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**PROMOTING POLLINATORS IN A TROPICAL URBAN LANDSCAPE: spatial
distribution of floral resources, interaction with flowers and a guide for good practices**

Belo Horizonte/MG
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Ingrid Naiara Gomes

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distribution of floral resources, interaction with flowers and a guide for good practices**

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Orientador: Dr. Pietro Kiyoshi Maruyama
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A todas as mulheres que questionam o óbvio,
desafiam o comum e seguem seus sonhos
ocupando espaços que por muito tempo lhes
foram negados. “The future is female!”

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“Não sei... se a vida é curta ou longa para nós, mas, sei que nada do que vivemos tem sentido, se não tocarmos o coração das pessoas”

Cora Coralina

RESUMO

Os polinizadores são essenciais para a integridade do ecossistema, mas sua diversidade está diminuindo devido a diversos impactos antrópicos como a urbanização. Entretanto, espaços verdes urbanos bem planejados podem sustentar uma comunidade diversa de polinizadores e seus serviços ecossistêmicos. Portanto, entender a distribuição de recursos, os efeitos das paisagens urbanas e identificar plantas atrativas para polinizadores é essencial, especialmente em cidades tropicais que permanecem sub-representadas. Dessa forma, esta tese teve como objetivo (1) avaliar a distribuição espaço-temporal de árvores atrativas aos polinizadores (2) avaliar o impacto da urbanização na diversidade de abelhas e suas interações com as flores e (3) identificar espécies de plantas atrativas. O Capítulo I analisou a distribuição de árvores de rua atrativas para polinizadores, considerando a origem das árvores, a estação de floração e os grupos funcionais de visitantes. Também foi testada a hipótese do "efeito luxo" em relação à disponibilidade desses recursos. O Capítulo II explorou o efeito dos fatores ambientais urbanos na diversidade e características funcionais das abelhas e o impacto da urbanização nas interações entre as abelhas e as flores. O Capítulo III apresenta um livro que tem como objetivo conscientizar o público sobre a importância dos polinizadores e de um paisagismo mais amigável. No Capítulo I, foi encontrada uma dominância de poucas espécies de árvores, com as abelhas sendo o grupo de polinizadores mais favorecido. A disponibilidade de recursos foi semelhante nas estações seca e chuvosa, mas a densidade de árvores foi reduzida na maior parte da paisagem. O "efeito luxo" foi evidente, com bairros mais ricos apresentando uma maior riqueza e abundância de recursos. No Capítulo II, espécies generalistas de abelhas dominaram as áreas urbanas, com a riqueza de plantas influenciando positivamente a riqueza e abundância de abelhas, mas com a maior proporção de plantas nativas impactando negativamente a abundância. Os fatores urbanos moldaram a distribuição de abelhas através de suas características funcionais, com as abelhas especialistas sendo mais afetadas pela urbanização. As redes de interação abelha-planta não foram afetadas pela urbanização. Esse estudo enfatiza a necessidade de um melhor planejamento urbano que promova uma maior diversidade de recursos florais em toda a cidade para dar suporte aos polinizadores. Isso ajudará a garantir que as áreas urbanas possam contribuir melhor para a conservação dos polinizadores.

Palavras-chave: Ecologia Urbana; Polinizadores; Conservação; Traços Funcionais; Interações Abelha-Planta.

ABSTRACT

Pollinators are essential for ecosystem integrity, but their diversity is declining due to anthropogenic impacts. Urbanization is a major threat, although well-planned urban green spaces can support diverse species and ecosystem services. Understanding resource distribution, the effects of urban landscapes on pollinators, and identifying plants that support them are key, especially in tropical cities. This thesis aimed to (1) evaluate the spatiotemporal distribution of street trees attractive to pollinators, (2) assess urbanization's impact on bee diversity, their functional traits, and bee-plant interactions, and (3) identify plant species that can support pollinators in urban areas. In the chapter I we evaluated the distribution of trees attractive to pollinators across Belo Horizonte's streets, considering tree origin, flowering season, and visitor groups. In addition, we tested the "luxury effect" hypothesis regarding floral resource availability. Chapter II we evaluated how urban environmental factors affected bee diversity and traits, and how urbanization influenced bee-plant interactions. Chapter III presents a book aimed at raising public awareness about pollinators and their floral preferences based on urban plants. In Chapter I, we found that streets were dominated by a few tree species, with bees being the most favored pollinator group, and bats and moths the least. Resource availability was similar across dry and wet seasons, but tree density was reduced in many areas. The "luxury effect" was evident, with wealthier neighborhoods having more richness and abundance of resources. Chapter II showed that generalist bee species dominated urban areas, with plant richness positively influencing bee richness and abundance and the higher proportion of native plants negatively impacted bee abundance. Urban factors shaped bee distribution by functional traits, with specialist bees were most affected by urbanization. The richness of plants played a key role in supporting larger bees and those that nest in the ground. Bee-plant interaction networks were not significantly affected by urbanization. Our study emphasizes the need for better urban planning that promotes diverse floral resources across the city to support pollinators. This will help ensure that urban areas can better contribute to pollinator conservation and biodiversity.

Keywords: Urban Ecology; Pollinators; Conservation; Functional Traits; Bee-Plant Interactions.

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GENERAL INTRODUCTION

In the last three centuries, there has been an increasing expansion of the human population with consequent intensification of land use transformations (Güneralp *et al.*, 2020; Seto *et al.*, 2011). Currently, much of the natural landscapes have been converted into pastures, agricultural land, and urban areas and the forecast is that urban expansion increases in the coming years (Ellis *et al.*, 2010; Seto *et al.*, 2012). Urbanization is one of the main drivers of natural habitat loss and fragmentation, resulting in ecosystem changes that affect the dispersal, distribution, and persistence of many species (Alberti, 2010; Wang *et al.*, 2019; Garcia Nieto *et al.*, 2018; Li *et al.*, 2016; Zhou *et al.*, 2018). Therefore, it is important to evaluate how species and ecosystem services respond to changes caused by urbanization, aiming to evaluate and implement sustainable strategies to reduce the impact on biodiversity (Grimm *et al.*, 2008; Wang *et al.*, 2019).

Among the ecosystem services deemed essential for sustaining terrestrial ecosystems, pollination stands out (Ollerton *et al.*, 2011; Klein *et al.*, 2007). Approximately 75% of crops and 87.5% of flowering plant species depend on pollination by animals (Klein *et al.*, 2007, Ollerton *et al.*, 2011). In natural environments, pollination assures plant reproduction and gene flow, promotes the maintenance of populations, which are in turn essential resources for the survival of several organisms (Potts *et al.*, 2010). Pollinators also contribute to increasing the productivity and quality of various crops in agricultural environments increasing their commercial values (Klein *et al.*, 2007; Klatt *et al.*, 2013). On a global level, the value of this service was estimated at around 153 billion per year in 2005, equivalent to 9.5% of the value of world agricultural production (Gallai *et al.*, 2009). In Brazil, the economic contribution of pollinators is estimated to be 30% (US\$12 billion) of the total annual agricultural income from pollinator-dependent crops, with 85 out of 141 analyzed crops relying on animal pollination (BPBES, 2019; Giannini *et al.*, 2015). Furthermore, a recent study has shown this dependence varies depending on the origin, with 71.4% of native food crops are highly dependent on pollinators, compared to 30.2% of exotic crops (Oliveira *et al.*, 2024). Pollination also can offer various economic benefits beyond those that have been quantified, including the reproduction of ornamental species, the cultivation of forage crops for domestic animals, and the provision of sustenance for wildlife in natural habitats, with the value of this service being underestimated (Lautenbach, 2019).

In urban areas, pollinators play a crucial role in the reproduction of various plant species and provide essential pollination services for urban agriculture, thereby enhancing local food

security (Lowenstein *et al.*, 2016; Nicholls *et al.*, 2020; Potter and LeBuhn, 2015). Therefore, developing sustainable urban agricultural practices combined with the conservation of pollinators can significantly advance several United Nations Sustainable Development Goals (SDGs). For instance, it directly supports SDG 2 (Zero Hunger) by fostering sustainable agriculture and improving food availability for those in need. Additionally, maintaining diverse pollinator populations contributes to SDG 11 (Sustainable Cities and Communities) by creating more resilient urban ecosystems and promoting sustainable food production practices. Indirectly, improvements in food security and agriculture can help advance SDG 1 (No Poverty) by enhancing economic opportunities and access to food, and SDG 3 (Good Health and Well-Being) by promoting better nutrition for the population. Ultimately, to ensure that pollinators effectively support these goals, it is essential to preserve the diversity of functional of these groups within urban environments (Kremen, 2018).

For a long time, cities were not considered when developing conservation strategies for biodiversity (Hall *et al.*, 2017). However, recent research has shown that the diversity of some groups, including pollinators, can be maintained in cities (Baldock *et al.*, 2015; Lowenstein *et al.*, 2014; Theodorou *et al.*, 2017). Depending on the management practices, urban areas can provide diverse resources for pollinators, such as pollen, nectar, and nesting sites (Hennig e Ghazoul, 2011; Osborne *et al.*, 2008). Furthermore, due to aesthetic concerns, urban green spaces can provide floral resources throughout the year, in contrast to natural areas which may show strong seasonality (Hoyle *et al.*, 2017; Mach and Potter, 2018). For this reason, some studies have reported that urban areas may present a greater diversity of some groups of pollinators, especially bees, when compared to other types of environments, such as rural areas (Leong *et al.*, 2014; Lowenstein *et al.*, 2014 Theodorou *et al.*, 2017). This change in perspective has aroused the interest of researchers in urban areas as alternative habitats for pollinators, which can aid in defining strategies that contribute to their conservation (Baldock *et al.*, 2019).

For cities to contribute to the conservation of pollinators and the ecosystem services they provide, it is important to understand how their diversity can be promoted (Aronson *et al.*, 2017; Turo and Gardiner, 2019). Some studies report that pollinator diversity increases in more heterogeneous urban areas with greater plant diversity and floral abundance (Hennig e Ghazoul, 2011; Hülsmann *et al.*, 2015). The surrounding urban matrix, connectivity, and extension of green spaces can also influence the pollinator community in these spaces (Aronson *et al.*, 2017; Hennig e Ghazoul, 2011; Patrício-Roberto e Campos, 2014). Street trees also play an important role in promoting biodiversity (Pena *et al.*, 2017, 2023; Some *et al.*, 2016). The uniform

distribution of these trees across the landscape, the availability of resources throughout the year, and diverse afforestation schemes benefit biodiversity in cities (Liu and Slik, 2022; Ikin *et al.*, 2015). Another important aspect is the use of native plants in urban landscaping (McKinney 2002; Threlfall *et al.*, 2017; Threlfall *et al.*, 2015; Burghardt *et al.*, 2009; Salisbury *et al.*, 2015). Native plants share a longer evolutionary history of interactions with native pollinators than non-native plants, and can represent more specialized interactions (Fenster *et al.*, 2004). Thus, the reduction of native plants to the detriment of the increase in non-native ones may result in a decrease of specialist pollinators, favoring, on the other hand, a community with more generalist species (Seitz *et al.*, 2020). However, all these factors are influenced by the public policies that govern cities and towns, the aesthetic preferences of the population, and the logistical limitations imposed by the availability of seedlings, including their cost and accessibility (Todorova *et al.*, 2004). Therefore, the distribution of vegetation in the urban landscape varies according to the socioeconomic gradients as well as environmental factors, which generates an uneven distribution of vegetation and consequently of the resources in the urban landscape (Landry and Chakraborty, 2009; Leong *et al.*, 2018). Besides various social implications, this unequal distribution of urban vegetation can exert a notable influence on urban biodiversity (Baldock *et al.*, 2019; Leong *et al.*, 2018). Therefore, for urban green spaces to benefit pollinators, it is important to conduct research to determine how resources are distributed throughout the urban landscape. Additionally, it is crucial to identify the plant species that have the greatest potential to support pollinators and to understand which landscape features could increase pollinator diversity in cities (Hall *et al.*, 2017; Hennig e Ghazoul, 2011; Garbuzov *et al.*, 2015; Turo and Gardiner, 2019).

Another key aspect in understanding how green spaces can contribute to biodiversity in cities is to examine how urban landscapes affect pollinators, aiming to develop strategies that minimize the impact of urban expansion on this group (Ayers and Rehan, 2021; Banaszak-Cibicka and Żmihorski, 2012). Among pollinators, bees are the most representative group (Potts *et al.*, 2010; Wardhaugh, 2015). Despite the evident importance of this group, several threats are contributing to the decline of bees, including urbanization (Lima *et al.*, 2022; Potts *et al.*, 2010). Research concerning the effect of urbanization on bees has grown in recent years due to the need to make cities more sustainable for biodiversity and conserve this important group of pollinators (Aronson *et al.*, 2016; Harrison and Winfree, 2015; Turo and Gardiner, 2019). However, many of these studies are limited to describing the abundance and richness of bees (Ahrné *et al.*, 2009; Banaszak-Cibicka, e Żmihorski, 2011; Geslin *et al.*, 2016; Zanette *et al.*,

2005), without considering their interactions. In addition, bees' responses can vary according to their functional traits, such as sociality, size, trophic specialization, and nesting location (Buchholz and Egerer, 2020). Furthermore, factors linked to urbanization can also alter interactions between plants and bees, affecting the structure and stability of communities (Harrison and Winfree, 2015; Geslin *et al.*, 2013; Kaiser-Bunbury *et al.*, 2017). Therefore, for a more complete assessment, it is essential to include responses to the functional traits of bees and their interactions with plants in studies to understand the effect of urbanization on bee communities and how to promote different species in cities (Buchholz and Egerer, 2020; Geslin *et al.*, 2013).

Despite the interest in making cities more sustainable for biodiversity, there is an uneven global distribution of these studies, with most research conducted in temperate cities rather than tropical ones (Brancher *et al.*, 2024; Zanette *et al.*, 2005; Stewart *et al.*, 2018; Stewart and Waitayachart, 2020; Silva *et al.*, 2023; Maruyama *et al.*, 2021). This gap is particularly concerning for tropical cities, which are not only underrepresented in research but also located in regions with high endemism and specialized pollination systems (Vizentin-Bugoni *et al.*, 2018). Furthermore, because tropical urban landscapes often lack marked seasonality, they typically offer year-round floral resources due to continuous flowering. This can support a higher diversity of pollinator groups (Nascimento *et al.*, 2020). However, these cities also face significant challenges, including high social inequality and inadequate urban planning, which can lead to spatial and temporal disparities in resource availability (Dobbs *et al.*, 2019). In poorer areas, for example, there may be more bare soil and fewer street trees and green areas, altering the resources available to pollinators on a spatial scale (Gomes *et al.*, 2023). Therefore, tropical cities present unique ecological and social contexts that must be considered in research on urban biodiversity (Dobbs *et al.*, 2019; Pena *et al.*, 2017; 2024). Addressing these disparities is crucial for improving urban ecological contexts and enhancing biodiversity conservation efforts in this region.

Given the knowledge gap regarding pollinators in urban tropical landscapes and the need to conserve diverse pollinator communities, especially bees, this thesis was structured into three chapters to address these issues. In Chapter I, we assessed the spatiotemporal distribution of trees attractive to different functional groups of pollinators (bees, wasps, butterflies, flies, beetles, moths, hummingbirds, non-hummingbird birds, bats, and others) across the streetscape of Belo Horizonte. We analyzed their geographical origin, flowering season, and the groups of floral visitors attracted to them, and tested the 'luxury effect' hypothesis on the availability of

floral resources to pollinators. Chapter II focused on evaluating how bee taxonomic diversity (e.g., richness and abundance) and functional traits (e.g., sociality, nesting type, trophic specialization, and body and wing size) respond to various urban environmental characteristics (e.g., urbanization gradient, average building height, proportion of vegetation, plant richness, flower abundance, and percentage of native plants). We also investigated the effect of urbanization on bee-plant interactions. In Chapter III, we present a book aimed at the public, providing information about the importance of pollinators and lists of floral preferences for each pollinator group based on the results from the previous chapters. This book serves as a tool to raise awareness among urban residents about the significance of conserving pollinators and to promote actions that support greater pollinator diversity in cities.

The main hypotheses of this thesis were that the tropical urban landscape evaluated is possibly poorly planned and managed, leading to an uneven spatiotemporal distribution of trees with a greater concentration of resources in areas of higher socioeconomic status within the city. We also expected a decrease in bee diversity and specialization in interaction networks in more urbanized areas and that bee functional traits would be affected differently by urbanization. Finally, we expected that some landscape variables, such as the proportion of vegetation, the richness and abundance of resources, and the proportion of native plants would be associated with a greater diversity of bees, including their functional traits. Understating the distribution of floral resources, the pollinators' use of flowers, and the effects of urban environmental factors on bees will foster a deeper understanding of which species and traits are most vulnerable to urbanization. This knowledge is crucial for devising effective strategies to mitigate these effects by fostering increased biodiversity within tropical cities.

CHAPTER I

Spatiotemporal availability of pollinator attractive trees in a tropical streetscape:

Unequal distribution for pollinators and people

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ABSTRACT

Street trees integrate the urban green infrastructure and are important elements for the maintenance of biodiversity, including pollinators. Thus, assessments of the spatiotemporal distribution and composition of these trees can subsidize strategies of conservation for different groups of pollinators in the cities. Here, we evaluated the spatiotemporal distribution of trees attractive to pollinators across the streetscape of a large Brazilian metropolis with more than 2.5 million inhabitants. We used the georeferenced data of ca. 300,000 woody plant individuals cataloged across the streetscape. These plants were characterized according to their geographical origin, flowering season, and the floral visitor groups that are attracted based on a literature survey. We also tested the “luxury effect” hypothesis on the resource availability to pollinators by evaluating the relationship between the average family income of the population and the richness and abundance of trees. We found that the streetscape was characterized by the dominance of a few tree species, with a balanced representation of both native and non-native species. Bees were the most favored group (94.86%) while bats (1.43%) and moths (1.73%) were the least. The potential supply of resources was homogeneous across dry and wet seasons, but the density of trees was reduced in most of the landscape. We found a strong luxury effect since tree richness and abundance were positively related to regions with higher average family income. Our study highlights the need for better planning and management practices of urban green spaces to support pollinators more uniformly across streetscapes. This will allow the benefits provided by pollinators to be more evenly shared among residents of urban landscapes.

Keywords: Conservation, Green infrastructure, Luxury effect, Street trees, Tropical cities, Urban ecology

1. INTRODUCTION

The urban green infrastructure constitutes a mosaic of natural and semi-natural areas of different sizes, partially or completely dominated by permeable surfaces (Chatzimentor et al., 2020). These areas provide multiple ecosystem services that increase the well-being of the human population, including improvement of air quality, the reduction of water runoff, and attenuation of noise pollution (Jones, 2021; Nowak et al., 2018). Incorporating green infrastructure into streetscapes can offer additional benefits, such as the reduction of the impacts of climate change through carbon dioxide sequestration and the amelioration of microclimate conditions through shading that provides thermal comfort for citizens (Escobedo et al., 2010; Li et al., 2018). In this sense, although streetscapes are associated with several environmental impacts and disturbances, e.g., degradation and loss of natural habitats, biodiversity reduction, pollution, heat island effect, and floods, green infrastructures may improve the ecological and social context at the landscape level (Razzaghmanesh et al., 2016). Accordingly, street trees represent one of the key elements that integrate the urban green infrastructure, and both their density and composition are important to ensure the provision of ecosystem services in cities (Tomson et al., 2021; Wood and Dupras, 2021).

Considering trees in the streetscapes, a higher proportion of native species, higher species diversity and the maintenance of large and old individuals are associated with the promotion of more diverse wildlife (Ikin et al., 2015; Pena et al., 2023, 2017b; Stagoll et al., 2012). The planting of nectar and fruit-producing trees that provide such resources at different periods of the year and for distinct animal groups also contributes to support more diverse communities (Liu and Slik, 2022). Furthermore, more evenly distributed trees across the streetscape can improve the connectivity between green spaces, increasing the permeability of the urban matrix and facilitating the movement of different animals (Benedict and McMahon, 2006). Despite the many potential benefits to biodiversity, the distribution and composition of urban trees result mostly from the aesthetic preferences of the population, logistical limitations imposed by the availability of seedlings (including their cost), and by the restriction linked to the city's infrastructure, i.e., trees can't be planted in areas occupied by roads and buildings (Todorova et al., 2004). Such tendencies may vary according to socioeconomic gradients in many cities, which generates uneven distribution of trees and green spaces across the streetscape (Landry and Chakraborty, 2009; Wood and Esaian, 2020). This is often referred as the "luxury effect", in which regions more impoverished of the city harbor a lower amount of green cover than the wealthier ones (Leong et al., 2018). In addition to several social

implications, such pattern leads to an unequal distribution of biodiversity which can affect specific groups, such as pollinators and the respective ecosystem services they provide (Baldock et al., 2019; Leong et al., 2018). However, support for the luxury effect on the resource provisioning to pollinators is still limited.

