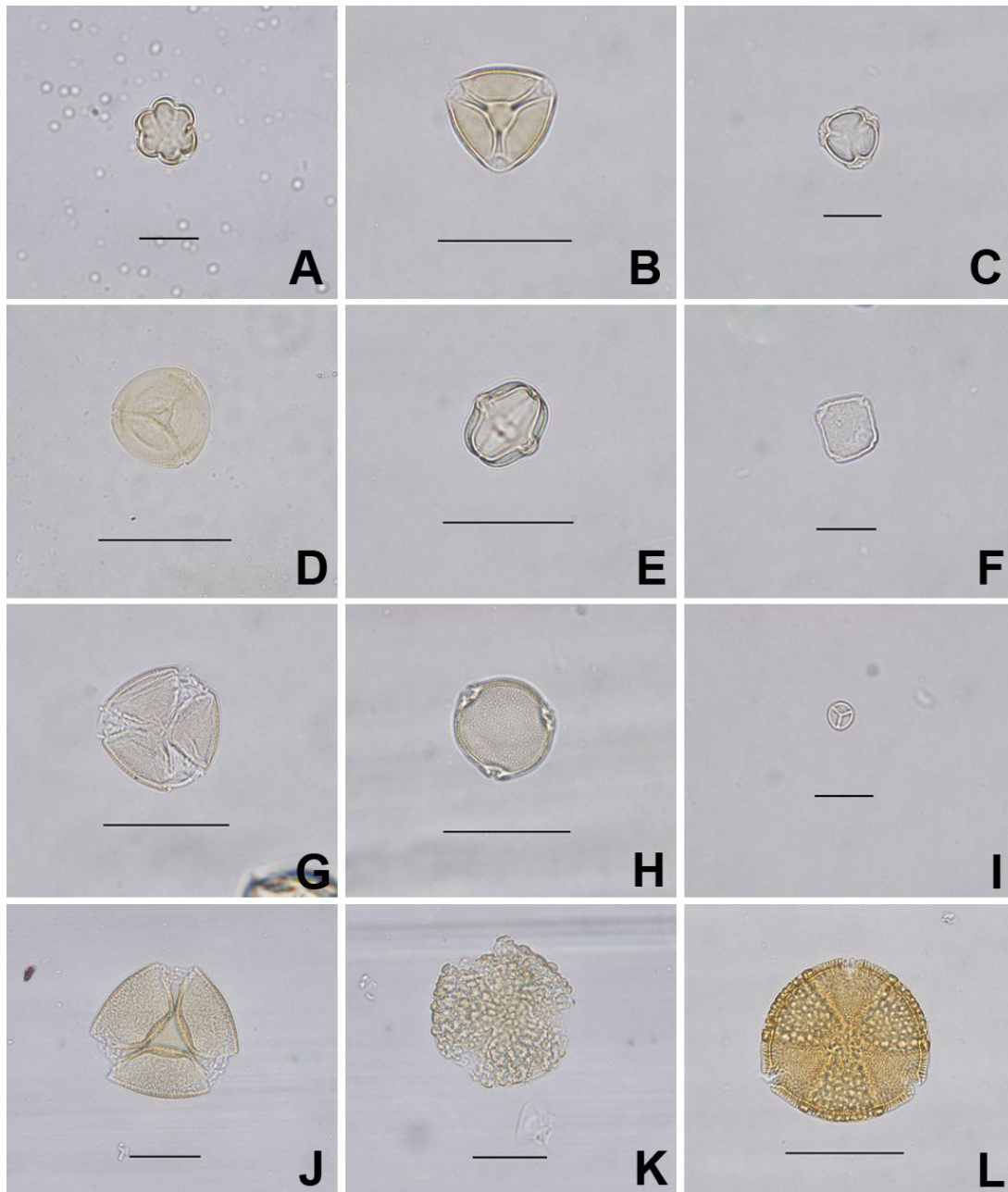


Fig 1. Photomicrographs of the most important pollen grains, displayed by order of percentage, counted and identified in pollen samples removed from *Pseudaugochlora graminea* females' scopae at the campus Santa Mônica in Uberlândia, Brazil. A - *Pleroma granulosum*, B - *Senna spectabilis*, C - *Solanum palinacanthum*, D - *Solanum sisymbriifolium*, E - *Chamaecrista rotundifolia*, F - *Psidium guajava*, G - *Cassia fistula*, H - *Apeiba tibourbou*, I - *Mimosa skinneri*, J - *Bauhinia variegata*, K - Type 1, and L - *Cenostigma pluviosum*. Scale bars: A, C, F, I = 20 µm; B, D, E, G, H, J, K, L = 50 µm.

Even in plants with funnel-shaped corolla such as *Turnera subulata* Sm. (Turneraceae) (Fig S1), females collected nectar without touching the anthers or the stigma, thus not performing pollination.