Pollinators constitute an important group of animals found in urban areas, benefiting from trees by collecting floral resources, such as pollen, nectar, and oils, the latter collected exclusively by specialized bees (Hausmann et al., 2016; Maruyama et al., 2021; Policarová et al., 2019). They provide important ecosystem services through their interactions with flowering plants, since approximately 87.5% of these require biotic pollination for reproduction (Ollerton et al., 2011). Thus, they contribute to the maintenance and conservation of biodiversity and agricultural productivity (IPBES, 2016; Ollerton, 2017). In urban areas, pollinators may contribute to the reproduction of many native plants, promoting their conservation (Lowenstein et al., 2015), and provide pollination services to urban agriculture, increasing local food security (Nicholls et al., 2020; Potter and LeBuhn, 2015). However, for pollinators to provide effective ecosystem services in cities, it is essential to maintain the diversity of different functional groups, which depends on the resources offered by a diverse community of flowering plants (Kremen, 2018).

Assessments on the spatiotemporal patterns and composition of urban trees can help us to understand whether the resources provided support different groups of pollinators in the streetscape and increase their diversity in cities (Freitas et al., 2020). Previous studies have shown that there is an uneven spatial distribution of street trees in many cities regarding their abundance and species diversity (Pham et al., 2012; Threlfall et al., 2022). It has also been reported that there is a seasonal variation in the flowering periods of urban trees, which can lead to periods of low resource availability for pollinators (Aleixo et al., 2014). Some studies have also suggested that the availability of floral resources is spatially unequal for different groups of pollinators in the urban area (e.g., Freitas et al., 2020). Notwithstanding, few studies evaluated the relationship between pollinators and vegetation in large tropical cities so far (e.g., Freitas et al., 2020; Maruyama et al., 2019; Stewart et al., 2018). Such scarcity of data compromises truly global efforts in the conservation of urban pollinators (Maruyama et al., 2021; Nascimento et al., 2020). Moreover, past studies were usually conducted in smaller urban settlements and used simplistic assumptions of pollination syndromes to infer the group of pollinators that would be benefited by specific plant species (Aleixo et al., 2014; Freitas et al., 2020). Although such classifications may capture some of the most relevant pollinators for

driving eco-evolutionary dynamics of plant-pollinator interactions (Rosas-Guerrero et al., 2014), they may also fail to capture many of the interactions and resource use by more generalized pollinators (Maruyama et al., 2019). Thus, we still lack a more detailed assessment on the availability of floral resources provided by trees for specific pollinator groups in tropical metropolises with millions of inhabitants.

In this study, we aim to characterize the spatiotemporal distribution of resources provided by street trees for different pollinator groups across the streetscape of a tropical metropolis in Brazil. Since urban trees are usually planted in monospecific groups for aesthetic purposes (Liu and Slik, 2022; Todorova et al., 2004), we expect a dominance of few tree species, which may indicate that floral resources for different groups of pollinators are unevenly distributed across the streetscape. The distribution and diversity of street trees can be strongly affected by public and private investments on urban afforestation (Leong et al., 2018). We therefore tested the hypothesis of a luxury effect influencing the distribution of potential resources for all pollinators evaluated (e.g., bees, wasps, butterflies, flies, beetles, moths, hummingbirds, non-hummingbird birds, bats, and others). We predicted that wealthier urban microregions will have higher densities of street trees, thus potentially providing more floral resources. Finally, we expect that the temporal availability of resources is affected by the spatial biases of trees' distribution, so that the availability of resources during dry and wet seasons would also be unevenly distributed across the streetscape. The results of this study can contribute with information for the planning and management of urban areas with the aim of providing a better distribution of resources and improving the connectivity between green spaces for different groups of pollinators. These strategies are especially important in tropical regions, where there is higher diversity of both plants and pollinators, that provide important urban ecosystem services.

2. MATERIALS AND METHODS

2.1. Study area and street tree community data

The study was conducted in Belo Horizonte city, the capital of the state of Minas Gerais, Southeastern Brazil-19° 48' 57" S, 43° 57' 15" W (Fig. 1). Estimated population in the city is 2,530,701 inhabitants (IBGE, 2021). It is one of the first planned cities in Brazil, designed with the concept of a “garden city”(Duarte, 2009). Climate in the region is Cwb according to the Köppen's classification, showing 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).

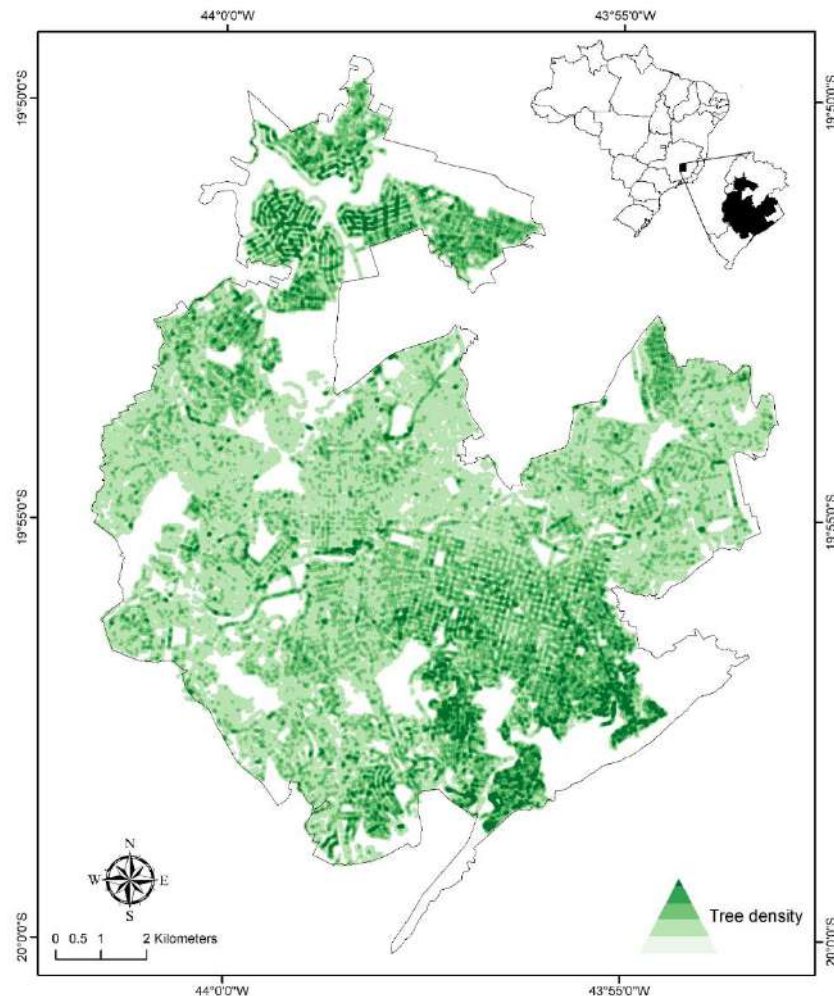


Fig. 1. Spatial distribution of the density of trees that provide potential floral resources for all pollinators across the streetscape of Belo Horizonte. More intense colors indicate regions with higher tree density for the pollinators.

We obtained information on street trees from the Belo Horizonte's Tree Information System (SIIA-BH). It provides georeferenced data on trees located across the streetscape of the city, including small green spaces (Belo Horizonte, 2021). The database provides information about the street tree community as a feature-point map, including scientific names and geographic coordinates. This database originally consisted of 559 species and 300,000 individuals of trees and shrubs recorded across the five administrative regions of Belo Horizonte.

Since we aimed to evaluate the spatiotemporal distribution of trees that potentially provide resources for pollinators via flowers, we excluded gymnosperms and pteridophytes (15 species and 13,296 individuals). Subsequently, we used the REFLORA (2021) website to categorize species according to their geographic origin (i.e., native or not native to Brazil). Species classified on the website as naturalized or cultivated were considered non-native plants. For the species not found on REFLORA, we carried out a search on the Google Scholar platform (<https://scholar.google.com/>) with the name of the species and the term “origin” as keywords (Appendix 1). Plant species were also classified according to their floral visitor groups to assess which animals potentially use flowers as a resource according to focal observations of interactions in previous studies. To do so, we used information compiled recently in a review of urban pollinators in Brazil by Nascimento et al. (2020). For species that were not found in this study, we conducted a survey in the Google Scholar using the scientific name of the tree species and "pollinators" as keywords (Appendix 1). For all plants, native and not native to Brazil, the information on the functional group of pollinators was extracted from studies conducted in different countries, but prioritizing observations carried out in Brazil whenever possible. The last search was conducted on July 21, 2021. The floral visitors recorded for each plant species were classified into the following functional groups: bees, wasps, butterflies, flies, beetles, moths, hummingbirds, birds (i.e., other than hummingbirds), bats, and others (i.e., thrips, geckos, and lizards, when these were considered as pollinators in the original study). We excluded records of ants, bed bugs, and dragonflies because these are unlikely to be pollinators. We also removed those plant species from which we did not find information related to floral visitors. In the end, we were able to find information about 67.6% (359) of the species and 75.60% (216,797) of the individuals in our database (Appendix 1).

Plant species were also classified according to their reproductive period as flowering in the dry (April-September), wet (October-March), or both seasons. The phenological information of the species was surveyed in specific scientific literature (i.e., Aleixo et al., 2014; Freitas et al., 2020; Lorenzi, 2009, 1998, 1992). When not available, we searched for additional sources in Google Scholar database using the scientific name of the tree species and the words “phenology” and “Brazil” as keywords (Appendix 1). Since flowering periods can vary in space according to climatic conditions, we only considered studies that observed the flowering phenology in the Southeastern region of Brazil. If the study described only the flowering peak (one or two months), then we used this same description in our classification. We did not find information for the flowering period of 89 species (7,586 individuals) out of the 359 species

with information on floral visitors. Thus, regarding phenology, we found information for 75.21% of species and 96.50% of individuals. At all stages of the literature search, we only included scientific articles, books, thesis, and dissertations as sources for data extraction (Appendix 1).

2.2. Spatiotemporal distribution of floral resources for pollinators

From the street trees database, we used a binary classification to indicate which group of pollinators is a flower visitor of each tree individual across the streetscape (an excel sheet with a column for each group of pollinators). This method allows classifying more than one pollinator functional group for a given plant species. Then, we estimated the spatial distribution of trees that potentially provide floral resources for each group of pollinator using the *point density* tool on ArcGIS® 10.6 software (ESRI, 2017) by calculating the number of trees (i.e., points) within a 50 m radius buffer surrounding each tree. The buffer size was defined considering the average size of the city blocks (100 m) in Belo Horizonte. This procedure resulted in nine raster surfaces (i.e., one raster for each pollinator group) indicating regions with low to high number of trees that potentially provide floral resources for each pollinator group. We reclassified each raster surface into five classes (1 to 5) of density of trees by applying Jenks Natural Breaks. To characterize the regions across the streetscape that provide resources for different groups of pollinators, we overlapped all raster surfaces. This procedure resulted in a final map indicating regions that provide a low density of resources for only one group of pollinators (scores equal to 1), until regions that provide a high density of resources for all pollinators (scores equal to 45). Thus, across the streetscape, if there was a tree that provides resources for at least one pollinator in a 50m radius buffer, the minimum score would be one. It is important to highlight that we focused on street trees only, thus large empty spaces in the resulted raster surfaces indicate regions without streets (i.e., outside of the streetscape), such as urban parks and lakes. Regions of the streetscape without trees in a 50m radius buffer received a score equal to zero.

To assess the temporal distribution of trees that potentially provide floral resources for pollinators, we also adopted a binary classification to indicate the flowering period of each tree individual (wet and/or dry season). We applied the *point density* tool to produce a raster surface indicating the distribution of trees across the streetscape during each season. To assess the spatiotemporal variation on the availability of resources according to seasons, we also used Jenks Natural Breaks to reclassify the dry season tree density map into five classes between 1

and 5, and the wet season density map into five classes between 10 and 50. This procedure allowed us to identify if there are regions that provide a low density of resources during only one season (i.e., values equal to 1 during dry season and equal to 10 during the wet season), regions with low density of resources during both seasons (i.e., values equal to 11, 21, and 12) and regions with intermediate to high density of resources during one and/or both seasons (other combinations e.g., 13, 54, etc.; Fig. 5)

2.3. The luxury effect hypothesis

To investigate if there is a luxury effect in the distribution of trees that provide floral resources to pollinators, we obtained data on average family income from the most recent survey of the Brazilian Institute of Geography and Statistics (IBGE, 2012). The information is provided as a shapefile in which the census sectors are represented by polygons containing specific socioeconomic data. These represent the microregions within the city where information was collected and made available by the government. In total, 2,013 microregions were defined, ranging from 0.16 to 327.34 hectares, with a mean of 6.67 (± 12.92 sd). For each microregion, we extracted the richness (number of species) and abundance (number of individuals) of trees, which represent the floral resources used by all pollinators. We removed those microregions represented by only one building, those with zero income characterized by green spaces (e.g., parks), and those that did not have information about the average population income.

We fitted linear models to investigate if both the richness and abundance of trees in the streetscape is related to population average family income across microregions. Since polygons have variable sizes, we took the ratio between the richness or abundance of trees and the area (in hectares) of the respective microregion to create our response variables: the densities of tree richness and abundance. We applied logarithmic transformation to the predictor variable to improve the distribution of models' residuals. After finding a significant effect of residual spatial autocorrelation for both richness (Moran's I test; $p < 0.001$) and abundance models (Moran's I test; $p < 0.001$), we fitted spatial models by using the respective coordinates of the centroids of microregions. We incorporated the spatial dependence in models by specifying a structured covariance matrix based on exponential autocorrelation using maximum likelihood estimation in the R-package *glmmTMB* version 1.1.3 (Brooks et al., 2017; Kristensen and McGillicuddy, 2022). The spatial dependence and models' validation were conducted by simulating the residuals 1,000 times using the R-package *DHARMa* version 0.4.5 (Hartig,

2022). We tested the significance of models using type II Wald chi-square tests in the R-package *car* version 3.1.0 (Fox and Weisberg, 2019). Using the R-package MuMIn version 1.47.1 (Bartoń, 2022), we calculated the amount of variance explained by the whole model ($R^2_{\text{conditional}}$: i.e., including fixed effects and spatial covariance structure) and by the fixed effect alone (R^2_{marginal}) (Nakagawa et al., 2017). We used the *ggpredict* function in the R-package *ggeffects* version 1.1.2 (Lüdtke, 2018) to extract and plot the model adjusted predicted probabilities and the respective 95% CIs. We also plotted the raw data points and added jittering (i.e., random noise) to prevent overplotting.

Due to the uneven distribution of resources for specific pollinator groups (see Results), the respective datasets per pollinator group had an excessive number of zeros. Thus, we did not perform any modelling for specific groups. However, we conducted pairwise Spearman's rank correlations between data for each group to show that the patterns found are representative for pollinator groups in separate as well. All analyzes were conducted using R software version 4.2.1 (R Core Team., 2021).

3. RESULTS

3.1. Street trees composition overview

Considering the geographic origin of the trees distributed in the streetscape, we found that 55.71% ($n = 200$) of the species were native while 42.06% (151) were non-native. Regarding the number of individuals, 40.44% (87,669) of the trees were native while 59.50% (129,008) were non-native. We did not find information for 2.22% (8) of the species, that constituted 0.06% (120) of the total individuals. We found that 47 out of the 359 species had more than 1,000 tree individuals distributed in the streetscape of Belo Horizonte, with 14 species exceeding 5,000 individuals. Among these most abundant, the native species were *Caesalpinia peltophoroides* (8.37% of the total; represented by 18,139 individuals; Fabaceae), *Syagrus romanzoffiana* (5.65%; 12,251; Arecaceae), *Tibouchina granulosa* (4.75%; 10,302; Melastomataceae), and *Handroanthus chrysotrichus* (2.71%; 5,894; Bignoniaceae). The most abundant non-native species were *Murraya exotica* (8.53%; 18,503; Rutaceae), *Dyopsis lutescens* (4.58%; 9,924; Arecaceae), *Tabebuia rosea* (4.03%; 8,752; Bignoniaceae), *Ligustrum lucidum* (3.11%; 6,745; Oleaceae), *Lagerstroemia indica* (2.90%; 6,289; Lythraceae), *Bauhinia variegata* (2.78%; 6,028; Fabaceae), *Terminalia catappa* (2.65%; 5,765; Combretaceae), *Leucaena leucocephala* (2.65%; 5,748; Fabaceae), *Michelia champaca* (2.51%; 5,453; Magnoliaceae), and *Lagerstroemia speciosa* (2.37%; 5,144; Lythraceae). Although these 14

most abundant species represent only 3.90% of the total species pool, they comprise 57.63% (124,937) of all individuals recorded in the streetscape.

Regarding seasonality, 24.07% (65 out 270) of species flowered in the dry season, 26.67% (72) in the wet season, and 49.26% (133) in both (Fig.2a). Concerning the number of individuals that offer resource to pollinators in the streetscape, we found that 18.23% (38,131) flowered in the dry season, 28.94% (60,546) in the wet season, and 52.83% (110,534) in both. (Fig.2b). Among the groups of pollinators evaluated, bees were the group most commonly associated with the floral resources provided by trees in the streetscape. We found that this group interacted with 80.50% (289) of the species, which represented most of the trees comprising 94.86% (205,652) of the individuals (Fig. 2c, d). The second most abundant group included hummingbirds, which were associated with 16.43% (59) of the species and 20.12% (43,633) of the individuals. Next, wasps were associated with 13.93% (50) of the species and 13.55% (29,372) of the individuals while butterflies were associated with 12.81% (46) of the species and 19.08% (41,372) of the individuals. Finally, bats and moths were the pollinator group associated with fewest trees providing resources. Bats were associated with only 3.62% (13) of the tree species and 1.43% (3,108) of the individuals and moths with 7.52% (27) of the species and 1.73% (3,758) of the individuals (Fig. 2c, d).

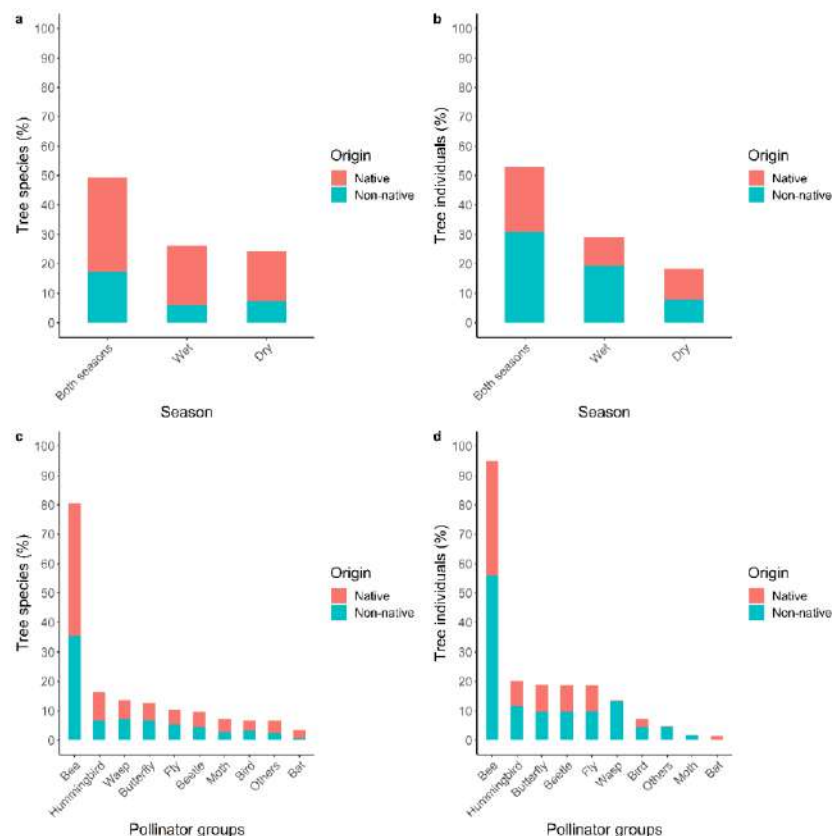


Fig. 2. Percentage of number of tree species – richness (a) and tree individuals – abundance (b) that flower in the dry, wet and both seasons. Percentage of tree species (c) and tree individuals (d) that provide resources for different groups of pollinators. The pink and blue bars indicate the percentage of native and non-native species, respectively.

3.2. Spatiotemporal distribution of floral resources for pollinators

The assessment of the spatial distribution of trees for different functional groups of pollinators indicated that most of the landscape provides resources for a few groups of pollinators concomitantly, without any part of the landscape providing resources for all functional groups of pollinators (Fig. 3). However, the Northern and Southeastern regions were those that favored more pollinators at the same time when compared to other regions (Fig. 3).

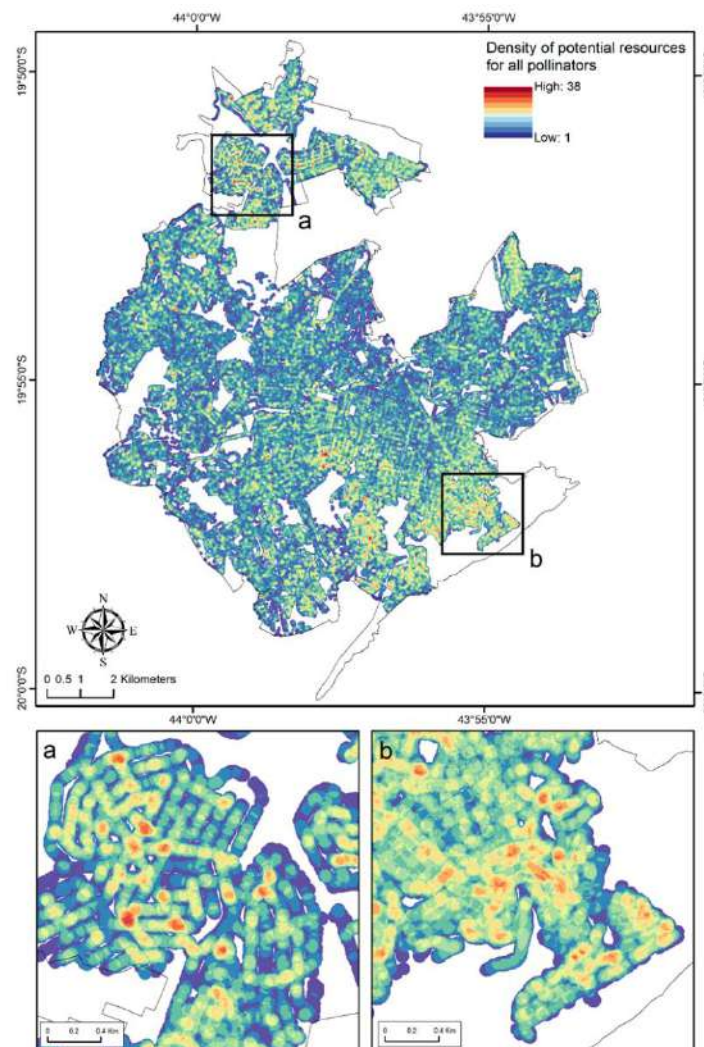


Fig. 3. Spatial distribution of the density of trees that provide potential floral resources for different functional groups of pollinators across the streetscape of Belo Horizonte. Cold and warm colors indicate a smaller and larger density of favored pollinator groups, respectively. Letters (a and b) are the zooming of regions in the streetscape that favor a greater number of functional groups of pollinators.

The spatial distribution of trees for each group of pollinators indicated that the tree density was the highest for bees when compared to the remaining pollinator groups, especially bats and moths which were the least favored (Figs. 4a, d, S1). The densities of trees providing floral resources for bees, beetles, hummingbirds, moths, butterflies, flies, and other non-hummingbird bird species were concentrated mainly in the Northern and/or Southeastern parts of the city (Figs. 4a, b, c, S1, S2, S3, S4). On the other hand, the densities of trees providing floral resources for bats and wasps, showed a more homogeneous distribution in the landscape (Figs. 4d, S5).

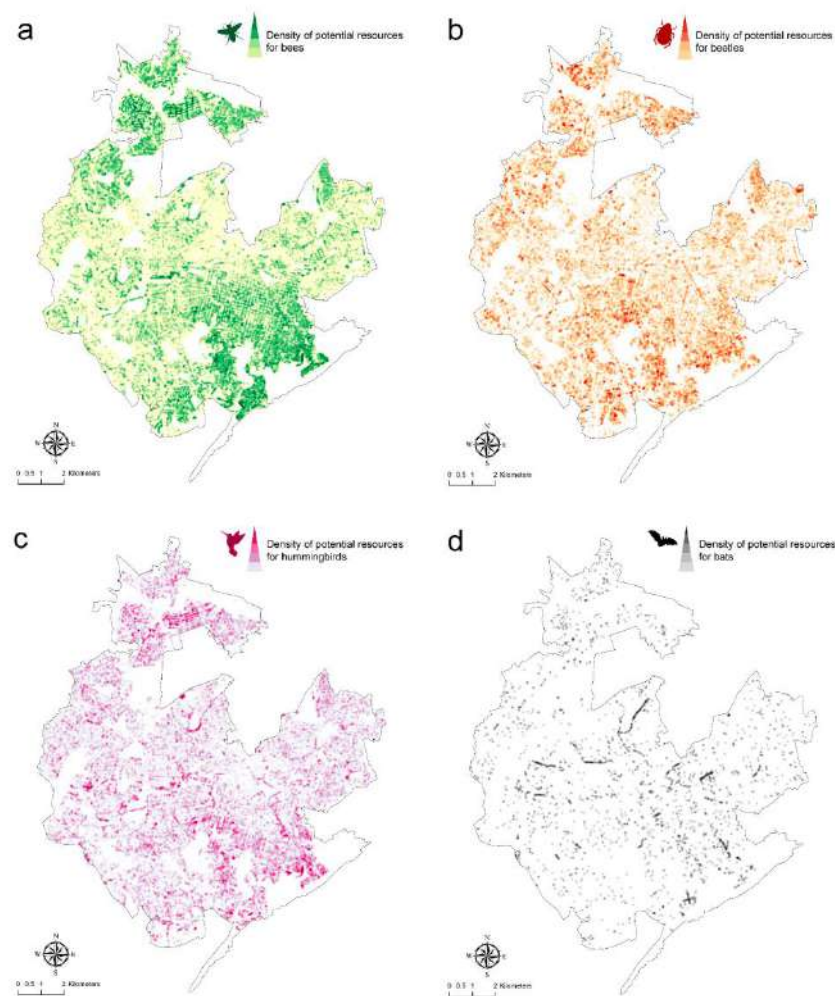


Fig.4. Spatial distribution of the density of trees that provide potential floral resources for (a) bees (green points), (b) beetles (orange points), (c) hummingbirds (pink points), and (d) bats (black points) across the streetscape of Belo Horizonte. More intense colors indicate regions with higher tree density for the pollinators.

The spatiotemporal distribution of the tree density showed that the availability of resources was homogeneous across both dry and wet seasons. The density of trees was low in most of the landscape, regardless of the season (Fig. 5a, b). Independent of whether considering

the rainy, dry or both seasons, areas with high tree density were concentrated in a few regions, mainly in the North and Southeast parts of the city (Fig. 5c).

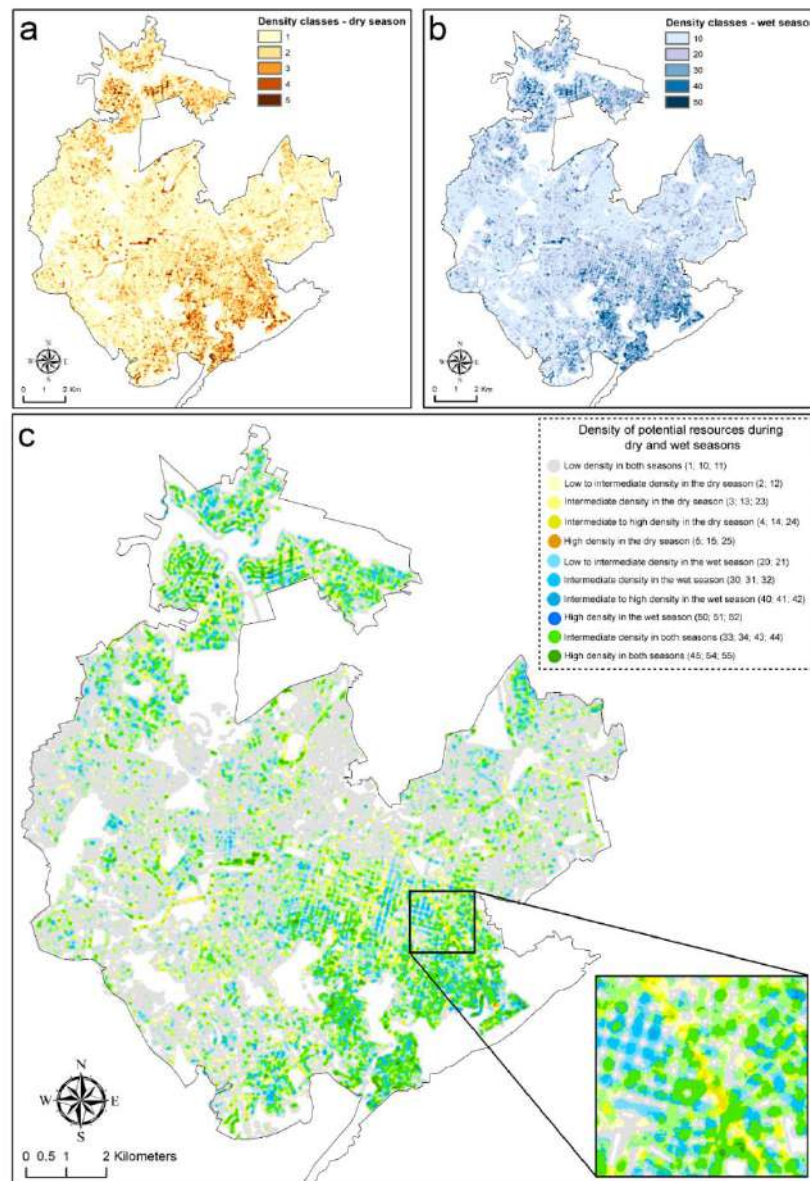


Fig. 5. Spatiotemporal distribution of the density of trees that potentially provide floral resources for pollinators during the dry (a), wet (b), and both seasons (c) across the streetscape of Belo Horizonte. In (c) gray points indicate regions in the streetscape that have a low density of floral resources for pollinators, regardless of the season. Yellow and blue points indicate areas in the streetscape that provide low to high density of floral resources in the dry and wet seasons, respectively. Green points indicate areas in the streetscape that provide intermediate to high density of floral resources in both seasons.

3.3. The luxury effect hypothesis

In a similar way to previous results of tree density, there was a greater concentration in the density of the average family income in the Northern and Southern portions of the city (Fig.

6a). Consequently, the variation on richness and abundance of trees highly overlapped with the variation of the average family income across the landscape (Fig. 6a, b). The richness of trees providing potential floral resources to pollinators was positively related to the average family income across microregions, with an R^2_{marginal} of 0.103 and an $R^2_{\text{conditional}}$ of 0.413, explaining 10.3% of the variation ($\chi^2 = 90.91$; $df = 1$; $p < 0.001$; Fig. 6c). Concerning tree abundance, we found an even stronger positive relationship, with an R^2_{marginal} of 0.344 and an $R^2_{\text{conditional}}$ of 0.694, with 34.4% of variance explained ($\chi^2 = 392.73$; $df = 1$; $p < 0.001$; Fig. 6d). The comparison of marginal and conditional R^2 s indicates that although there is influence of spatial dependency, average family income still explains a considerable amount of variance. Our correlation analyses also indicated a strong association between the abundance of attractive trees to distinct groups of pollinators (mean Spearman $r = 0.67$; Fig. S6). Altogether, these results indicated a luxury effect determining the spatial distribution of potential resources for pollinators across the assessed streetscape.

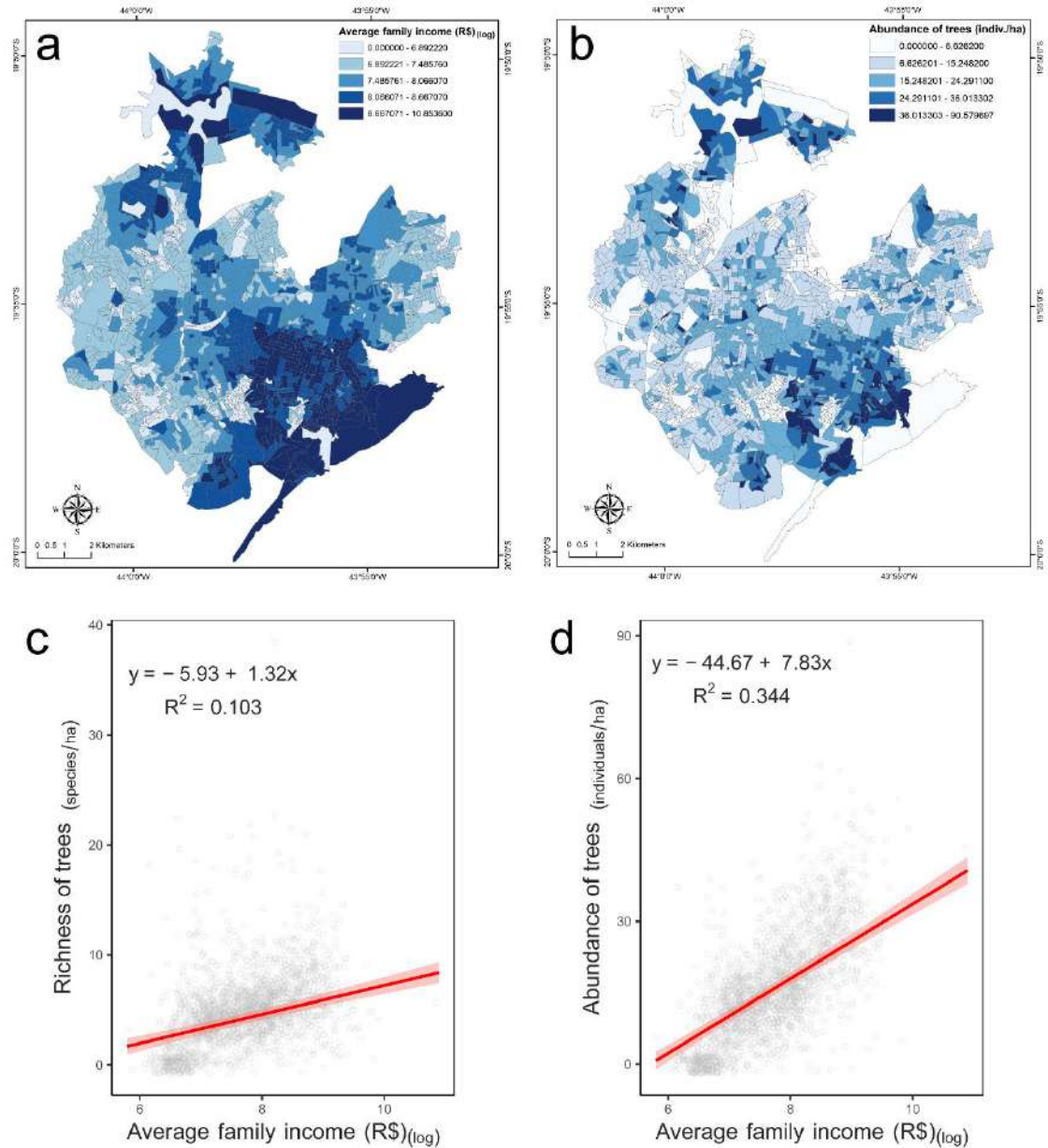


Fig. 6. Relationship between average family income and the richness and abundance of trees. Spatial distribution of (a) average family income and (b) abundance of trees variables, respectively. Effect of average family income on the (c) richness and (d) abundance of trees that potentially provide floral resources for all pollinators across the streetscape of Belo Horizonte. The red lines and shadows show model-adjusted (predicted) values and their 95% confidence intervals, respectively. Points in (c) and (d) show the raw data jittered with 0.8 and 2.0 units in y, respectively.

4. DISCUSSION

Street trees are essential for the maintenance and conservation of pollinators in cities, providing food resources and nesting structures (Hausmann et al., 2016; Mach and Potter,

2018). Using a large database from a tropical metropolis as study system, we found that the streetscape was characterized by the dominance of a few tree species, with similar representation of native and non-native species. We also found that not all pollinator groups were equally benefited, with bees the most benefited in relation to other groups, especially when compared to bats and moths. However, it is important to emphasize that this result is based on the interactions we found using data available in the literature, and not from direct field observations in our study area. Concerning the flowering season, the supply of trees potentially offering resources was similar during both dry and wet seasons. However, the density of these trees was reduced in most of the landscape, being more concentrated in regions whose residents had a higher average family income. This pattern confirms that the luxury effect is influencing the distribution of trees that may offer floral resources to pollinators.

Although non-native plants are dominant in many cities around the world, (Stewart et al., 2018; Wilson and Jamieson, 2019; Wood and Esaian, 2020), this was not the case of the streetscape of Belo Horizonte. Studies carried out in different urban areas evaluating the capacity of non-native plants in supporting pollinators show contrasting results (Bergerot et al., 2010; Tasker et al., 2020). Some studies consider the use of non-native plants as a threat to urban biodiversity (Banerjee and Dewanji, 2017; Fenoglio et al., 2021; Paż-Dyderska et al., 2020). On the other hand, other studies report that these plants can complement the resources provided by the native ones in cities, especially during periods of low resource supply or in regions with low green area coverage (Salisbury et al., 2015; Staab et al., 2020; Stewart et al., 2018). At the same time, pollinators seem flexible in using resources from native and non-native plants, and both can play important structural roles in the interaction networks (Nascimento et al., 2020). Therefore, an interesting strategy could be to include different native species in the urban greening, diversifying the quality and quantity of resources for different groups of pollinators, and including ecologically important non-native plants when necessary (Staab et al., 2020). However, this should be done considering the potential negative effects of non-native plants, such as a “hogging effect” that hinders visitation to native species (Cuadra-Valdés et al., 2021; Koptur and Barrios, 2020) and the risk of biological invasion (Moro and Castro, 2015; Tasker et al., 2020). In addition, the support of specialist pollinators that may be less prone in using non-native plants should be considered (Bergerot et al., 2010; Threlfall et al., 2015).

Bees are the most dominant group of pollinators, especially when considering the diversity of plant species that depend on them (Ollerton, 2017). In agreement, this group was the most

associated with the trees found across the streetscape of Belo Horizonte, especially when compared to other pollinators, such as bats and moths. The predominance and importance of bees in pollination systems from natural communities was reported by Ollerton (2017), which demonstrated that most plants are pollinated by generalist insects (most of them bees) (~47%), exclusively by bees (~18%), and flies (~15%), with very few plants pollinated by other functional groups, such as bats, wasps, and thrips that represented less than 1%. In addition, this predominance of bees also is associated with their dependence on several floral resources throughout their life cycle, since they require resources other than nectar to feed their offspring and maintain their nests, such as pollen, oil, and resin (Aleixo et al., 2014; Ollerton, 2017; Rocha-Filho et al., 2018). Despite their importance in pollination, bee diversity has been decreasing due to several anthropic impacts, such as the use of agrochemicals, habitat fragmentation, and urban expansion (Banaszak-Cibicka and Dylewski, 2021; Cardoso and Gonçalves, 2018; Potts et al., 2010). Therefore, strategies that increase the diversity of resources in urban green spaces are essential for the conservation of different bee species in cities (Baldock, 2020; Dylewski et al., 2020). However, for a more holistic conservation strategy, greening choices in the city must also include plant species that are also used as a resource by groups of pollinators other than bees (Fontaine et al., 2016; Maruyama et al., 2019). This is especially important for groups less favored by current landscaping practices and that are also threatened by the urbanization processes, such as beetles, moths, and bats (Magura and Lövei, 2021; Russo and Ancillotto, 2015; Straka et al., 2021). The conservation of different pollinator groups in cities is essential to ensure the reproductive success of many plants including those that are not bee-pollinated, many of them consisting of economically important crops (Albuquerque-Lima et al., 2022; Rader et al., 2016; Ratto et al., 2018). Our spatial evaluation indicated that some large avenues in the city have a concentration of trees that provide resources for bats, one of the least favored groups. Furthermore, some of these areas also provide resources in both seasons and are not located in the wealthier regions of the city. Therefore, the landscaping strategy adopted in these specific avenues can be considered a good starting point in guiding biodiversity-friendly management practices, increasing the conservation potential of cities for different functional groups of pollinators, and improving the population's access to urban green spaces and their important ecosystem services.

One recurrent trend regarding the composition and distribution of trees in the urban matrix is that the streetscapes are generally characterized by the dominance of a few species (Liu and Slik, 2022; Pena et al., 2016; Thaweeproradej and Evans, 2022). In agreement, we

found that a subset of only 14 species (out of 359) represented more than half (57.63%) of all cataloged tree individuals with information on the potential floral visitors. Considering the response of urban ecosystems to global climate change, it is recommended that a single species should not exceed 10-20% of the total number of individuals, since a low diversity of plants may decrease ecosystem resistance and resilience (Kendal et al., 2014; Paquette et al., 2021). Moreover, for urban afforestation to support different species of pollinators and their associated ecological functions, landscaping practices must diversify the plant species that are used in the streetscape (Baldock et al., 2019; Stewart and Waitayachart, 2020). In this context, landscaping practices must include an ecological perspective and go beyond the aesthetic value of the streetscape, since the management of trees and green spaces influences the functionality and provision of resources that support biodiversity (Salomaa et al., 2017). Such biodiversity-friendly practices could be one among several strategies to mitigate the negative impacts of urbanization.