All plant species recorded as floral sources were located within the campus, and most of them were near the nest aggregation (around 250 m from the nests) (Fig 2). The two primary pollen sources, *P. granulosum* and *S. spectabilis*, were represented by only eight and two individuals, respectively (Fig 2). While *S. palinacanthum* individuals occurred in a great spot within the campus, *S. sisymbriifolium* was recorded by only one specimen nearby the nest aggregation until February 2022, when this single plant was killed by a mowing conducted in the same month. Likewise, specimens of other *Solanum* species, *M. skinneri*, and the three *Chamaecrista* species (Fabaceae) identified in the study area were constantly mowed during the rainy season. Individuals of some nectar sources such as *T. subulata*, *Luffa cylindrica* (L.) M.Roem. (Cucurbitaceae) and *Centratherum punctatum* Cass. (Asteraceae) were also mowed.

Bee-plant interaction networks

All interaction networks between *P. graminea* females and plant species were highly specialized ($C = 0.25$, $H_2' = 0.997$ for March 2019; $C = 0.142$, $H_2' = 0.987$ for March 2022; $C = 0.099$, $H_2' = 0.979$ for the total network). From the 20 females sampled in 2019, 16 (80%) collected pollen on flowers of a single plant species (Fig 3). This percentage was much lower in 2022, with 11 females (44%) visiting only one plant species (Fig 3). For the total network, the plants with the highest numbers of interactions, were the primary pollen sources: *P. granulosum* ($D = 28$), *S. spectabilis* ($D = 9$), and *S. palinacanthum* ($D = 7$). As for females, in both years, 11 bees interacted with two plant species; six females interacted with three plants, and only one *P. graminea* female (I43) interacted with four floral sources (Fig 3). Among these 18 females, most of them had a very low proportion of pollen grains belonging to other plant species (less than 12 grains), which might indicate pollen contamination rather than active pollen collection. Only four females (I4, I14, I32, and I36) (Fig 3) presented similar proportions of two pollen sources, which suggests a concomitant pollen gathering on flowers of two plant species.