The supply of floral resources in the streetscape of Belo Horizonte was similar between the two seasons, and providing resources throughout the year is essential to support different species of pollinators in urban areas (Stewart and Waitayachart, 2020). Nevertheless, this temporal distribution is possibly not sufficient when the resources are not spatially well distributed. Based on the spatial arrangement of the trees in our study, pollinators probably concentrate in a few areas in the city for foraging, especially the groups other than bees that also have a lower density of available potential resources to exploit. We also found that the richness and abundance of trees offering potential resources for pollinators were positively related to the average family income across city microregions, with 10.3% and 34.4% of variance explained, respectively. Such strong relationship confirms our hypothesis of the luxury effect determining the availability of potential resources to pollinators (Leong et al., 2018). The wealthiest areas are in the Northern and Southeastern parts of the city, which are dominated by large properties with gardens. However, despite providing a higher density of resources, these microregions still do not supply the needs of all groups of pollinators, such as bats that had an overall low density of potential resources. On the other hand, the reduced richness and abundance of trees and green spaces in impoverished microregions of the city is one of the problems linked to social inequality and can impact the health and quality of life of the local population (Leong et al., 2018). The luxury effect is also expected to change the distribution of species and key ecological processes, such as species interactions (Schell et al., 2020). Cities in South America are experiencing one of the most rapid and intense urbanization processes

worldwide, and are characterized by high social inequality, lack of urban planning, low community participation in the management of urban areas and several ineffective public policies (Dobbs et al., 2019; Pena et al., 2017a). Thus, the trend regarding inequality found here is expected to get worse in the future, especially when considering the current management practices common around the world, such as the reduction of street trees and urban vegetation cover (Richards and Belcher, 2020; Roux et al., 2014). All these factors can produce severe consequences for biodiversity, especially because many of the countries where urbanization is rapidly progressing are in biodiversity hotspots (Güneralp and Seto, 2013), including Belo Horizonte located in the transition zone between the Atlantic Forest and Cerrado biomes (Myers et al., 2000).

Finally, despite providing important information about the spatiotemporal distribution of resources for pollinators, some limitations of our study must be considered. First, we only considered the distribution of part of the floral resources available, as we did not consider herbaceous, epiphytic, and climbing plants that may also contribute to the maintenance of pollinators in urban areas (Twerd et al., 2021). Second, our methodology to assess the resources provided by trees did not consider important factors that influence the supply of such resources in the field, such as management practices (e.g., pruning), the size and age of the trees, the amount of light received by the plant, among others (Aronson et al., 2017). Future studies should consider these limitations in mind to provide an even more comprehensive assessment of resource availability when data become available.

5. CONCLUSION

Our study is the first to investigate the spatiotemporal distribution of potential resources provided by street trees to pollinators and test the luxury effect hypothesis on the availability of resources in a tropical metropolis with millions of inhabitants, based on a database comprising 216,797 inventoried trees. In summary, our results indicate that planting different tree species in regions with low density of potential floral resources could improve and increase the availability of resources for different groups of pollinators. We hope that our results contribute with information for the planning and management of the street tree community that aim to provide a better distribution of resources for different groups of pollinators, guiding government actions to regions where there are less amount and diversity of resources. Such initiatives could improve the accessibility and the equitability of the distribution of multiple ecosystem services

across the streetscape, increasing the well-being and quality of life of the citizens, especially of less affluent communities, and the sustainability of the urban landscape.

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SUPPLEMENTARY DATA

FIGURE CAPTIONS

Fig. S1. Spatial distribution of the density of floral resources provided by street trees for moths across the streetscape of Belo Horizonte.

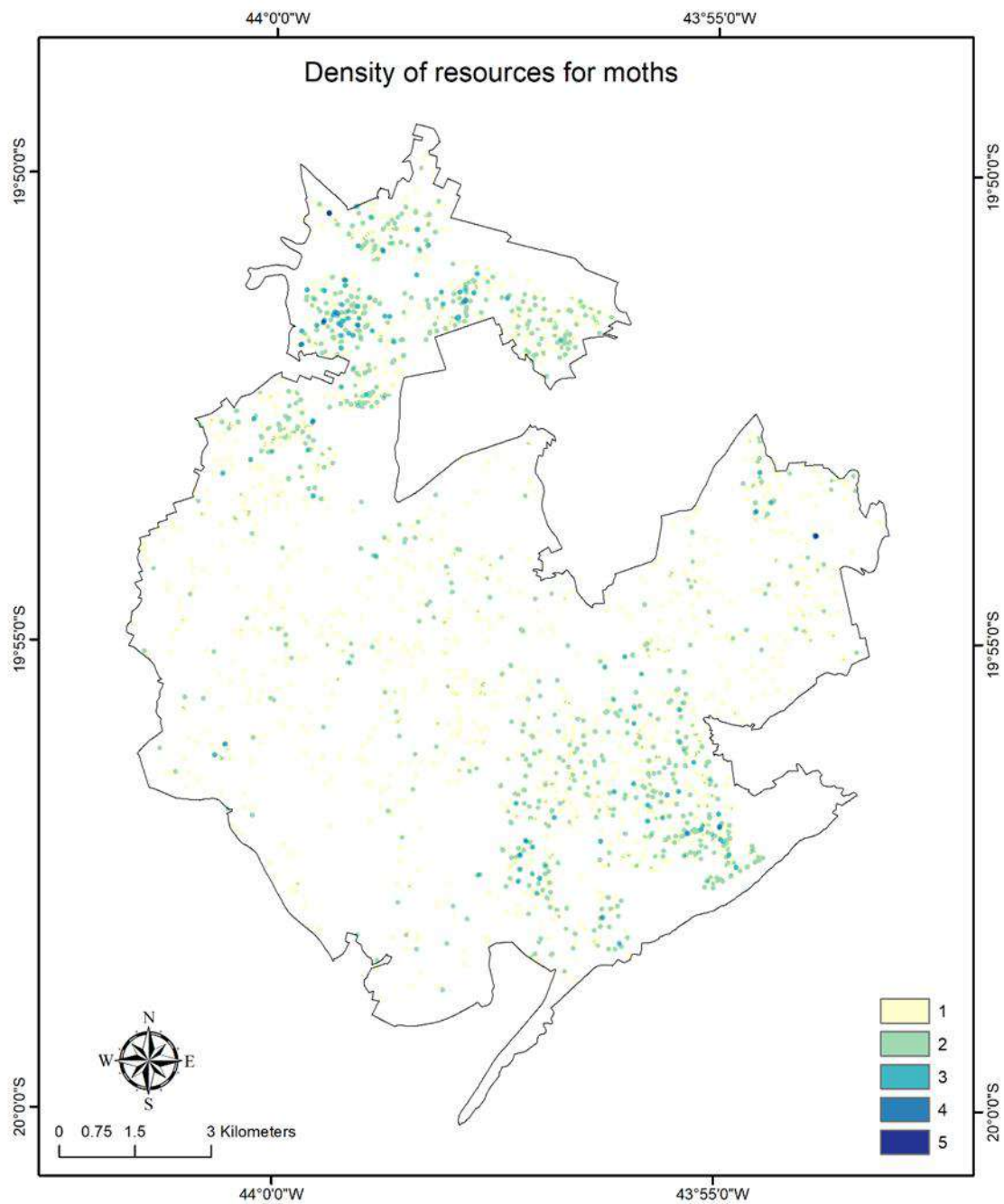


Fig. S2. Spatial distribution of the density of floral resources provided by street trees for butterflies across the streetscape of Belo Horizonte.

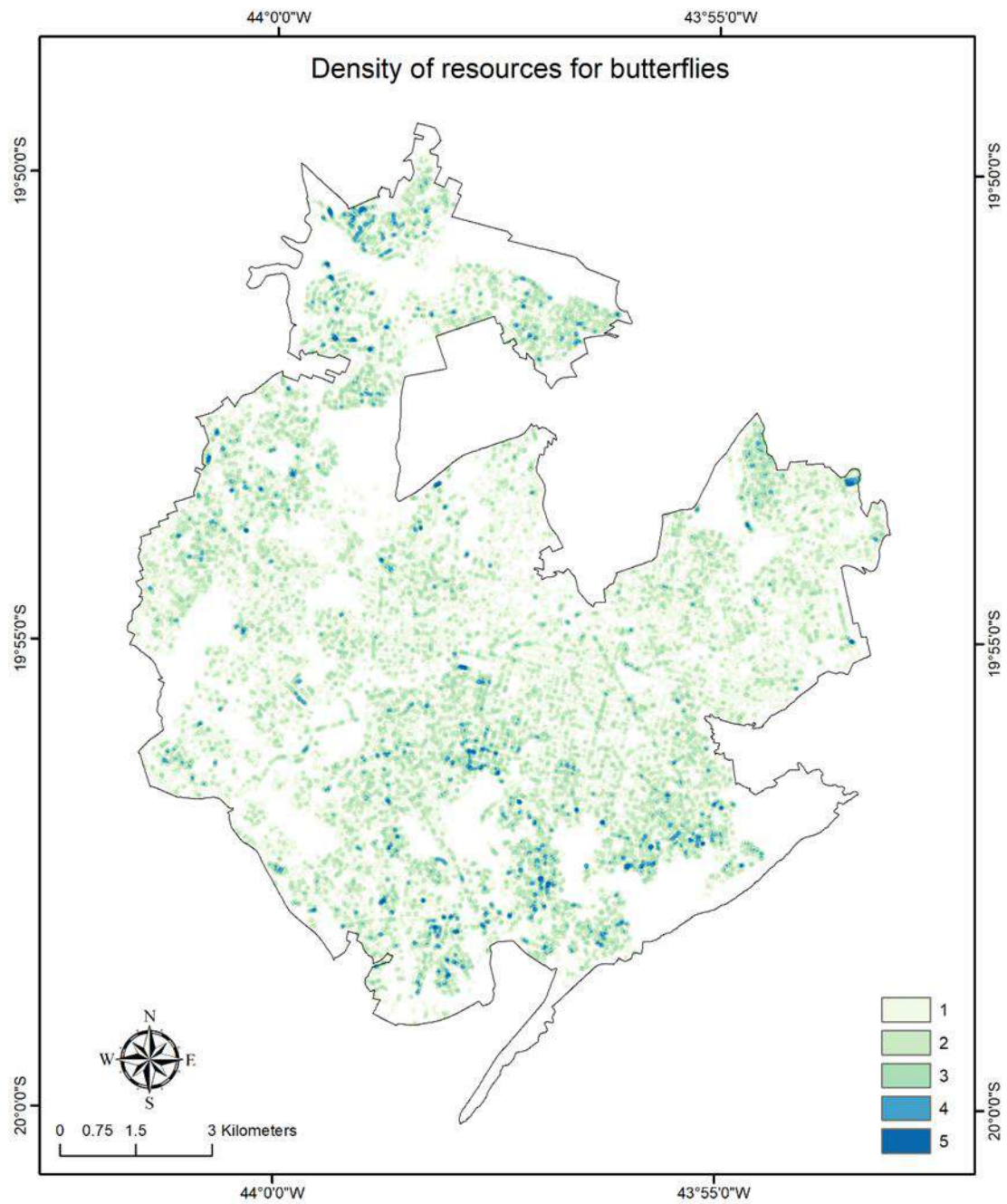


Fig. S3. Spatial distribution of the density of floral resources provided by street trees for flies across the streetscape of Belo Horizonte.

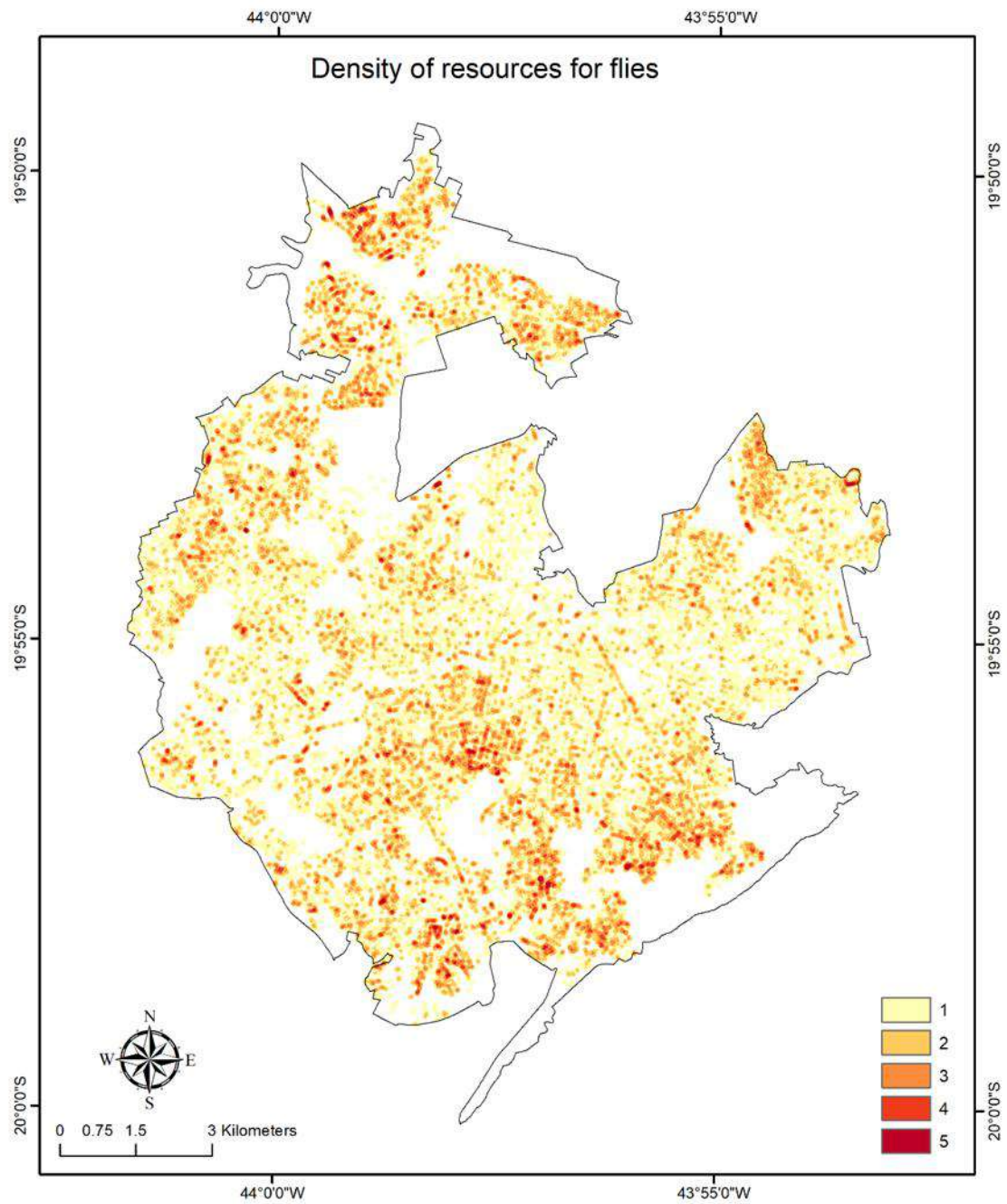


Fig. S4. Spatial distribution of the density of floral resources provided by street trees for non-hummingbird birds across the streetscape of Belo Horizonte.

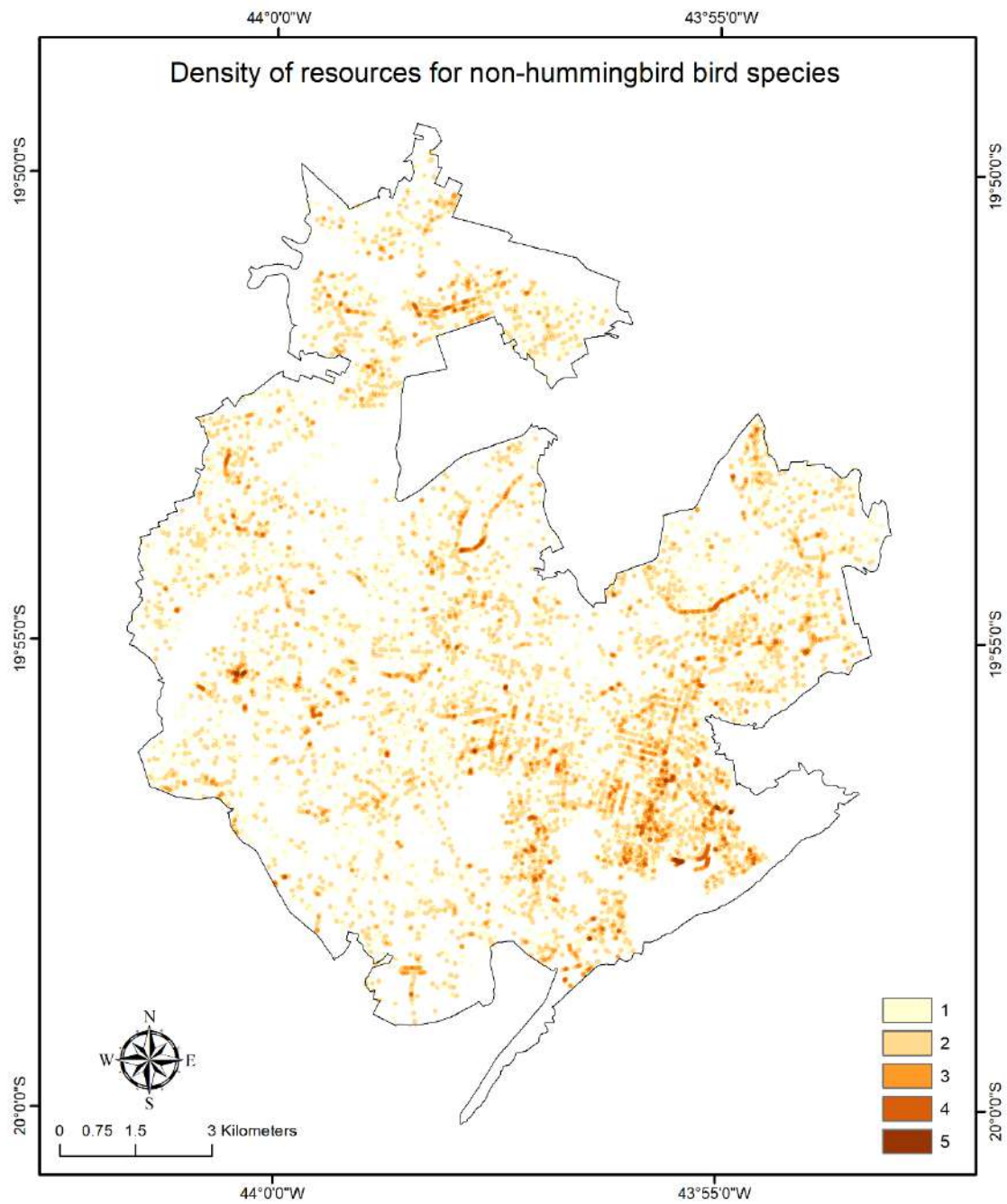


Fig. S5. Spatial distribution of the density of floral resources provided by street trees for wasps across the streetscape of Belo Horizonte.