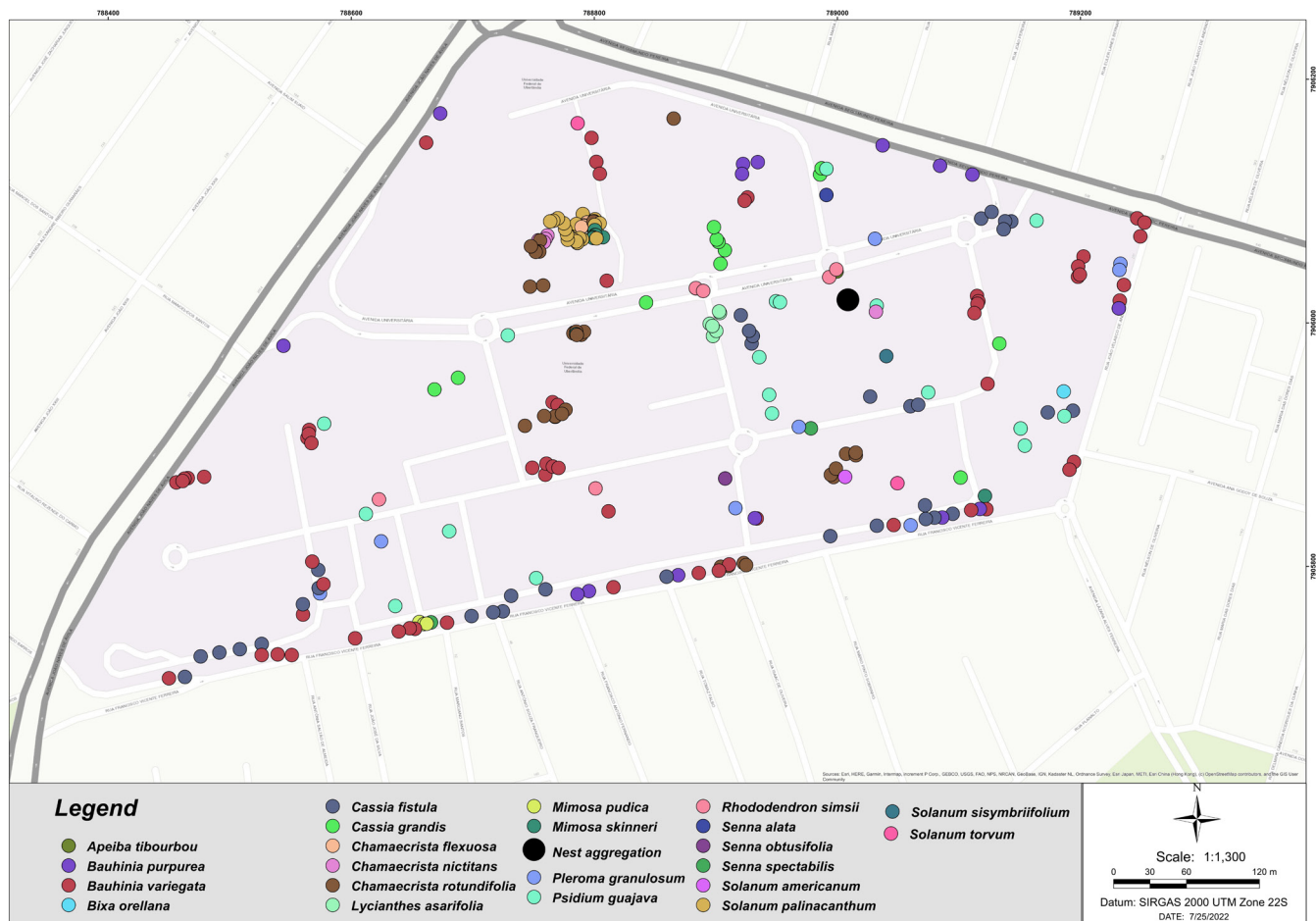


Fig 2. Locations at the campus Santa Mônica of the plant individuals belonging to the species identified in pollen samples from *Pseudaugochlora graminea* females, as well as from plant species belonging to the same genera of the species found in the samples.

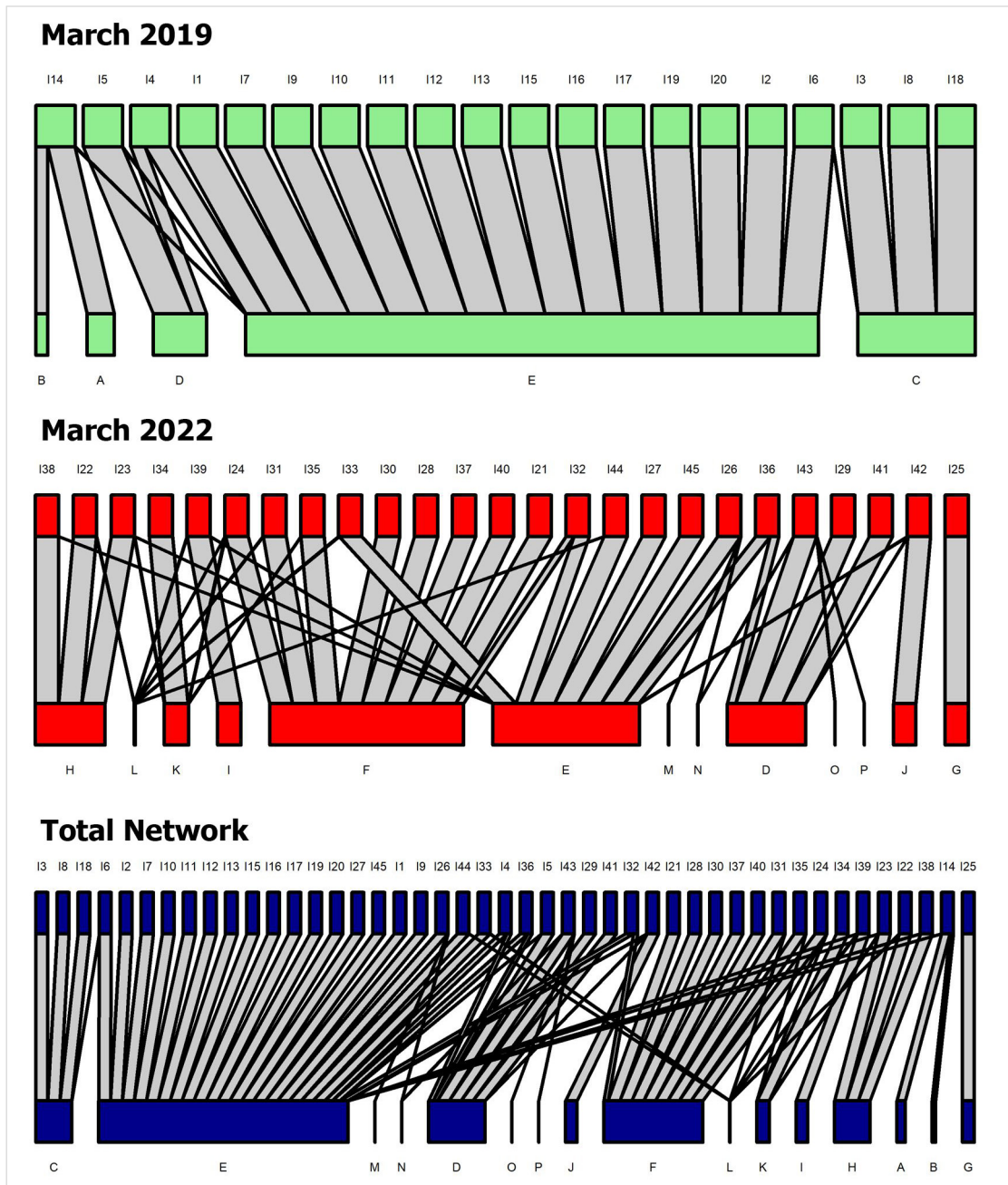


Fig 3. Interaction networks of *Pseudaugochlora graminea* females with plant species at the campus Santa Mônica, Uberlândia, Brazil. Females are represented by numbers (upper side), while plant species are defined by letters (lower side). The link width represents the number of interactions between females and plant species and the width of plant rectangles denote the number of pollen grains sampled.