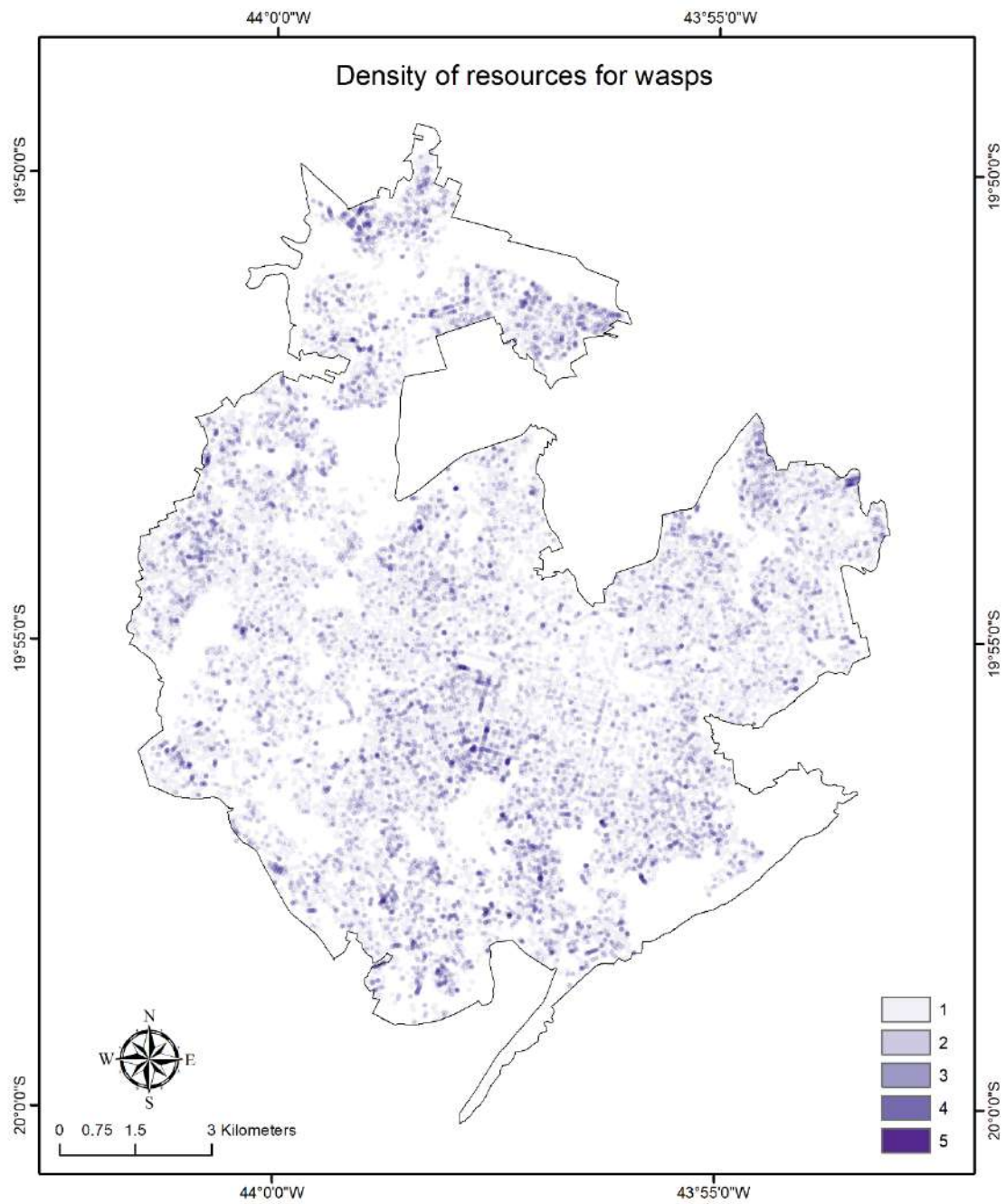
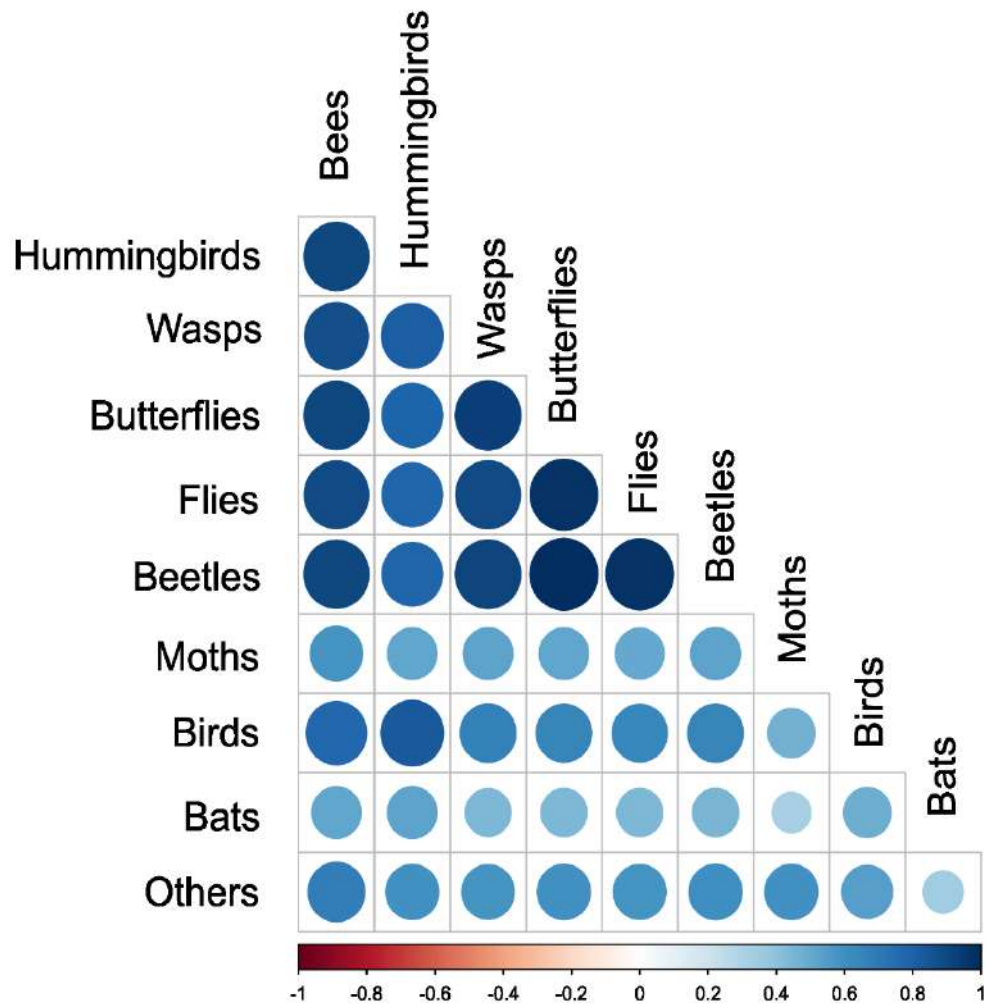


Fig. S6. Correlation analysis of the number of attractive trees for the different groups of pollinators evaluated. Red and blue colors indicate negative and positive correlations, respectively. Larger circles with more intense colors represent a high degree of correlation between groups.



CHAPTER II

Exploring bee diversity and interactions with flowers in a tropical city: implications for conservation

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ABSTRACT

Although urbanization significantly impacts biodiversity and ecosystem functioning, urban green spaces have demonstrated an ability to sustain a diverse bee community. Therefore, understanding the specific characteristics that promote this biodiversity is crucial. However, research on urban biodiversity in tropical cities remains limited and little is known about how bees and their interactions with flowers respond to urbanization depending on their functional characteristics. Thus, we investigated how a heterogeneous tropical urban matrix influences the taxonomic (richness and abundance) and functional diversity (body size, sociality, nesting preference, and trophic specialization) of bees, as well as their interactions with plants, using network specialization and nestedness metrics. We found that generalist bees were the dominant species group across the studied tropical urban landscape, representing 79% of all observed interactions. Regarding urban environmental factors that better explained bee richness, plant species richness played a crucial role, positively impacting bee richness. Meanwhile bee abundance responded positively and negatively by plant species richness and the proportion of native plants, respectively. We also found that urban environmental factors shaped bee species distribution based on their functional traits. Highly eusocial and above-ground nesting bees responded negatively to plant richness while ground-nesting bees responded positively. Generalist bees (i.e., polilectic) responded positively to the higher proportion of impermeable surfaces in urban areas, while specialist bees responded negatively. Larger bees are more abundant in areas with more plants and flowers. Finally, the structure of bee-plant interaction networks was unaffected by urbanization intensity. Our findings underscore the importance of a more comprehensive approach to better understand the mechanisms that shape bee communities through environmental filters linked to urbanization. Moreover, we emphasize the importance of implementing landscaping practices that incorporate a greater diversity of plants, including natives, in urban landscape to supports a wider range of bee species and their functional traits.

Keywords: Functional traits, Urban landscape, Interaction networks, Floral resources

1. INTRODUCTION

Urbanization is one of the primary threats to biodiversity. However, the impact of urbanization varies depending on the region and group being evaluated, due to the complex and heterogeneous nature of cities (Fenoglio et al., 2020). Most urban biodiversity studies focus on non-tropical cities, overlooking the distinct characteristics and challenges faced by cities in the Global South, such as social inequality, ineffective public policies, and low community participation in urban planning (Roberts, 2005, Dobbs *et al.*, 2019, Pena et al 2024; Silva et al., 2023). This underrepresentation highlights the need to develop strategies to mitigate the impacts of urbanization on biodiverse tropical communities, particularly for groups that play essential roles in ecosystem services, such as pollinators (Wenzel et al., 2020). Among pollinators, bees are the most representative group, and are therefore essential for plant reproduction in all ecosystems, including urban areas (Lowenstein et al. 2015; Ollerton et al., 2017; Oliveira et al. 2019, Nascimento et al. 2020). Despite the threat of urbanization, some research has shown that cities can maintain a considerable diversity of bees (Baldock et al., 2015; Lowenstein et al., 2014; Theodorou et al., 2017). This is because urban areas can provide diverse resources for pollinating insects, such as pollen, nectar, and nesting sites, especially for bees that build their nests in pre-existing cavities (Hennig e Ghazoul, 2011; Osborne et al., 2008; Lynch et al., 2021). Furthermore, depending on how they are managed, urban landscapes can provide different floral resources throughout the year due to aesthetic concerns, which does not occur in other environments (Theodorou et al., 2017). This change in perspective has aroused the interest in urban habitats for bee conservation (Baldock et al., 2019). However, for cities to promote biodiversity, it is essential to understand how bees respond to different characteristics of the urban landscape to think about effective strategies for sustainable development (Ayers and Rehan, 2021).

Bees are part of a highly diverse group, evidenced by different life history characteristics that vary between species, such as morphology, dietary preferences, social behavior, and nest biology (Michener, 2007). This variety of strategies linked to adaptation shapes the ecology and evolution of bee species, suggesting distinct responses of species to anthropogenic disturbances, such as urbanization (Banaszak and Dylewski, 2021; Montoya-Pfeiffer et al., 2019). Thus, urbanization can act as an environmental filter in which species will experience different pressures depending on their tolerances defined by these functional traits (Buchholz et al., 2020), possibly leading to simplification of the community with a predominance of ecologically similar species that tolerate the same urban conditions (Lokatis and Jeschke, 2022). Therefore,

understanding the relationships of traits with urbanization can help identify the most threatened functional characteristics. In addition, understanding the relationship between which characteristics of urban landscape, could reduce the impact of urbanization on bee traits and species is essential to develop effective strategies that promote the sustainable development and conservation (Buchholz and Egerer, 2020).

The simplification of communities resulting from urbanization may have consequences for the interaction with plants (Buchholz and Egerer, 2020). In environments such as cities, these changes in community composition can occur due to the loss of interaction partners, i.e., specialists that are more vulnerable to urbanization, or the gain of partners, i.e., in the planting of non-native ornamental species commonly used in urban landscaping (Harrison and Winfree, 2015; Tylianakis e Morris, 2017). Furthermore, urbanization can also change the probability and frequency of interactions, due to a decrease of some species or increase in the abundance of highly generalist species (Tylianakis and Morris, 2017). These changes in interactions can alter the structure and stability of communities and lead to potential impacts on the pollination and consequently on the functioning of urban ecosystems (Geslin et al., 2013; Harrison and Winfree, 2015; Kaiser-Bunbury et al., 2017). In this context, applying interaction network approaches across anthropic gradients, such as urbanization, can increase our understanding of community responses to environmental changes and create strategies for the conservation of biodiversity (Tylianakis e Morris, 2017).

In this context, our objective was to understand how a heterogeneous urban matrix influences the taxonomic and functional diversity of bees, as well as their interactions with plants. We were interested in understanding which local and landscape characteristics can mitigate the commonly associated negative effects of urbanization on bee diversity. Thus, we evaluated how the taxonomic diversity of bees (richness and abundance) and their different functional traits (sociality, nesting preference, trophic specialization, body size, and wing length) respond to local and landscape characteristics including: (i) the proportion of impermeable surfaces, ii) proportion of vegetation cover, iii) average height of buildings, iv) richness and v) abundance of floral resources. Furthermore, we evaluated the structure of bee-plant-interaction networks (nestedness, and specialization) along the urbanization gradient to gain further insights into bee responses to urbanization. We expected to find a negative effect of urbanization on bee richness and abundance, with lower taxonomic diversity in urban areas with a high proportion of impermeable surfaces and surrounded by the tallest buildings. In contrast, areas with higher proportion of vegetation cover, native plants, and richness and

abundance of floral resources would be related to a greater diversity of bees. We also expected that local and urban landscape factors would have distinct effects on bee functional traits, predicting, for example, an association between the increase in generalist bees with the proportion of impermeable surfaces and, between specialist bees with an increase in flowering species. Regarding interactions, we expected that urban areas with a higher percentage of impervious surfaces would have a lower richness of interactions, less specialized networks, and greater nestedness.

2. MATERIALS AND METHODS

2.1 Study area

The study was conducted in Belo Horizonte city, the capital of the state of Minas Gerais, Southeastern Brazil (19° 48' 57" S, 43° 57' 15" W) (Fig. 1). Climate in the region is Cwb according to the Köppen's classification, showing 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). Estimated population in the city is 2,530,701 inhabitants (IBGE, 2021). Belo Horizonte is in the transition between the Cerrado and the Atlantic Forest biomes, both considered biodiversity hotspots (Myers et al., 2000). It is one of the first planned cities in Brazil, designed with the concept of a "garden city" and even today it maintains many parks, public squares, and conservation units, despite the high level of urbanization (Belo Horizonte, 2019; Duarte, 2009). These characteristics make the region particularly interesting for research aimed at increasing the potential of urban landscapes conserve biodiversity in tropical cities.

2.2 Landscape characteristics

We selected twelve landscapes distributed across the city of Belo Horizonte to obtain information about the bee community and different local and landscape characteristics (Fig 1).

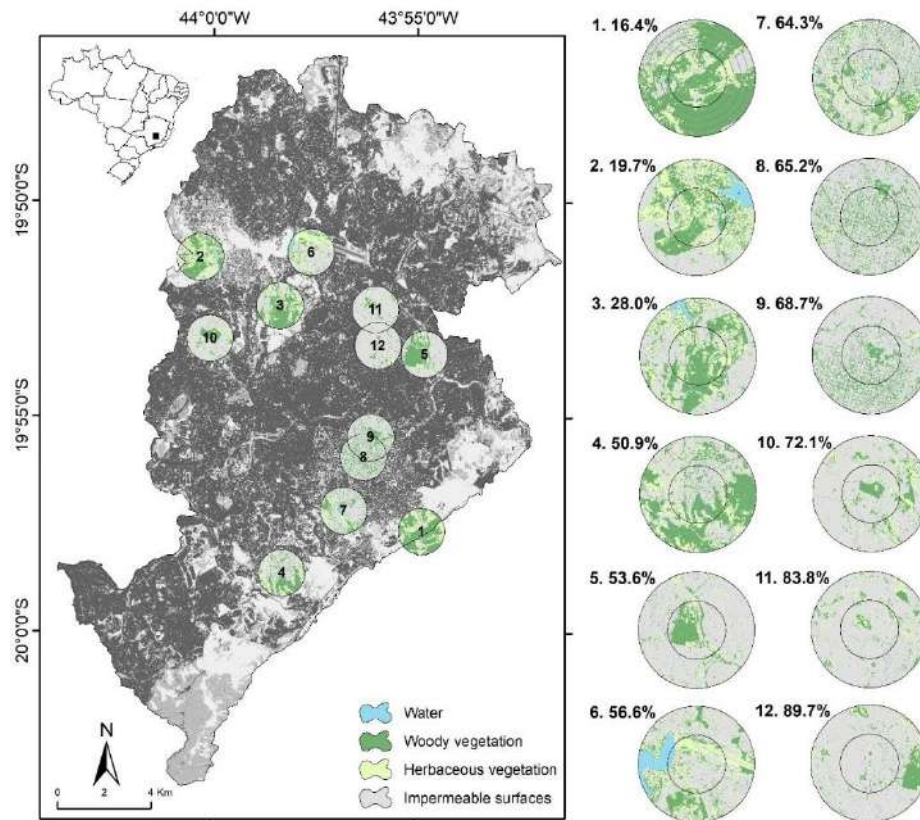


Fig.1. The 12 points sampled for bee-plant interactions, with their respective percentage of impermeable surfaces in Belo Horizonte city, Brazil.

We aimed for random selection but always prioritizing collector safety, ensuring an even distribution across the gradient and including areas with plants under 2 meters in height for our observations. These landscapes were selected to characterize an urbanization gradient with the percentage of impervious surfaces being a proxy for urbanization intensity. The increasing percentages of impervious surfaces varied from 14.7% (least urbanized) to 83.9% (most urbanized) (Fig1; Tab. S1). Each of these landscapes is highly heterogeneous and the urban vegetation is distributed across different land uses such as gardens, parks, small green spaces, and streets. The land cover map of Belo Horizonte was obtained through a supervised classification (applying the Maximum Likelihood algorithm) of PlanetScope satellite imagery with 3m resolution and four spectral bands from 2021 (Bhakti et al 2023). Each landscape is comprised of a 1km radius buffer from which we extracted the percentage of impervious surfaces that describes the urbanization intensity gradient across Belo Horizonte (Fig. 1). Although many bee species can fly distances greater than 1 km, depending on body size, they often limit their foraging activity to distances smaller than those predicted for their size (Greenleaf et al., 2007). Therefore, we believe that a 1 km radius was adequate to understand

the scale at which bee populations respond to the landscape. The impervious surface is defined as areas where there is no infiltration of water into the soil due to road paving, sidewalks, parking lots, and housing constructions, among others. This metric is considered an important factor to characterize the degree of urbanization (Gao et al., 2023). Furthermore, it has a strong influence on the environmental quality and biodiversity that occurs in the surroundings (Herman et al., 2023; Yan et al., 2019; Pena et al 2023).

From each landscape, we also extracted other metrics describing attributes that may influence bee communities across urban landscapes. Besides the percentage of impervious surfaces, we calculated the proportion of woody and herbaceous vegetation in each landscape. For each land cover class, we also extracted the mean patch size, the edge density, and the largest patch index. All these metrics were calculated using the package *landscapemetrics* in the R programming environment (Hesselbarth et al., 2024). Furthermore, we calculated the average height of buildings using a vector map comprised of polygons containing as attributes the estimated buildings' height obtained through LiDAR flights in 2007 (Pinto, 2015). In the urban matrix, buildings, as well as roads and other forms of paved areas, can act as barriers affecting the movement of flying insects, especially small species with low dispersal capacity (Andersson et al., 2017). Finally, we obtained a raster file describing the soundscape of Belo Horizonte that combines three geospatial layers: motorized traffic volume, the height of buildings, and commercial density (see Bhakti et al., 2023). For each landscape, we extracted the average soundscape value as a measure of human activity. The raw data containing all landscape metrics extracted for each landscape can be assessed in the Supplementary Material (Appendix 1). These landscape variables with local characteristics related to flower composition and availability (see below) were selected to evaluate how urbanization characteristics influence the taxonomic and functional diversity of bee communities. The selection of these variables was carried out considering a literature review combined with our knowledge of bee ecology (Ayers and Rehan, 2021; Pardee et al., 2023).

2.3 Bee sampling and local characteristics

Field 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 site. Bee sampling was carried out whenever possible on sunny days, avoiding cloudy or rainy days due to reduced bee activity. In each of the twelve urban landscapes, we covered one-kilometer transects observing the interactions between bees and flowers for 10 minutes in each

flowering plant, with the aim of describing the bee and plant community for each landscape. During the observations, the bees that interacted with the flowers were captured with entomological nets by two collectors and later transferred to a "Killer Jug", packed in paper envelopes, and taken to the lab. Collections were carried out on all plants located on the transect whose flowers were within reach, that is, on plants less than two meters tall. In the laboratory, these bees were prepared for identification on entomological pins, dried at temperatures between 40 and 60 °C for approximately three days, labeled, identified, and recorded. Species identification followed the classification proposed by Melo and Gonçalves (2005), which treats the whole group as a single family (Hymenoptera, Apoidea, Apidae sensu lato). Genera were identified using Silveira et al. (2002), and for the species level, we considered specific taxonomic revisions. To avoid a destructive sampling of bees, we did not collect all individuals of the most common bees found in urban areas such as *Apis mellifera*, *Trigona spinipes*, and *Plebeia* sp. However, due to the similarity in the field, *Nannotrigona testaceicornis*, *Paratrigona lineata*, and *Plebeia* sp. needed to be grouped into a single morphospecies (defined as *Meliponini* sp.) in our study.

To assess the influence of urbanization on the functional traits of bees, we used five functional traits: body size, wing size, sociality, nesting preference, and trophic specialization. All these traits are known to respond to environmental gradients (Coutinho et al., 2018; Eggenberger et al., 2019; Wilians et al., 2010). The body size of the bees was classified based on measures of intertegular distance (ITD), a proxy for body size (Cane, 1987). Wing size was measured from the tegula up to the apex of the forewing (Eggenberger et al., 2019). For ITD and wing size, we randomly selected ten female individuals from each species, whenever possible, using less when ten individuals were not available. Thereafter, we used a microscope and its accompanying software (Leica Application Suite 5.2) to capture the image and make the measurements of each bee. Finally, we calculated the mean value of these measurements to assign a value for each species. Categorical traits (e.g., sociality, nesting preference, and trophic specialization) were classified using the information available in Michener (2007). For sociality bees were separated into solitary, cleptoparasitic, and eusocial, the latter being divided into primitively eusocial (totipotent reproductive caste) and highly eusocial (fixed reproductive caste). Regarding nesting preferences, bees were divided into species that nest in the soil and species that nest above ground, such as exposed nests, cavities, and other substrates. At last, for the trophic specialization, bees were classified as generalists (i.e., polilectic) and specialists

(i.e., oligolectic or that collect specific resources such as oil and fragrance) through literature data. All the data were validation by a bee specialist.

Regarding local characteristics, comprising flower composition and availability, we quantified floral abundance during observations of bee-plant interactions by counting the number of flowers per plant. For the plants that produced many flowers, we quantified the average number of flowers per inflorescence, obtaining an estimated number of flowers per individual. All plants used by bees as resources were collected and prepared for identification by a specialist to obtain data on the richness of floral resources. To classify the plant species according to their geographic origin (i.e., native or non-native to Brazil) we used the Flora and Funga of Brazil (REFLORA 2021). Species classified as naturalized or cultivated were considered non-native plants in our study.

2.4 Data analysis

2.4.1 Effects of urbanization on bee diversity

To avoid multicollinearity of the predictor variables we first conducted a pairwise Pearson correlation analysis (Quinn and Keough, 2002) considering local and landscape variables (Fig. S1). Variables with a high correlation ($r > 0.70$) were removed from the subsequent analysis (Santis et al., 2023). Five variables remained: percentage of impermeable surfaces, average height of buildings (landscape variables) and percentage of native plants, richness of plants used as a resource by bees, and abundance of flowers (local variables).

We used these variables to build the models to assess which characteristics of urban areas better explained the variation in bee richness and abundance across our urbanization gradient. We used the R package *glmulti* (Calcagano et al. 2020) to generate all possible models considering out predictors and, given our small sample size ($n = 12$), we used the standard correction of Akaike's Information Criterion (AICc) to rank the candidate models (Burnham and Anderson 2004). We also calculated Akaike weights for each model, the value varying from 0 to 1 and indicating the probability of that model being the best among the other models tested (Symonds and Moussalli, 2011). We selected our final model based on the lowest AICc value and the highest Akaike weight (Tab. S2, S3). To evaluate the relationship between the response variables (richness and abundance of bees) and the predictor variables included in the best model, we performed generalized linear models (GLM). We used Poisson and binomial negative distribution for the richness and abundance, respectively, based on preliminary

explanatory analyses. We ensured that the assumptions of heteroscedasticity and normality were met by examining residuals after model fitting and we found no evidence of overdispersion, both assessed using the respective function of the DHARMA package (Hartig, 2022).

To evaluate whether there are relationships between urban environmental variables and different bee traits, we employed the combined RLQ analysis and fourth corner approach (Dray and Dufour 2007; Dray et al., 2014). RLQ analysis aims to identify the main co-structures and relationships between the environmental characteristics (R matrix) and the bee traits (Q matrix) weighted by a matrix of species abundance distribution between urban areas (L matrix), providing a classification score to summarize the joint structure between the three tables (Dolédéc et al., 1996). In the fourth corner approach, tests are carried out to evaluate direct relationships between individual bee traits and each environmental characteristics (Dray and Legendre 2008; Dray et al. 2014).

Together these methods can identify trait syndromes associated with environmental gradients (Dray et al., 2014). To Q matrix the selected bee traits were body size, sociality, nesting preference, and trophic specialization. We removed wing size because it is highly correlated with bee body size ($r = 0.94$). Regarding the matrix of environmental data, we included the same local (richness of plants, abundance of flowers and proportion of native plants) and landscape variables (impervious surfaces and height of buildings) previously described. Before the analyzes, we removed the species classified in sociality trait as cleptoparasitic, as they did not present data for other characteristics, such as nesting preference and trophic specialization. In total, sixteen individuals represented by six species were removed of the trait (Q) and abundance (L) matrix.

In RLQ analysis we order each matrix. For the matrix of the species (L) we logarithmized the data due to the large difference between abundances and subsequently applied a correspondence analysis (`dudi.coa`). For the bee trait matrix (Q), we performed a principal components analysis using the Hill-Smith method (`dudi.hillsmith`) that allows us to evaluate for both continuous and categorical variables (Hill and Smith, 1976). Finally, for the environmental data matrix (R) we applied a principal components analysis (`dudi.pca`).

The overall significance was evaluated via a global Monte-Carlo test using 9,999 random permutations. We used the type 6 model which combines the type 2 model, testing the null hypothesis that species distribution is not influenced by environmental conditions and type 4 model which tests whether species composition is not influenced by species traits (Dray et

al., 2014). Both models were combined to obtain a corrected level of Type I error by applying an a priori significance level of 5% (Dray et al., 2014). Finally, we use the combination of RLQ and fourth corner analysis to assess the significance of associations between traits and environmental variables identified by RLQ. We used 9,999 permutations and the sidak correction factor (less conservative and appropriate for the number of comparisons in our study) to correct p-values for multiple-test comparisons and to avoiding type I error. We performed these analyses with *vegan* (Oksanen and Guillaume Blanchet, 2017) and *ade4* (Chessel et al., 2004) packages in R (R Core Development Team, 2021).

2.4.2 Plant-bee interactions

To assess the effect of urbanization on bee-plant interaction networks, we built 12 networks that were sampled along the urbanization gradient described previously. As urban landscapes are generally characterized by planned vegetation and our main objective is to understand how to improve urban areas for improving urban bee diversity, we considered all the interactions observed, since it essentially means resource consumption by bees, regardless of the potential to pollination (legitimate and illegitimate interactions). We calculated the sampling completeness of interactions for all 12 interaction networks using the *iNEXT* package (Chao et al. 2016). Sampling completeness is measured as the percentage of observed interaction richness in relation to the expected richness estimated by the *Chao 1* richness estimator (Chacoff et al. 2012, Dalsgaard et al. 2017). For more information about sampling completeness of the networks see the supplementary material (Fig.S2; Tab. S4).

For each network, we calculated metrics that characterize different aspects of network structure, such as, specialization (H_2'), and nestedness (wNODF). These metrics were defined due to the capacity to be influenced by local and landscape features on plant-pollinator interactions (Pardee et al., 2023, Theodorou et al., 2017, Weiner et al., 2014). Specialization (H_2') measures the degree of specialization of interactions in different networks (Blüthgen et al. 2006). The value of H_2' ranges from 0 to 1, where 0 indicates high generalization and 1 high specialization (Blüthgen et al. 2006). Nestedness assesses whether species that interact with specialists (those with few links) are a subset of species that interact with generalists (those with many links) and was estimated by the wNODF index (Almeida-Neto & Ulrich, 2011). The values vary from 0 to 100, where 100 represents perfect nestedness (Almeida-Neto & Ulrich, 2011). The nestedness interaction structure provides a protection against loss and temporal fluctuations in the abundance of specialized pollinators, decreasing the chances of secondary

extinctions. Therefore, even with the loss of specialists, the remaining species will still have others to interact with (Tylianakis et al., 2010).

To assess the significance of these metrics, we generated 1,000 randomized networks using the *r2dtable* function, which constrains the marginal totals and network size, and compared the observed values with the values for each of these networks (Dormann et al. 2008). All network analyses were carried out in the R package 'bipartite' (Dormann et al. 2008; R Core Development Team, 2021). Following this, we performed Pearson correlation tests between the urban gradient and sampling completeness, and we found no strong and significant correlation between these variables ($r = 0.53$, $p = 0.07$). As a result, we proceeded to investigate the impact of urbanization on the network metrics described above using generalized linear models (GLM) implemented in the *stats* package. Given the continuous nature of the data, we adopted a Gaussian distribution family for the model.

3. RESULTS

3.1 Flowering plants and the bee community structure across the urban landscape

We found a total of 97 bee species (7,801 individuals) that interacted with 226 plant species (57.47% native of Brazil). The flowering plant community belonged to 70 plant families. In terms of species richness, Asteraceae was the most diverse family (14%), followed by Fabaceae (11%), Acanthaceae (5%), Bignoniaceae (3%), Verbenaceae (3%), Convolvulaceae (3%), Lamiaceae (3%), Lythraceae (3%), Rubiaceae (3%) and Solanaceae (3%). Together these ten plant families represent 53% of all plant species used by bees (Tab. S5).

The plant species with the highest number of interactions were *Sphagneticola trilobata* representing 8% of all interactions, followed by, *Lagerstroemia indica* (5%), *Callistemon viminalis* (4%), *Tridax procumbens* (2%), *Ipomoea horsfalliae* (2%), *Muntingia calabura* (2%), *Antigonon leptopus* (2%), *Turnera subulata* (2%), *Bauhinia forficata* (2%) and *Ocimum basilicum* (2%), totaling 31% of all interactions. The plant species that attracted the greatest number of bee species were *Sphagneticola trilobata* representing 26% of all species observed, followed by, *Agapanthus africanus* (16%), *Pleroma granulatum* (15%), *Psychotria carthagenensis* (13%), *Alpinia zerumbet* (11%), *Leucanthemum vulgare* (11%), *Tecoma stans* (10%), *Crotalaria micans* (9%) and *Ocimum basilicum* (9%) (Tab. S5).

Bees belonged to five subfamilies (Apinae, Halictinae, Megachilinae, Colletinae, and Adreninae). The most abundant subfamily was Apinae (94% of individuals), followed by Halictinae (5%), whereas the remaining subfamilies did not exceed 1% (Tab. S6). Concerning species richness, Apinae accounted for 58%, followed by Halictinae (27%) and Megachilinae (13%). Adreninae and Colletinae represented 1% of the richness with only one species recorded for each subfamily (Tab. S6). The introduced honeybee *Apis mellifera* was the most abundant species representing 25% of all individuals and interactions observed. Regarding native bees, the most abundant species were *Trigona spinipes* (21%), *Meliponini* spp (20%), *Tetragonisca angustula* (13%), *Tetragona clavipes* (2%) and *Bombus morio* (2%), all from the Apinae subfamily. On the other hand, 57 species were observed less than 10 times during the study, representing only 3% of all individuals and interactions observed. Regarding bee traits, 52% of the species nest above ground and 42% below ground, 45% are solitary, 33% primitively eusocial, 16% highly eusocial and 6% cleptoparasitic. Concerning the trophic specialization 73% of the bees are classified as generalist and 21% as specialist.

3.2 Effects of urbanization on taxonomic diversity and functional traits of bees

The model that best explained the richness of bees is the one that included the richness of plant species used by bees, showing a positive association ($z = 4.31$, $p < 0.0001$, Fig.2). When it comes to bee abundance, the model that better explained it was the one incorporating plant species richness and the percentage of native plants. Plant species richness had a positive effect ($z = 6.18$, $p < 0.0001$), while the percentage of native plants had a negative one ($z = -6.43$, $p < 0.0001$, Fig.2). For a complete overview of all possible models with the different combinations of predictors, see the Supplementary material (Tab. S2, S3).

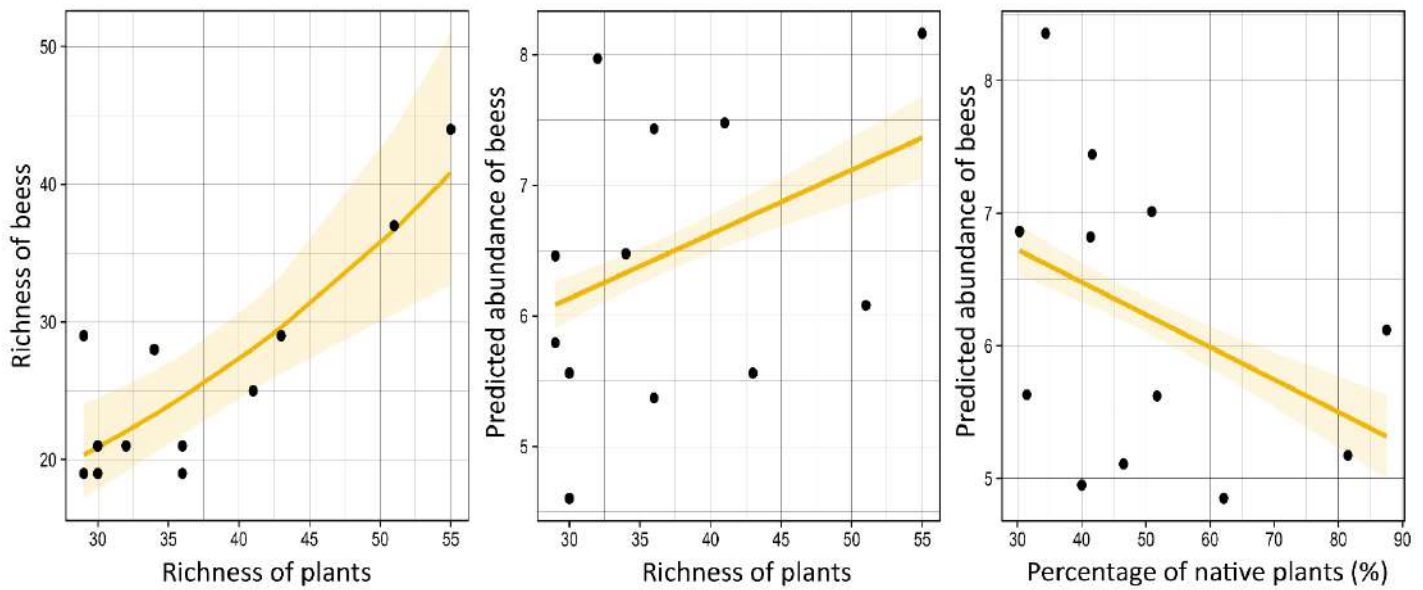


Fig. 2. Effect of urban variables that best explained variation in bee richness and abundance, based on model selection.

The global RLQ test indicated that the species distribution is influenced by environmental conditions (model 2, $p = 0.008$) and that the species composition is influenced by species traits (model 4, $p = 0.001$). We focused on the first RLQ axis to assess the relationships among variables, given that it explained most of the variability (i.e., 92% vs. 5% for the second axis). We observed a positive relationship between specialist bees and ground-nesting bees with the richness of plants. In contrast, species with these traits were negatively related to the percentage of impervious surfaces and average height of buildings. Generalist and above-ground nesting bee species were positively related to the percentage of impervious surfaces and average building height but negatively related to plant richness (Fig. 3).

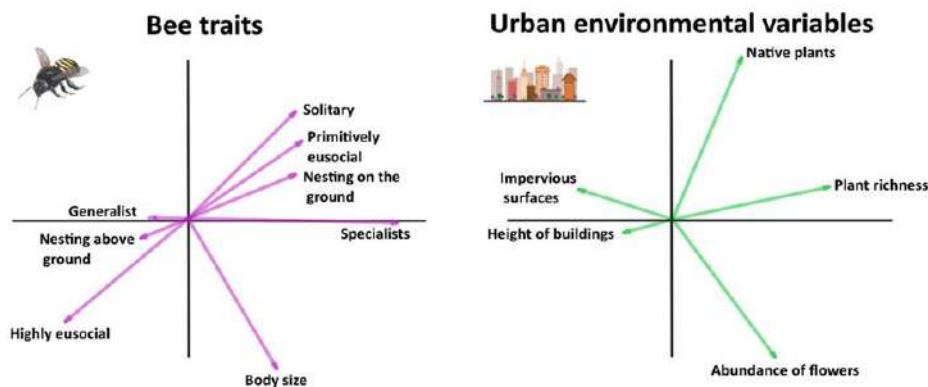


Fig. 3. Axis 1 (horizontal) and axis 2 (vertical) of the RLQ analysis indicating the relationships found between (a) bee traits and (b) urban environmental variables.

The correlation matrix derived from the fourth corner analysis detected seven significant correlations between environmental variables and bee traits (Fig. 4). Highly eusocial bees and above-ground nesting species were negatively related to plant richness. In contrast, ground-nesting bees were positively related to plant richness. Generalist bees were positively related to the percentage of impervious surfaces while specialist bees were negatively affected. Finally, the body size of the bees was positively related to plant richness and flower abundance (Fig. 4).

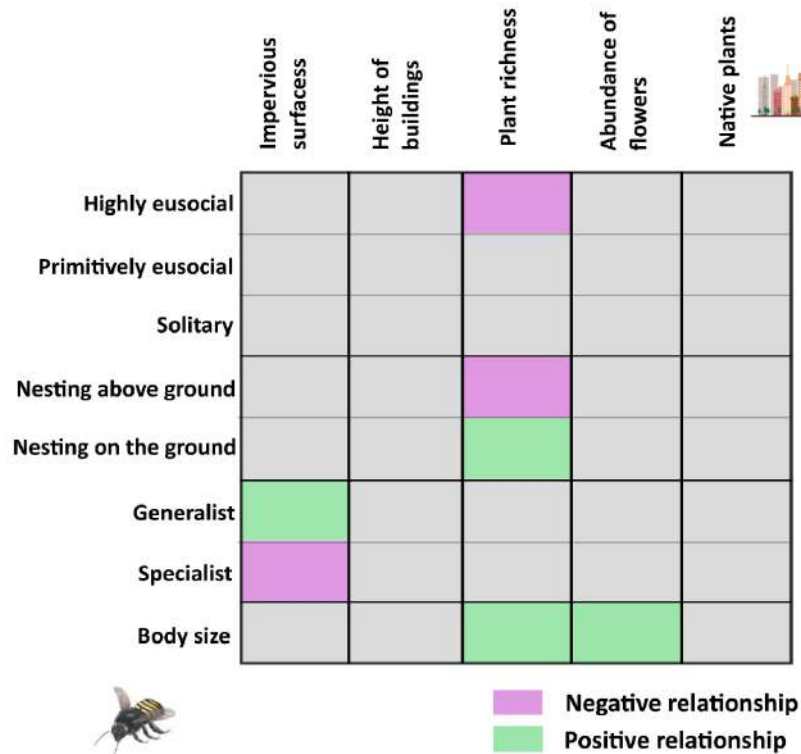


Fig. 4. Relationships between bees' functional traits and urban environmental variables resulting from the fourth corner analysis. Positive associations are represented by green cells while negative associations are by pink cells ($p < 0.05$). Non-significant associations are in gray.

We also assessed the relationships between individual traits and the first RLQ environmental axes (which explained the most) and individual environmental variables and the first RLQ trait axes by combining both RLQ and fourth-corner analysis. The first environmental axis (AxcR1, combination of environmental variables) was negatively related to highly eusocial bees, while the first RLQ trait axis (AxcQ1, combination of traits) was positively related to plant richness.

3.3 Effect of urbanization on bee-plant interactions

We counted 7,801 interactions, the number of bee-plant interactions ranged from 1,588 to 164 at each locality, while the number of unique bee-plant combinations (interaction richness), ranged from 165 to 55. For more details about the interactions, metrics, and richness of bees and plants areas across landscapes see Tab. S1. The degree of urbanization, defined as the percentage of impervious surface, did not influence the structure of bee-plant interaction networks (specialization H_2' , $t = -0.712$, $p = 0.493$; and nestedness $wNODF$, $t = 0.926$, $p = 0.376$, Fig. 5 and S3-S14).

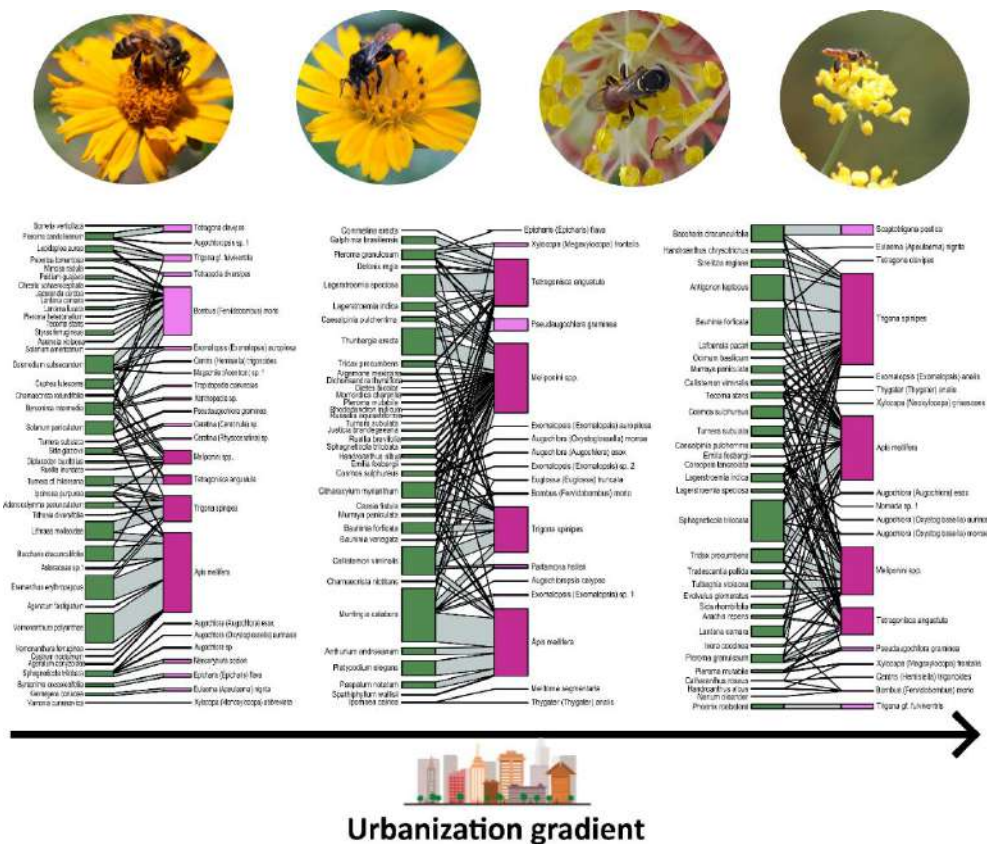


Fig. 5. Bee-plant interaction networks along an urbanization gradient. The first network has the lowest level of urbanization (16.38%), the second intermediate level (64.30%) and the third the highest level (89.74%). The bees in the image, depicted in the sequence *A. mellifera*, *T. spinipes*, Meliponini spp, and *T. angustula*, represent the most abundant species found in the urban landscape (highlighted in darker pink in the networks). Meliponini spp included only *N. testaceicornis*, *P. lineata*, and *Plebeia sp*.