Discussion

Despite the rich flora composition found in the campus (Table S1) and its adjacent areas (Rocha-Filho et al., 2018), we identified 24 plant species that acted as floral sources for *P. graminea* nesting females, all of them located near the nest aggregation. Among the floral sources observed, both exotic and native species were visited by females for pollen and nectar collection. Moreover, considering only the results of pollen analysis, it was verified that the number of pollen types found was much higher in 2022 than in 2019, despite

mowing and plant replacements that occurred throughout this interval of three years. Considering that we have studied only one species in a single area, it is important to stress that our results may not represent distinct cases of bee species in urban areas, even other generalist species such as *P. graminea* or other *Pseudaugochlora* species. Further studies encompassing different bee species with distinct habitats are needed, especially research focusing on the studied species' functional diversity aspects. Additionally, as we have analyzed data from only two different periods, the long-term impact of gardening practices on *P. graminea* females' choices is unknown.

Our first hypothesis on the polylecty of *P. graminea* females was corroborated because this species undoubtedly behaved as a generalist, i.e., the number of pollen sources identified in pollen analysis exceeded four genera from three plant families (Müller & Kuhlmann, 2008). However, the second assumption on low levels of specialization in bee-plant networks was rejected, considering that *P. graminea* females were highly specialized in the use of pollen types. Similar results were documented for two sympatric *Xylocopa* species (Apidae) in Brazilian savanna areas, where both species presented generalist diets, but females were highly specialized (Araújo et al., 2021). Specialist individuals can select and canalize information more efficiently when seeking resources than generalists (Bernays, 2001), which could represent a pertinent advantage to optimizing foraging strategies.

Interestingly, in the same study area, females of the oligolectic bee species *Centris collaris* Lepeletier (Apidae) presented higher connectance and lower specialization ($C = 0.314$, $H_2' = 0.744$) (Rocha-Filho et al., 2018) than what was calculated for *P. graminea*. Studies carried out in urban environments have shown floral specializations of pollinators, including several bee species (e.g., Baldock et al., 2015; Martins et al., 2017; Theodorou et al., 2017; Beal-Neves et al., 2020; Suni et al., 2021). This pattern observed may reflect the high speciose flora found in cities, as well as in the study area and its surroundings, which hosts plant species from the Brazilian savanna, Amazon, Atlantic rainforest, and exotic species (Table S1; Rocha-Filho et al., 2018).

A high prevalence of pollen grains from plants with poricidal anthers was observed on *P. graminea* samples, indicating a preference for gathering this floral resource on flowers requiring sonication to release the grains. Plant species with poricidal anthers belong to numerous botanical families and tend to have protein-rich pollen grains (Roulston et al., 2000), which could explain the selection of these species by females to the detriment of pollen from flowers with non-poricidal anthers.

One important aspect to discuss is that, regardless of the *P. graminea* polylecty, females concentrated their pollen collection on a few plant species, such as *P. granulosum*, a common tree species used in Uberlândia afforestation. Likewise, other generalist bee species such as *Tetrapedia diversipes* Klug (Apidae) (Rocha-Filho & Garófalo, 2016), *Xylocopa frontalis* (Olivier), and *X. grisescens* Lepeletier (Araújo et al., 2021) also exhibited selective diets, which could reflect the long blooming period of their preferred pollen sources, as observed for *Pereskia grandifolia* Haw. (Cactaceae), the main species visited by *T. diversipes* females (Rocha-Filho et al., 2016), and also in the present study for *P. granulosum*, which was represented by few individuals at the campus but had long-lasting flowerings.

Apparently, the gardening practices adopted in the study site influenced, to a certain degree, the preference for

pollen gathering by the *P. graminea* females, even though we have yet to study the influence of abiotic factors such as temperature or humidity on plant species blooming. The second most important pollen source in 2019, *S. sisymbriifolium*, was not recorded in pollen samples in 2022 since the single individual in the area was mowed. Frequent mowing causes a decrease in the number of flowers for bees. It disrupts the continuity in the availability of floral resources (Dylewski et al., 2019), reducing the bee diversity in urban areas (Wastian et al., 2016). Also, only a single female used the native *Apeiba tibourbou* Aubl. (Malvaceae) as a pollen source, a species represented in the area by only one individual near the nest aggregation. Hence, it is likely to assume that plant replacements performed on the campus using these native species would be highly advantageous to *P. graminea* females and other bee species that perform buzz pollination. The plant replacement performed on the campus seemed beneficial for *P. graminea* females since species such as *Asystasia gangetica* (L.) T. Anderson (Acanthaceae) and *Lantana camara* L. (Verbenaceae), both visited by bees for nectar collection, are used to cover areas with bare soil when seedlings are available.

Nonetheless, the species *Syngonium angustatum* Schott (Araceae), which females do not use for gathering floral resources, is the most used in gardening due to the ease of its propagation and resistance. Native plant species are more attractive to pollinators at a community level than exotic species (Zaninotto et al., 2023). Therefore, City halls in urban afforestation, parks, squares, and other green spaces should prioritize these native plant species.

Our findings demonstrate that gardening practices impacted the female floral choices of a generalist bee species. Based on our results, the University landscaping department staff was advised to conduct mowing cautiously to preserve entomophilous plant species and to prefer native plant seedlings to use in plant replacements rather than exotic species. Authorities and city dwellers should also consider these recommendations to provide a suitable habitat for bees and other pollinators.

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Authors' Contributions

LCRF: Review and editing, methodology, writing-original draft, fieldwork, data processing, data analysis, design and conceptualization.

TNA: Review and editing, methodology, fieldwork, data processing, data analysis.

ALSCM: Review and editing, methodology, fieldwork.

TDF: Review and editing, methodology, fieldwork, data processing.

SCA: Review and editing, methodology, design and conceptualization.

Disclosure statement

The authors declare that they have no conflict of interest.

References

- Almeida, E.A.B. (2008). Revision of the Brazilian Species of *Pseudaugochlora* Michener 1954 (Hymenoptera: Halictidae: Augochlorini). *Zootaxa*, 1679: 1-38. <https://doi.org/10.11646/zootaxa.1679.1.1>
- Araújo, T.N., Pires, L.P., Meireles, D.A.L. & Augusto, S.C. (2021). Individual-resource network between *Xylocopa* bees and plant resources: generalist species, specialist individuals? *Ecological Entomology*, 46: 1273-1282. <https://doi.org/10.1111/een.13072>
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M., Potts, S.G., Robertson, K.M., Scott, A.V., Stone, G.N., Vaughan, I.P. & Memmott, J. (2015). Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences*, 282: 20142849. <https://doi.org/10.1098/rspb.2014.2849>
- Banaszak-Cibicka, W. & Żmihorski, M. (2012). Wild bees along an urban gradient: winners and losers. *Journal of Insect Conservation*, 6: 331-343. <https://doi.org/10.1007/s10841-011-9419-2>
- Banaszak-Cibicka, W., Twerd, L., Fliszkiewicz, M., Giejdasz, K. & Langowska, A. (2018). City parks vs. natural areas – is it possible to preserve a natural level of bee richness and abundance in a city park? *Urban Ecosystems*, 21: 599-613. <https://doi.org/10.1007/s11252-018-0756-8>
- Beal-Neves, M., Ely, C.V., Esteves, M.W., Blochtein, B., Lahm, R.A., Quadros, E.L.L. & Ferreira, P.M.A. (2020). The influence of urbanization and fire disturbance on plant-floral visitor mutualistic networks. *Diversity*, 12: 1-20. <https://doi.org/10.3390/d12040141>
- Bernays, E.A. (2001). Neural limitations in phytophagous insects: Implications for diet breadth and evolution of host affiliation. *Annual Review of Entomology*, 46: 703-727. <https://doi.org/10.1146/annurev.ento.46.1.703>
- Blüthgen, N., Menzel, F. & Blüthgen, N. (2006). Measuring specialization in species interaction networks. *BMC Ecology*, 6: 1-12. <https://doi.org/10.1186/1472-6785-6-9>
- Bonet-Ferrer, M. & Vergara, C.H. (2019). Abejas silvestres de un cafetal orgánico en Veracruz, México. Puebla: Fundación Universidad de las Américas, 499 p.
- Cane, J.H., Minckley, R.L., Kervin, L.J., Roulston, T.A.H. & Williams, N.M. (2006). Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications*, 16: 632-644. [https://doi.org/10.1890/1051-0761\(2006\)016\[0632:crwadb\]2.0.co;2](https://doi.org/10.1890/1051-0761(2006)016[0632:crwadb]2.0.co;2)
- Czech, B., Krausman, P.R. & Devers, P.K. (2000). Economic associations among causes of species endangerment in the United States. *BioScience*, 50: 593-601. [https://doi.org/10.1641/0006-3568\(2000\)050\[0593:EAACOS\]2.0.CO;2](https://doi.org/10.1641/0006-3568(2000)050[0593:EAACOS]2.0.CO;2)
- Dormann, C.F. (2011). How to be a specialist? Quantifying specialisation in pollination networks. *Network Biology*, 1: 1-20.
- Dormann, C.F., Gruber, B. & Fründ, J. (2008). Introducing the bipartite package: analysing ecological networks. *R News*, 8: 8-11.
- Dormann, C.F., Fründ, J., Blüthgen, N. & Gruber, B. (2009). Indices, graphs and null models: analyzing bipartite ecological networks. *Open Journal of Ecology*, 2: 7-24.
- Dylewski, Ł., Maćkowiak, Ł. & Banaszak-Cibicka, W. (2019). Are all urban green spaces a favourable habitat for pollinator communities? Bees, butterflies and hoverflies in different urban green areas. *Ecological Entomology*, 44: 678-689. <https://doi.org/10.1111/een.12744>
- Erdtman, G. (1960). The acetolysis method. A revised description. *Svensk Botanisk Tidskrift*, 54: 561-564.
- Fortel, L., Henry, M., Guilbaud, L., Guirao, A.L., Kuhlmann, M., Mouret, H., Rollin, O. & Vaissière, B.E. (2014). Decreasing abundance, increasing diversity, and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. *PLoS ONE*, 9: e104679. <https://doi.org/10.1371/journal.pone.0104679>
- Guimarães-Alves, S. & Gaglianone, M.C. (2021). Bee guilds' responses to urbanization in Neotropics: A case study. *Diversity*, 13: 365. <https://doi.org/10.3390/d13080365>
- Hall, D.M., Camilo, G.R., Tonietto, R.K., Ollerton, J., Ahrné, K., Arduser, M., Ascher, J.S., Baldock, K.C.R., Fowler, R., Frankie, G., Goulson, D., Gunnarsson, B., Hanley, M.E., Jackson, J.I., Langellotto, G., Lowenstein, D., Minor, E.S., Philpott, S.M., Potts, S.G., Sirohi, M.H., Spevak, E.M., Stone, G.N. & Threlfall, C.G. (2017). The city as a refuge for insect pollinators. *Conservation Biology*, 31: 24-29. <https://doi.org/10.1111/cobi.12840>
- Hülsmann, M., von Wehrden, H., Klein, A.M. & Leonhardt, S.D. (2015). Plant diversity and composition compensate for negative effects of urbanization on foraging bumble bees.