4. DISCUSSION

We found that urbanization can lead to functional homogenization of bee communities, with local variables such as the number of plant species exerting a stronger influence on bees

and their interactions with flowers than predictors at the landscape scale. There was a predominance of generalist species across the city that represented 79% of all individuals and interactions recorded in the urban gradient. Plant species richness was the primary explanatory factor for bee richness, showing a positive correlation. Bee abundance was influenced by both plant species richness and the proportion of native plants, exhibiting positive and negative associations, respectively. Furthermore, we found that urban environmental variables influenced the distribution of bee species based on their functional traits, which could lead to a simplification of the communities. Surprisingly, the structure of bee-plant interaction networks remained unaffected by the degree of urbanization.

Research around the world shows that increased urbanization reduces bee richness (Bates et al., 2011; Geslin et al., 2016; Graf et al., 2022; Tavares-Brancher et al., 2023). However, it is also reported that the distribution and abundance of some species seem not to be affected by urbanization, especially for social and generalist species including invasive ones. (Banaszak-Cibicka and Żmihorski, 2012; Silva et al., 2023; Tavares-Brancher et al., 2024). This pattern is supported by our findings, which indicate a predominance of highly generalist bees, such as *A. mellifera* and *T. spinipes* that dominated interactions across the evaluated landscapes. These bees form perennial colonies with thousands of individuals and have an efficient communication system between them (Michener, 2007; Nieh et al., 2004). Such characteristics allow these bees to have a wide occurrence in different types of environments, including urban landscapes (Banaszak-Cibicka and Żmihorski, 2012). The introduced species *A. mellifera*, the most abundant one found in our study, has a highly competitive potential with native bees for floral resources and nesting sites, resulting in significant ecological impacts (Cunningham et al., 2022; Geslin et al., 2017). This threat may be more intense in urban landscapes, where the distribution and abundance of many species may be limited by environmental filters imposed by urbanization (Gathof et al., 2022).

Among the urban environmental variables evaluated, plant richness stands out as the main factor that explains the increase in bee richness and abundance. This relationship was also found in other cities with different sizes and levels of urbanization (Gruver and CaraDonna, 2021; Wilson and Jamieson, 2019; Hülsmann et al., 2015). The urban matrix imposes a series of challenges for the maintenance of pollinators due to different factors (Wenzel et al., 2020). However, our results indicate that local factors, such as resource diversity, may be better predictors of bee communities than variables at the landscape scale, such as the percentage of impervious surfaces and the presence of large buildings (Geslin et al., 2016; Tavares-Brancher

et al., 2023). Therefore, diverse landscaping including different floral resources are needed to reduce the negative effects of urbanization.

Plant richness and the proportion of native plants were the urban variables that most explained the abundance of bees. Similarly, plant richness had a positive relationship with bee abundance. However, the increase in the percentage of native plants decreased bee abundance. In urban landscapes, the contribution of non-native plants to supporting pollinators show divergent trends (Bergerot et al., 2010; Tasker et al., 2020). Some research considers them a threat to biodiversity (Banerjee e Dewanji, 2017; Fenoglio et al., 2021), while others suggest that they can complement native plant resources in cities, especially in periods of scarcity or in urban landscapes with little vegetation (Salisbury et al., 2015; Staab et al., 2020; Stewart et al., 2018, Anselmo et al. 2023). The relationship found in our study is possibly due to the predominance of generalist bees, since they are more flexible in resource use and may be favored by the presence of highly rewarding non-native plants (Ayers and Rehan et al., 2021; Giannini et al., 2015). However, to promote the maintenance of a more diverse community of bees, it is crucial to include a variety of attractive native plants, not only based on their aesthetic value but also considering supporting specialized pollinators, which are less attracted to non-native plants (Ayers and Rehan et al., 2021; Bergerot et al., 2010; Threlfall et al., 2015).

In our assessment of the relationships between urban environmental variables and the functional traits of bees, we also found a strong influence of plant richness. We found that the plant richness, had a negative relationship with highly eusocial and above-ground nesting bees, in contrast to a positive relationship observed with ground-nesting bees. As demonstrated in other studies in tropical cities, the most abundant species in our study were highly eusocial bees that nest above ground, among which *A. mellifera* and *T. spinipes* stand out, recognized as highly generalists due to their interactions with multiple groups of species in ecological networks (Giannini et al., 2015; Nascimento et al., 2020; Silva et al., 2023; Zotarelli et al., 2014). However, despite this wide breadth of diet, these species are not able to access resources in specialized flowers (e.g. pollen flowers or flowers with longer corollas (King and Buchmann, 2003; Saskia et al., 2019; Klumpers et al., 2019; Vallejo-Marín, 2022). This influences bees' flower preferences as they seek to maximize efficiency, minimizing the time spent collecting (De Luca and Vallejo-Marín, 2013; Saskia et al., 2019). Hence, such restrictions may explain the absence of a direct relationship between increased resource richness and increased occurrence of these bees. Conversely, many of the species identified in our study that nest in the ground, such as those belonging to the genera *Centris*, *Epicharis*, *Exomalopsis*, and the

subfamily Halictinae exhibit buzzing behavior (Rosi-Denadai et al., 2020; Vallejo-Marín, 2022), which, together with other biological characteristics, allow these bees to be functionally specialized and benefit from higher diversity of plants (De Luca and Vallejo-Marín, 2013; Laha et al., 2020).

Another environmental factor that influenced bee traits was the increased percentage of impervious surfaces that was positively associated with generalist bees, while negatively related with the presence of specialist bees (Ayers and Rehan et al., 2023; Deguines et al., 2016; Wilson and Jamieson et al., 2019; Zanette et al., 2005). Across cities, it is common to observe a predominance of a few plant species in the landscape with a high level of urbanization, influenced both by logistical restrictions related to the availability of seedlings and by the aesthetic preferences of the population (Gomes et al., 2023; Matteson et al., 2012; Todorova et al., 2004). This condition results in a lower diversity of resources available to bees, especially those that depend on specific plants or that require resources other than pollen and nectar, such as oils and perfumes, limiting the distribution of these species in cities (Buchholz and Monika, 2020; Kearns et al., 1998).

We also observed a positive relationship between plant richness, flower abundance and larger body size. The increase in body size of animals is often associated with a higher energy demand to support its metabolic functions (Blanckenhorn et al., 2000). In contrast to regions abundant in green spaces, highly urbanized landscapes frequently present limitations in the availability of resources for bees, which may prove inadequate to fulfill their dietary requirements (Matteson et al., 2012). However, bees with larger body sizes have a greater flight distance, which enable higher mobility in urban landscapes and capacity to track green spaces with greater availability of floral resources (Greenleaf et al., 2007). Hence, larger bees can forage further depending on the availability of the resource and energy demand, which may explain the relationship found in our study (Beekman e Ratnieks 2000; Greenleaf et al., 2007; Steffan-Dewenter and Arno 2003, Torné-Noguera et al., 2014).

Contrary to our hypothesis, we did not observe difference in network specialization and nestedness patterns along the urbanization intensity gradient. Other studies carried out in urban landscapes found this same lack of pattern (Prendergast and Ollerton, 2021; Tavares-Brancher et al., 2024; Fisogni et al. 2022). We expected that in less urbanized landscapes some bee species would interact with specific sets of plant species, increasing the specialization of the network. However, the network with the second highest level of specialization was the most urbanized one, with 83.80% of impermeable surfaces. The transects in this landscape crossed less

managed areas containing native plants with functionally more specialized flowers, such as pollen flowers, flowers that offer oil, and keel-flowers pollination systems (e.g., *Solanum lycocarpum*, *Banisteriopsis* sp., *Stylosanthes guianensis*). These characteristics contributed to an increase in bees that are more specialized in collecting these resources, such as species of the genus *Epicharis* and bees of the Megachilidae family, reflecting on the result we found. Therefore, it indicates the importance of the composition of floral resources for the maintenance of different species of bees in urban landscapes (Lanner et al., 2020; Hulsmann et al., 2015; Wilson and Jamieson, 2019).

5. CONCLUSION AND MANAGEMENT AND PLANNING IMPLICATIONS

The patterns we find here can help in the development of practices that help reduce the negative effects of urbanization on bees. We observed that local variables, such as the number of plant species, exerted a stronger influence on bees and their interactions with flowers than landscape predictors related to urbanization. The presence of specialist bees was also observed in highly urbanized landscapes, but which maintained specialized flowers. Therefore, even in highly urbanized landscapes, it is possible to observe a diverse community of bees including specialist species depending on local characteristics, mainly related to the composition, richness and functional traits of the flowers used as a resource by bees. These results emphasize the importance of management strategies that promote greater plant diversity in urban landscapes, including more species with functionally specialized flowers. We recommend planting species that attracted a greater number of bee species in our study, such as *Sphagneticola trilobata*, *Agapanthus africanus*, and *Pleroma granulosum*, which were responsible for attracting 25, 16 and 15 bee species, respectively, in the evaluated landscapes. Additionally, we recommend growing flowers with more specialized pollination systems, such as pollen flowers and keel floral morphology, as they attract a community of bees with more specialized resource collection behaviors. Among the pollen flowers, we highlight *Senna multijuga*, *Senna pendula*, *Pleroma mutabile*, *Solanum lycocarpum*, *Solanum paniculatum*, and *Lyciantes asarifolia*. Among the flowers with keel floral morphology, we indicate *Crotalaria micans*, *Stylosanthes guianensis*, and *Arachis pintoii*, the latter being a good option for soil coverage. Furthermore, we recommend increasing the number of plant species belonging to the Malpighiaceae family, that offer oil as a resource, such as *Galphimia brasiliensis*, *Byrsonima intermedia*, and *Malpighia emarginata*, as they are fundamental to the life cycle of bee genera, such as *Centris*

spp. and *Epicharis spp.* Lastly, we suggest planting species from the Convolvulaceae family, particularly those belonging to the *Ipomoea spp.* genus, as they provide resources for oligolectic bees, such as species from the *Melitoma spp.* genus. These practices could support a more diverse bee community in cities, in addition to allowing a greater distribution of specialist species in urban landscapes. However, it is important to highlight that our list of plants is limited to species found in urban landscapes in our study. Therefore, we strongly encourage and highlight the importance of research focused on plant selection of native species that are generally not commercialized and managed in urban landscaping to enhance further the capacity of the urban landscapes in maintaining and conserving biodiversity.

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SUPPLEMENTARY DATA

FIGURES, TABLES AND CAPTION

Tab. S1 Sampling sites, geographic coordinates, percentage of impermeable surface, and richness of species (bees and plants) and network metrics along an urbanization gradient in Belo Horizonte, Minas Gerais.

Site name	Latitude	Longitude	Urbanization (%)	Richness (bee)	Richness (plant)	Nº (interactions)	Richness (interactions)	H2'	wNODF
Serra do curral	-19.960813	-43.914086	16.38	25	41	327	71	0.74	8.02
Zoobotânica	-19.854994	-44.005302	19.70	44	55	1588	165	0.57	12.52
Estação ecológica	-19.873608	-43.972575	28.03	29	29	164	59	0.53	7.52
Aggeo pio	-19.977102	-43.971338	50.96	19	29	510	76	0.40	27.53
Museu	-19.892272	-43.913291	53.63	21	30	353	64	0.62	13.54
Ruas	-19.852902	-43.959977	56.59	19	36	660	89	0.55	22.69
Eduardo Couri	-19.952778	-43.946056	64.30	21	36	817	93	0.51	25.65
Praça da liberdade	-19.932166	-43.938038	65.21	28	34	813	106	0.48	18.86
P. Municipal	-19.924375	-43.935063	68.73	29	43	620	115	0.56	13.94
P. ursulina	-19.886438	-44.001205	72.14	37	51	646	120	0.54	7.90
P. Renato Azeredo	-19.874939	-43.933462	83.80	19	30	335	55	0.70	10.16
P. Ismael de Oliveira	-19.888953	-43.932411	89.74	21	32	931	93	0.51	18.89

Model Richness of bees	AICc	Weights
bees_richness ~ 1 + plant_richness_only_bees	73.08950479	0.51719018
bees_richness ~ 1 + prop_urb + plant_richness_only_bees	76.13548057	0.112778167
bees_richness ~ 1 + plant_richness_only_bees + percentage_plant_native	76.17244863	0.11071272
bees_richness ~ 1 + mean_build_height_m + plant_richness_only_bees	76.54559669	0.091869097
bees_richness ~ 1 + plant_richness_only_bees + abundance_of_flowers_only_bees	76.62517371	0.088285528
bees_richness ~ 1 + mean_build_height_m + plant_richness_only_bees + percentage_plant_native	80.37720869	0.013525255
bees_richness ~ 1 + prop_urb + mean_build_height_m + plant_richness_only_bees	80.38179476	0.013494277
bees_richness ~ 1 + prop_urb + plant_richness_only_bees + abundance_of_flowers_only_bees	80.50237633	0.012704737
bees_richness ~ 1 + prop_urb + plant_richness_only_bees + percentage_plant_native	80.68478899	0.011597256
bees_richness ~ 1 + plant_richness_only_bees + abundance_of_flowers_only_bees + percentage_plant_native	80.88648155	0.010484755
bees_richness ~ 1 + mean_build_height_m + plant_richness_only_bees + abundance_of_flowers_only_bees	81.19210546	0.008998972
bees_richness ~ 1 + abundance_of_flowers_only_bees + percentage_plant_native	84.21635074	0.001983747
bees_richness ~ 1 + abundance_of_flowers_only_bees	85.77529003	0.000909844
bees_richness ~ 1 + prop_urb + mean_build_height_m + plant_richness_only_bees + percentage_plant_native	86.37147582	0.000675316

bees_richness ~ 1 + prop_urb + mean_build_height_m + plant_richness_only_bees + abundance_of_flowers_only_bees	86.44199582	0.000651919
bees_richness ~ 1 + mean_build_height_m + plant_richness_only_bees + abundance_of_flowers_only_bees + percentage_plant_native	86.51956873	0.000627118
bees_richness ~ 1 + prop_urb	86.54172569	0.000620208
bees_richness ~ 1 + prop_urb + plant_richness_only_bees + abundance_of_flowers_only_bees + percentage_plant_native	86.78140735	0.000550163
bees_richness ~ 1 + mean_build_height_m + abundance_of_flowers_only_bees + percentage_plant_native	86.84172324	0.000533819
bees_richness ~ 1 + prop_urb + abundance_of_flowers_only_bees	87.44402925	0.000395007
bees_richness ~ 1	87.77851859	0.000334173
bees_richness ~ 1 + percentage_plant_native	88.1882342	0.000272272
bees_richness ~ 1 + prop_urb + abundance_of_flowers_only_bees + percentage_plant_native	88.65762294	0.000215316
bees_richness ~ 1 + mean_build_height_m + abundance_of_flowers_only_bees	89.30357362	0.000155887
bees_richness ~ 1 + prop_urb + percentage_plant_native	90.04559143	0.000107568
bees_richness ~ 1 + prop_urb + mean_build_height_m	90.12409025	0.000103428
bees_richness ~ 1 + mean_build_height_m	90.64708683	7.96E-05
bees_richness ~ 1 + prop_urb + mean_build_height_m + abundance_of_flowers_only_bees	91.72315725	4.65E-05
bees_richness ~ 1 + mean_build_height_m + percentage_plant_native	91.78827766	4.50E-05
bees_richness ~ 1 + prop_urb + mean_build_height_m + abundance_of_flowers_only_bees + percentage_plant_native	92.41342698	3.29E-05
bees_richness ~ 1 + prop_urb + mean_build_height_m + percentage_plant_native	94.62057486	1.09E-05
bees_richness ~ 1 + prop_urb + mean_build_height_m + plant_richness_only_bees + abundance_of_flowers_only_bees + percentage_plant_native	95.17024534	8.30E-06

Tab. S2 Description of value the AICc and Akaike weight values for all possible bee richness models

Model abundance of bees	AICc	Weights
abundance_total_of_bees ~ 1 + plant_richness_only_bees + percentage_plant_native	163.794814	0.807608115
abundance_total_of_bees ~ 1 + plant_richness_only_bees + abundance_of_flowers_only_bees + percentage_plant_native	168.651475	0.071218058
abundance_total_of_bees ~ 1 + prop_urb + plant_richness_only_bees + percentage_plant_native	169.9156972	0.037850164
abundance_total_of_bees ~ 1 + mean_build_height_m + plant_richness_only_bees + percentage_plant_native	170.0347164	0.035663428
abundance_total_of_bees ~ 1 + abundance_of_flowers_only_bees + percentage_plant_native	172.1867624	0.012159402
abundance_total_of_bees ~ 1 + prop_urb + abundance_of_flowers_only_bees	172.5685623	0.010046284
abundance_total_of_bees ~ 1 + abundance_of_flowers_only_bees	172.8423743	0.008760884

abundance_total_of_bees ~ 1 + mean_build_height_m + abundance_of_flowers_only_bees	174.7645432	0.003350844
abundance_total_of_bees ~ 1 + prop_urb + mean_build_height_m + abundance_of_flowers_only_bees	175.9601001	0.001843072
abundance_total_of_bees ~ 1 + plant_richness_only_bees	176.3008524	0.00155435
abundance_total_of_bees ~ 1 + prop_urb + plant_richness_only_bees + abundance_of_flowers_only_bees	176.4369607	0.00145209
abundance_total_of_bees ~ 1 + plant_richness_only_bees + abundance_of_flowers_only_bees	176.9321216	0.001133628
abundance_total_of_bees ~ 1 + mean_build_height_m + plant_richness_only_bees + abundance_of_flowers_only_bees + percentage_plant_native	177.3022498	0.000942103
abundance_total_of_bees ~ 1 + prop_urb + plant_richness_only_bees + abundance_of_flowers_only_bees + percentage_plant_native	177.3165979	0.000935368
abundance_total_of_bees ~ 1 + prop_urb + abundance_of_flowers_only_bees + percentage_plant_native	177.5045449	0.000851472
abundance_total_of_bees ~ 1 + percentage_plant_native	177.5443944	0.000834675
abundance_total_of_bees ~ 1	177.5467551	0.00083369
abundance_total_of_bees ~ 1 + mean_build_height_m + abundance_of_flowers_only_bees + percentage_plant_native	177.6387604	0.000796207
abundance_total_of_bees ~ 1 + prop_urb + plant_richness_only_bees	178.4317253	0.000535594
abundance_total_of_bees ~ 1 + prop_urb + mean_build_height_m + plant_richness_only_bees + percentage_plant_native	178.6666052	0.000476247
abundance_total_of_bees ~ 1 + mean_build_height_m + plant_richness_only_bees + abundance_of_flowers_only_bees	180.2681413	0.000213827
abundance_total_of_bees ~ 1 + prop_urb + percentage_plant_native	180.4051482	0.00019967
abundance_total_of_bees ~ 1 + mean_build_height_m + plant_richness_only_bees	180.5075699	0.000189702
abundance_total_of_bees ~ 1 + prop_urb	181.2021892	0.000134041
abundance_total_of_bees ~ 1 + mean_build_height_m	181.2132075	0.000133304
abundance_total_of_bees ~ 1 + mean_build_height_m + percentage_plant_native	181.6860605	0.000105236
abundance_total_of_bees ~ 1 + prop_urb + mean_build_height_m + plant_richness_only_bees + abundance_of_flowers_only_bees	181.7381703	0.00010253
abundance_total_of_bees ~ 1 + prop_urb + mean_build_height_m + plant_richness_only_bees	184.4184815	2.68E-05
abundance_total_of_bees ~ 1 + prop_urb + mean_build_height_m + abundance_of_flowers_only_bees + percentage_plant_native	184.5749194	2.48E-05
abundance_total_of_bees ~ 1 + prop_urb + mean_build_height_m	185.9160085	1.27E-05
abundance_total_of_bees ~ 1 + prop_urb + mean_build_height_m + percentage_plant_native	186.3649003	1.01E-05

Tab. S3 Description of value the AICc and Akaike weight values for all possible bee abundance model.

Areas	S.obs	S.chao1	Sample completeness (%)	72
Serra do curral	71	114.5	62	
Zoobotânica	165	214.4	77	
Estação ecológica	59	96.8	61	
Aggeo pio	76	86.2	88	
Museu	64	83.71429	76	
Ruas	89	99.46154	89	
Eduardo Couri	93	108.3333	86	
Praça da liberdade	106	150.4	70	
P. municipal	115	143.9565	80	
P. ursulina	120	171.1304	70	
P. Renato Azeredo	55	70	79	
P. Ismael de Oliveira	93	104.7692	89	
All areas	785	1050.556	75	

Tab. S4 Sample completeness (%) total (all areas) and for each sampling site.