- Apidologie, 46: 760-770.
<https://doi.org/10.1007/s13592-015-0366-x>
- IBGE - Instituto Brasileiro de Geografia e Estatística (2024). Cidades. IBGE, Rio de Janeiro. <https://cidades.ibge.gov.br/brasil/mg/uberlandia/panorama>. (accessed date: 19 June 2024).
- Imperatriz-Fonseca, V.L., Alves-dos-Santos, I., Santos-Filho, O.S., Engels, W., Ramalho, M., Wilms, W., Aguilar, J.B.V., Pinheiro-Machado, C.A., Alves, D.A. & Kleinert, A.M.P. (2011). Checklist das abelhas e plantas melitófilas no Estado de São Paulo, Brasil. *Biota Neotropica*, 11: 631-655.
<https://doi.org/10.1590/S1676-06032011000500029>
- Lanner, J., Kratschmer, S., Petrović, B., Gaulhofer, F., Meimberg, H. & Pachinger, B. (2020). City dwelling wild bees: how communal gardens promote species richness. *Urban Ecosystems*, 23: 271-288.
<https://doi.org/10.1007/s11252-019-00902-5>
- Lowenstein, D.M., Matteson, K.C., Xiao, I., Silva, A.M. & Minor, E.S. (2014). Humans, bees, and pollination services in the city: the case of Chicago, IL (USA). *Biodiversity Conservation*, 23: 2857-2874.
<https://doi.org/10.1007/s10531-014-0752-0>
- Martins, K.T., Gonzalez, A. & Lechowicz, M.J. (2017). Patterns of pollinator turnover and increasing diversity associated with urban habitats. *Urban Ecosystems*, 20: 1359-1371. <https://doi.org/10.1007/s11252-017-0688-8>
- McDonald, R.I., Kareiva, P. & Forman, R.T.T. (2008). The implications of current and future urbanization for global protected areas and biodiversity conservation. *Biological Conservation*, 141: 1695-1703.
<https://doi.org/10.1016/j.biocon.2008.04.025>
- McKinney, M.L. (2008). Effects of urbanization on species richness: A review of plants and animals. *Urban Ecosystems*, 11: 161-176. <https://doi.org/10.1007/s11252-007-0045-4>
- Michener, C.D. & Kerfoot, W.B. (1967). Nests and social behavior of three species of *Pseudaugochloropsis* (Hymenoptera: Halictidae). *Journal of the Kansas Entomological Society*, 40: 214-232.
- Müller, A. & Kuhlmann, M. (2008). Pollen hosts of western palaeartic bees of the genus *Colletes* (Hymenoptera: Colletidae): the Asteraceae paradox. *Biological Journal of the Linnean Society*, 95: 719-733.
<https://doi.org/10.1111/j.1095-8312.2008.01113.x>
- Nimer, E. & Brandão, A.M.P.M. (1989). Balanço hídrico e clima da região dos cerrados. Rio de Janeiro: IBGE, 166 p.
- Osborne, J.L., Martin, A.P., Shortall, C.R., Todd, A.D., Goulson, D., Knight, M.E., Hale, R.J. & Sanderson, R.A. (2008). Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology*, 45: 784-792.
<https://doi.org/10.1111/j.1365-2664.2007.01359.x>
- Rocha-Filho, L.C. & Garófalo, C.A. (2016). Natural history of *Tetrapedia diversipes* (Hymenoptera, Apidae) in an Atlantic semi-deciduous forest remnant surrounded by coffee crops, *Coffea arabica* (Rubiaceae). *Annals of the Entomological Society of America*, 109: 183-197.
<https://doi.org/10.1093/aesa/sav153>
- Rocha-Filho, L.C., Ferreira-Caliman, M.J., Garófalo, C.A. & Augusto, S.C. (2018). A specialist in an urban area: Are cities suitable to harbour populations of the oligolectic bee *Centris (Melacentris) collaris* (Apidae: Centridini)? *Annales Zoologici Fennici*, 55: 135-149. <https://doi.org/10.5735/086.055.0101>
- Roulston, T.H., Cane, J.H. & Buchmann, S.L. (2000). What governs protein content of pollen: Pollinator preferences, pollen-pistil interactions, or phylogeny? *Ecological Monographs*, 70: 617-643.
[https://doi.org/10.1890/0012-9615\(2000\)070\[0617:WGPCOP\]2.0.CO;2](https://doi.org/10.1890/0012-9615(2000)070[0617:WGPCOP]2.0.CO;2)
- Roulston, T.H. & Goodell, K. (2011). The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology*, 56: 293-312.
<https://doi.org/10.1146/annurev-ento-120709-144802>
- Rundlöf, M., Andersson, G.K.S., Bommarco, R., Fries, I., Hederström, V., Herbertsson, L., Jonsson, O., Klatt, B.K., Pedersen, T.R., Yourstone, J. & Smith, H.G. (2015). Seed coating with a neonicotinoid insecticide negatively affects wild bees. *Nature*, 521: 77-80.
<https://doi.org/10.1038/nature14420>
- Samuelson, A.E., Gill, R.J., Brown, M.J.F. & Leadbeater, E. (2018). Lower bumblebee colony reproductive success in agricultural compared with urban environments. *Proceedings of the Royal Society B: Biological Sciences*, 285: 20180807.
<https://doi.org/10.1098/rspb.2018.0807>
- Senapathi, D., Carvalheiro, L.G., Biesmeijer, J.C., Dodson, C.A., Evans, R.L., McKerchar, M., Morton, R.D., Moss, E.D., Roberts, S.P.M., Kunin, W.E. & Potts, S.G. (2015). The impact of over 80 years of land cover changes on bee and wasp pollinator communities in England. *Proceedings of the Royal Society B: Biological Sciences*, 282: 20150294.
<https://doi.org/10.1098/rspb.2015.0294>
- Steiner, J., Zillikens, A., Kamke, R., Feja, E.P. & Falkenberg, D.B. (2010). Bees and melittophilous plants of secondary Atlantic Forest habitats at Santa Catarina Island, Southern Brazil. *Oecologia Australis*, 14: 16-39.
<https://doi.org/10.4257/oeco.2010.1401.01>
- Suni, S., Hall, E., Bahu, E. & Hayes, H. (2021). Urbanization increases floral specialization of pollinators. *Ecology and Evolution*, 12: e8619. <https://doi.org/10.1002/ece3.8619>
- Theodorou, P., Albig, K., Radzevičiūtė, R., Settele, J., Schweiger, O., Murray, T.E. & Paxton, R.J. (2017). The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. *Functional Ecology*, 31: 838-847.
<https://doi.org/10.1111/1365-2435.12803>

- Theodorou, P., Radzevičiūtė, R., Lentendu, G., Kahnt, B., Husemann, M., Bleidorn, C., Settele, J., Schweiger, O., Grosse, I. & Wubet, T. (2020). Urban areas as hotspots for bees and pollination but not a panacea for all insects. *Nature Communications*, 11: 576. <https://doi.org/10.1038/s41467-020-14496-6>
- Threlfall, C.G., Walker, K., Williams, N.S.G., Hahs, A.K., Mata, L., Stork, N. & Livesley, S.J. (2015). The conservation value of urban green space habitats for Australian native bee communities. *Biological Conservation*, 187: 240-248. <https://doi.org/10.1016/j.biocon.2015.05.003>
- United Nations (2018). *World Urbanization Prospects: The 2018 Revision*. Department of Economic and Social Affairs/Population Division. <https://population.un.org/wup/>. (accessed date: 2 March 2023).
- Vergeron, P. (1964). Interprétation statistique des résultats en matière d'analyse pollinique des miels. *Les Annales de l'Abeille*, 7: 349-364.
- Wastian, L., Unterweger, P.A. & Betz, O. (2016). Influence of the reduction of urban lawn mowing on wild bee diversity (Hymenoptera, Apoidea). *Journal of Hymenoptera Research*, 49: 51-63. <https://doi.org/10.3897/JHR.49.7929>
- Zambrano, L., Aronson, M.F.J. & Fernandez, T. (2019). The consequences of landscape fragmentation on socio-ecological patterns in a rapidly developing urban area: A case study of the National Autonomous University of Mexico. *Frontiers in Environmental Science*, 7: 152. <https://doi.org/10.3389/fenvs.2019.00152>
- Zanette, L.R.S., Martins, R.P. & Ribeiro, S.P. (2005). Effects of urbanization on neotropical wasp and bee assemblages in a Brazilian metropolis. *Landscape and Urban Planning*, 71: 105-121. <https://doi.org/10.1016/j.landurbplan.2004.02.003>
- Zaninotto, V., Thebault, E. & Dajoz, I. (2023). Native and exotic plants play different roles in urban pollination networks across seasons. *Oecologia*, 201: 525-536. <https://doi.org/10.1007/s00442-023-05324-x>



Material Supplementary



Fig S1. A- Nest aggregation of *Pseudaugochlora graminea* located right beside the stairs of an educational building of Federal University of Uberlândia. B- Nests constructed below the exposed roots of a mango tree. C- A nesting female preparing to leave her nest to forage.

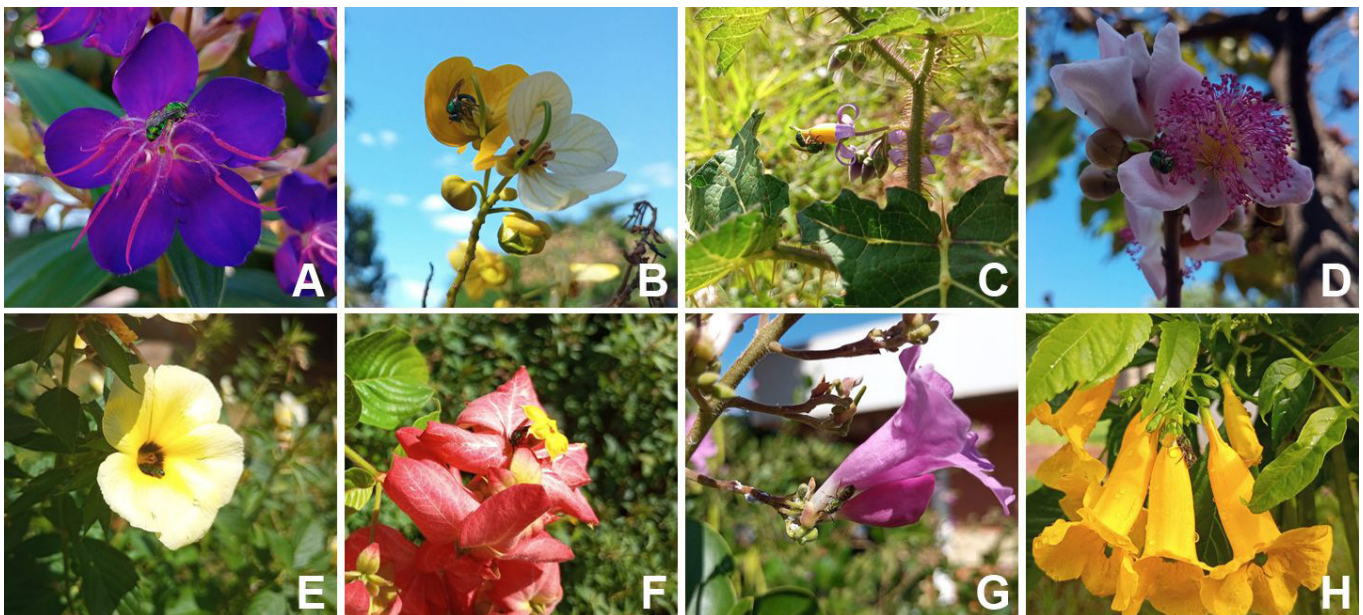


Fig S2. Flowering plants visited by *Pseudaugochlora graminea* females at the campus Santa Mônica, Uberlândia, Brazil. A - *Pleroma granulatum*, B - *Senna spectabilis*, C - *Solanum palinacanthum*, D - *Bixa orellana*, E - *Turnera subulata*, F - *Mussaenda philippica*, G - *Fridericia platyphylla*, and H - *Tecoma stans*.