Order	Family	Species	Number of interactions	Richness of bee species attracted	Origin
Alismatales	Araceae	<i>Anthurium andraeanum</i>	22	2	non-native
		<i>Spathiphyllum cannifolium</i>	63	5	non-native
		<i>Spathiphyllum wallisii</i>	6	2	non-native
Apiales	Apiaceae	<i>Anethum graveolens</i>	51	7	non-native
	Araliaceae	<i>Hydrocotyle bonariensis</i>	11	2	native
Arecales	Arecaceae	<i>Phoenix roebelenii</i>	17	1	non-native
Asparagales	Amaryllidaceae	<i>Agapanthus africanus</i>	127	16	non-native
	Asphodelaceae	<i>Bulbine frutescens</i>	57	3	non-native
	Asparagaceae	<i>Cordyline fruticose</i>	21	5	non-native
	Amaryllidaceae	<i>Crinum americanum</i>	76	5	native
		<i>Crinum x powellii</i>	64	6	non-native
		<i>Tulbaghia violacea</i>	29	2	non-native
	Asphodelaceae	<i>Hemerocallis x hybrida</i>	15	5	non-native
		<i>Hemerocallis flava</i>	30	7	non-native
	Iridaceae	<i>Dietes bicolor</i>	8	2	non-native
		<i>Iris domestica</i>	8	4	non-native
		<i>Neomarica candida</i>	24	7	native
Asterales	Asteraceae	<i>Ageratum conyzoides</i>	14	3	native
		<i>Ageratum fastigiatum</i>	1	1	native
		<i>Ambrosia artemisiifolia</i>	12	2	native
		<i>Asteraceae sp.1</i>	9	4	—
		<i>Baccharis dracunculifolia</i>	95	4	native
		<i>Chresta sphaerocephala</i>	1	1	native
		<i>Conyza bonariensis</i>	19	4	native
		<i>Coreopsis lanceolata</i>	9	5	non-native
		<i>Cosmos caudatus</i>	9	2	non-native
		<i>Cosmos sulphureus</i>	112	7	non-native

		<i>Cyrtocymura scorpioides</i>	8	3	native
		<i>Emilia fosbergii</i>	22	6	non-native
		<i>Eremanthus erythropappus</i>	36	2	native
		<i>Helenium amarum</i>	11	2	non-native
		<i>Lepidaploa aurea</i>	9	2	native
		<i>Lepidaploa cf. salzmännii</i>	3	1	native
		<i>Leucanthemum vulgare</i>	82	11	non-native
		<i>Mikania hirsutissima</i>	2	1	non-native
		<i>Moquiniastrium densicephalum</i>	1	1	native
		<i>Pseudelephantopus spicatus</i>	9	2	native
		<i>Sanvitalia procumbens</i>	3	1	non-native
		<i>Sonchus oleraceus</i>	88	5	native
		<i>Sphagneticola trilobata</i>	639	25	native
		<i>Symphyotrichum sp.</i>	45	5	—
		<i>Tilesia baccata</i>	9	5	native
		<i>Tithonia diversifolia</i>	94	8	non-native
		<i>Tridax procumbens</i>	198	10	non-native
		<i>Unxia kubitzkii</i>	27	5	native
		<i>Vernonanthura ferruginea</i>	1	1	native
		<i>Vernonanthura polyanthes</i>	43	1	native
		<i>Youngia japonica</i>	18	3	non-native
Boraginales	Boraginaceae	<i>Cynoglossum amabile</i>	1	1	non-native
	Cordiaceae	<i>Varronia curassavica</i>	1	1	native
Brassicales	Brassicaceae	<i>Brassica napus</i>	8	5	non-native
	Caricaceae	<i>Carica papaya</i>	9	2	non-native
	Moringaceae	<i>Moringa oleifera</i>	4	3	non-native
	Tropaeolaceae	<i>Tropaeolum majus</i>	3	1	non-native
Caryophyllales	Polygonaceae	<i>Antigonon leptopus</i>	175	5	non-native
	Nyctaginaceae	<i>Bougainvillea glabra</i>	2	1	native
	Phytolaccaceae	<i>Phytolacca thyrsoflora</i>	4	3	native
	Portulacaceae	<i>Portulaca umbraticola</i>	18	4	native
	Talinaceae	<i>Talinum paniculatum</i>	13	5	native
Commelinales	Commelinaceae	<i>Commelina erecta</i>	66	4	native
		<i>Dichorisandra thyrsoflora</i>	2	2	native
		<i>Tradescantia pallida</i>	91	4	non-native
		<i>Tradescantia zebrina</i>	8	4	non-native
Cornales	Hydrangeaceae	<i>Hydrangea macrophylla</i>	4	1	non-native
Cucurbitales	Begoniaceae	<i>Begonia coccinea</i>	2	1	native
	Cucurbitaceae	<i>Cucurbita maxima</i>	23	4	non-native
		<i>Luffa aegyptiaca</i>	7	2	non-native
		<i>Momordica charantia</i>	13	4	non-native
Dipsacales	Caprifoliaceae	<i>Abelia x grandiflora</i>	9	4	non-native
Ericales	Lecythidaceae	<i>Coroupita guianensis</i>	18	3	native
	Balsaminaceae	<i>Impatiens walleriana</i>	1	1	non-native
	Ericaceae	<i>Rhododendron indicum</i>	99	7	non-native
	Styracaceae	<i>Styrax ferrugineus</i>	8	3	native

Fabales	Fabaceae	<i>Acacia podalyriifolia</i>	31	1	non-native
		<i>Arachis repens</i>	31	7	native
		<i>Bauhinia forficata</i>	164	5	native
		<i>Bauhinia variegata</i>	16	5	non-native
		<i>Brownea grandiceps</i>	6	3	native
		<i>Caesalpinia pulcherrima</i>	70	5	non-native
		<i>Cassia fistula</i>	12	5	non-native
		<i>Cenostigma pluviosum</i>	5	4	native
		<i>Centrosema virginianum</i>	2	1	native
		<i>Chamaecrista nictitans</i>	3	3	native
		<i>Chamaecrista rotundifolia</i>	2	2	native
		<i>Crotalaria micans</i>	57	9	native
		<i>Delonix regia</i>	7	2	non-native
		<i>Desmodium subsecundum</i>	26	5	native
		<i>Erythrina speciosa</i>	5	3	native
		<i>Leucaena leucocephala</i>	5	1	non-native
		<i>Macroptilium cf. sabaraense</i>	1	1	native
		<i>Mimosa radula</i>	4	2	native
		<i>Peltophorum dubium</i>	26	2	native
		<i>Platypodium elegans</i>	73	6	native
		<i>Senna angulata</i>	1	1	native
		<i>Senna multijuga</i>	36	8	native
		<i>Senna pendula</i>	73	9	native
		<i>Senna spectabilis</i>	59	7	native
		<i>Stylosanthes guianensis</i>	20	3	native
		<i>Vachellia seyal</i>	9	2	non-native
	Polygalaceae	<i>Asemeia violacea</i>	1	1	native
Gentianales	Apocynaceae	<i>Allamanda cathartica</i>	3	2	native
		<i>Asclepias curassavica</i>	1	1	native
		<i>Catharanthus roseus</i>	6	3	non-native
		<i>Nerium oleander</i>	1	1	non-native
		<i>Plumeria rubra</i>	25	2	non-native
	Rubiaceae	<i>Borreria verticillata</i>	2	1	native
		<i>Ixora coccinea</i>	127	3	non-native
		<i>Pentas lanceolata</i>	3	1	non-native
		<i>Psychotria carthagenensis</i>	96	13	native
		<i>Richardia brasiliensis</i>	30	2	native
		<i>Rubiaceae sp.</i>	10	1	—
		<i>Serissa japonica</i>	1	1	non-native
Geraniales	Geraniaceae	<i>Pelargonium zonale</i>	10	6	non-native
Lamiales	Bignoniaceae	<i>Adenocalymma pedunculatum</i>	8	1	native
		<i>Anemopaegma prostratum</i>	14	2	native
		<i>Fridericia triplinervia</i>	7	1	native
		<i>Handroanthus albus</i>	15	5	native
		<i>Handroanthus chrysotrichus</i>	20	5	native
		<i>Jacaranda caroba</i>	1	1	native

		<i>Tabebuia roseoalba</i>	18	3	native
		<i>Tecoma stans</i>	45	10	non-native
	Verbenaceae	<i>Aloysia virgata</i>	3	1	native
		<i>Citharexylum myrianthum</i>	50	4	native
		<i>Duranta erecta</i>	45	5	non-native
		<i>Lantana camara</i>	45	5	non-native
		<i>Lantana fucata</i>	4	1	native
		<i>Lippia alba</i>	5	3	native
		<i>Petrea volubilis</i>	7	1	native
		<i>Stachytarpheta gesnerioides</i>	4	2	native
	Acanthaceae	<i>Asystasia gangetica</i>	93	7	non-native
		<i>Eranthemum pulchellum</i>	138	7	non-native
		<i>Justicia brandegeana</i>	122	6	non-native
		<i>Megaskepasma erythrochlamys</i>	6	3	non-native
		<i>Pachystachys lutea</i>	30	4	native
		<i>Ruellia brevifolia</i>	7	1	native
		<i>Ruellia geminiflora</i>	3	1	native
		<i>Ruellia inundata</i>	15	2	native
		<i>Ruellia simplex</i>	10	3	native
		<i>Ruellia sp.</i>	4	1	—
		<i>Sanchezia oblonga</i>	2	1	non-native
		<i>Thunbergia erecta</i>	90	6	non-native
	Lamiaceae	<i>Clerodendrum splendens</i>	8	1	non-native
		<i>Leonurus japonicus</i>	1	1	non-native
		<i>Ocimum basilicum</i>	143	9	non-native
		<i>Rotheca myricoides</i>	23	5	non-native
		<i>Salvia coccinea</i>	9	2	non-native
		<i>Salvia leucantha</i>	11	3	non-native
		<i>Vitex polygama</i>	3	3	native
	Oleaceae	<i>Jasminum officinale</i>	46	2	non-native
		<i>Ligustrum lucidum</i>	7	3	non-native
	Plantaginaceae	<i>Russelia equisetiformis</i>	2	1	non-native
Magnoliales	Magnoliaceae	<i>Magnolia grandiflora</i>	11	3	non-native
Malpighiales	Malpighiaceae	<i>Banisteriopsis sp.</i>	10	2	—
		<i>Byrsonima coccolobifolia</i>	5	5	native
		<i>Byrsonima intermedia</i>	18	7	native
		<i>Galphimia brasiliensis</i>	50	5	native
		<i>Peixotoa tomentosa</i>	4	2	native
	Salicaceae	<i>Casearia sylvestris</i>	8	3	native
	Clusiaceae	<i>Clusia mexiae</i>	19	3	native
	Euphorbiaceae	<i>Euphorbia hirta</i>	22	2	native
		<i>Euphorbia milii</i>	80	1	non-native
	Calophyllaceae	<i>Kielmeyera coriacea</i>	4	1	native
	Turneraceae	<i>Turnera cf. hilaireana</i>	14	2	native
		<i>Turnera subulata</i>	168	9	native
Malvales	Bixaceae	<i>Bixa Orellana</i>	11	6	native

	Malvaceae	<i>Dombeya wallichii</i>	11	1	non-native
		<i>Gossypium barbadense</i>	3	2	non-native
		<i>Luehea grandiflora</i>	1	1	native
		<i>Pavonia sepium</i>	11	2	native
		<i>Sida glaziovii</i>	9	3	native
		<i>Sida rhombifolia</i>	14	1	native
	Muntingiaceae	<i>Muntingia calabura</i>	179	9	native
Myrtales	Myrtaceae	<i>Callistemon viminalis</i>	281	8	non-native
		<i>Eugenia mattosii</i>	2	1	native
		<i>Eugenia uniflora</i>	22	2	native
		<i>Psidium guajava</i>	20	9	non-native
	Melastomataceae	<i>Miconia chamissois</i>	20	3	native
		<i>Pleroma candolleianum</i>	10	3	native
		<i>Pleroma granulatum</i>	141	15	native
		<i>Pleroma heteromallum</i>	4	4	native
		<i>Pleroma mutabile</i>	77	8	native
	Lythraceae	<i>Cuphea hyssopifolia</i>	121	7	non-native
		<i>Cuphea lutescens</i>	19	6	native
		<i>Diplusodon buxifolius</i>	3	1	native
		<i>Lafoensia pacari</i>	25	2	native
		<i>Lagerstroemia indica</i>	359	5	non-native
		<i>Lagerstroemia speciosa</i>	93	3	non-native
		<i>Punica granatum</i>	18	3	non-native
Oxalidales	Oxalidaceae	<i>Oxalis barrelieri</i>	1	1	native
		<i>Oxalis cf. hirsutissima</i>	1	1	native
		<i>Oxalis corniculata</i>	17	1	non-native
Poales	Poaceae	<i>Paspalum notatum</i>	21	1	native
Proteales	Proteaceae	<i>Grevillea banksii</i>	4	2	non-native
Ranunculales	Papaveraceae	<i>Argemone mexicana</i>	6	3	non-native
Rosales	Rosaceae	<i>Rosa x hybrida</i>	1	1	non-native
		<i>Rubus rosifolius</i>	18	2	native
Santalales	Loranthaceae	<i>Struthanthus flexicaulis</i>	100	1	native
Sapindales	Rutaceae	<i>Citrus x limonia</i>	13	3	non-native
		<i>Murraya paniculata</i>	89	4	non-native
	Anacardiaceae	<i>Lithraea molleoides</i>	27	2	native
		<i>Schinus molle</i>	10	3	native
		<i>Schinus terebinthifolia</i>	12	4	native
Solanales	Solanaceae	<i>Cestrum axillare</i>	9	1	native
		<i>Cestrum nocturnum</i>	1	1	non-native
		<i>Lycianthes asarifolia</i>	9	3	native
		<i>Solanum americanum</i>	2	2	native
		<i>Solanum didymum</i>	2	2	native
		<i>Solanum lycocarpum</i>	30	8	native
		<i>Solanum paniculatum</i>	43	8	native
	Convolvulaceae	<i>Distimake aegyptius</i>	38	2	native
		<i>Distimake macrocalyx</i>	12	2	native

		<i>Evolvulus glomeratus</i>	7	5	native
		<i>Ipomoea cairica</i>	18	5	native
		<i>Ipomoea horsfalliae</i>	190	7	non-native
		<i>Ipomoea purpurea</i>	11	4	native
		<i>Jacquemontia blanchetii</i>	7	2	native
Vitales	Vitaceae	<i>Leea coccinea</i>	1	1	non-native
Zingiberales	Zingiberaceae	<i>Alpinia zerumbet</i>	135	11	non-native
		<i>Hedychium coronarium</i>	5	1	non-native
	Cannaceae	<i>Canna indica</i>	17	2	native
	Costaceae	<i>Costus spiralis</i>	3	2	native
	Marantaceae	<i>Ctenanthe compressa</i>	3	1	native
		<i>Goeppertia cylindrica</i>	2	1	native
	Heliconiaceae	<i>Heliconia psittacorum</i>	22	2	native
	Strelitziaceae	<i>Strelitzia reginae</i>	28	1	non-native

Tab. S5 Flower species used by bees as resource found along the urban gradient in Belo Horizonte city, their total floral abundance and origin.

Subfamily	Species	Abundance	Sociability	Nesting preferences	Trophic specialization	Body size
Andreninae	<i>Oxaea flavescens</i>	9	SO	GR	GE	4,07
Apinae	<i>Apis mellifera</i>	1924	HE	AG	GE	2,78
	<i>Apoidea sp.</i>	1	—	—	—	—
	<i>Bombus (Fervidobombus) morio</i>	138	PE	AG	GE	4,86
	<i>Centris (Centris) varia</i>	15	SO	GR	SP	4,43
	<i>Centris (Hemisiella) trigonoides</i>	6	SO	AG	SP	3,49
	<i>Centris (Melanocentris) collaris</i>	20	SO	GR	SP	7,65
	<i>Centris (Melanocentris) discolor</i>	1	SO	GR	SP	8,05
	<i>Centris (Trachina) similis</i>	18	SO	GR	SP	6,81
	<i>Ceratina (Ceratinula) sp.</i>	4	PE	AG	GE	0,87
	<i>Ceratina (Crewella) sp.</i>	5	PE	AG	GE	1,67
	<i>Ceratina (Neoclavicera) sp.</i>	17	PE	AG	GE	1,39
	<i>Ceratina (Rhysoceratina) sp.</i>	3	PE	AG	GE	1,27
	<i>Coelioxoides waltheriae</i>	1	CL	CL	CL	1, 51
	<i>Epicharis (Epicharis) flava</i>	51	SO	GR	SP	5,51
	<i>Euglossa (Euglossa) truncata</i>	62	PE	AG	SP	3,43
	<i>Eulaema (Apeulaema) cingulata</i>	3	SO	AG	SP	6,42
	<i>Eulaema (Apeulaema) nigrita</i>	31	SO	AG	SP	5,72
	<i>Eulaema (Eulaema) helvola</i>	2	SO	AG	SP	4,48

	<i>Exomalopsis (Exomalopsis) analis</i>	38	SO	GR	GE	1,91
	<i>Exomalopsis (Exomalopsis) auropilosa</i>	21	SO	GR	GE	1,51
	<i>Exomalopsis (Exomalopsis) sp. 1</i>	21	SO	GR	GE	1,81
	<i>Exomalopsis (Exomalopsis) sp. 2</i>	3	SO	GR	GE	1,86
	<i>Frieseomelitta varia</i>	9	HE	AG	GE	1,31
	<i>Geotrigona subterranean</i>	19	HE	GR	GE	1,68
	<i>Lophopedia pygmaea</i>	11	SO	GR	SP	1,94
	<i>Melipona (Melipona) quadrifasciata</i>	5	HE	AG	GE	2,88
	<i>Meliponini spp.</i>	1571	HE	AG	GE	1,27
	<i>Melitoma segmentaria</i>	17	SO	GR	SP	2,91
	<i>Mezochaira bicolor</i>	1	CL	CL	CL	2,31
	<i>Nomada sp. 1</i>	8	CL	CL	CL	1,31
	<i>Nomada sp. 2</i>	3	CL	CL	CL	1, 15
	<i>Osiris sp.</i>	1	CL	CL	CL	1, 37
	<i>Paratetrapedia connexa</i>	2	SO	AG	SP	2,14
	<i>Paratetrapedia fervida</i>	7	SO	AG	SP	2,15
	<i>Paratetrapedia flaveola</i>	2	SO	AG	SP	1,81
	<i>Partamona helleri</i>	67	HE	AG	GE	1,71
	<i>Partamona sp.</i>	3	HE	AG	GE	1,78
	<i>Peponapis fervens</i>	4	SO	GR	SP	3,62
	<i>Ptilothrix plumate</i>	7	SO	GR	SP	3,15
	<i>Scaptotrigona postica</i>	35	HE	AG	GE	1,72
	<i>Tetragona clavipes</i>	156	HE	AG	GE	1,51
	<i>Tetragonisca angustula</i>	1031	HE	AG	GE	0,94
	<i>Tetrapedia diversipes</i>	19	HE	AG	SP	2,13
	<i>Thalestria spinosa</i>	2	CL	CL	CL	4,31
	<i>Thygater (Thygater) analis</i>	29	SO	GR	GE	3,23
	<i>Thygater (Thygater) palliventris</i>	6	SO	GR	GE	3,33
	<i>Trigona gf. Fulviventris</i>	29	HE	AG	GE	1,68
	<i>Trigona hyalinata</i>	1	HE	AG	GE	1,76
	<i>Trigona spinipes</i>	1680	HE	AG	GE	1,76
	<i>Tropidopedia carinata</i>	2	SO	AG	SP	1,90
	<i>Tropidopedia danunciae</i>	4	SO	AG	SP	1,66
	<i>Xanthopedia sp.</i>	3	SO	GR	SP	1,60
	<i>Xylocopa (Megaxylocopa) frontalis</i>	49	PE	AG	GE	9,01
	<i>Xylocopa (Monoxylocopa) abbreviate</i>	1	PE	AG	GE	3,04
	<i>Xylocopa (Neoxylocopa) grisescens</i>	55	PE	AG	GE	9,09

	<i>Xylocopa (Neoxylocopa) suspecta</i>	10	PE	AG	GE	6,97
Colletinae	<i>Ptiloglossa sp.</i>	1	SO	GR	GE	5,74
Halictinae	<i>Agapostemon (Notagapostemon) semimelleus</i>	2	SO	GR	GE	1,96
	<i>Augochlora (Augochlora) caerulior</i>	1	PE	AG	GE	1,61
	<i>Augochlora (Augochlora) esox</i>	54	PE	AG	GE	1,69
	<i>Augochlora (Augochlora) Hestia</i>	21	PE	AG	GE	1,62
	<i>Augochlora (Augochlora) scabrata</i>	12	PE	AG	GE	1,46
	<i>Augochlora (Oxystoglossella) aurinasis</i>	18	PE	GR	GE	1,24
	<i>Augochlora (Oxystoglossella) mendax</i>	2	PE	GR	GE	1,21
	<i>Augochlora (Oxystoglossella) morae</i>	32	PE	GR	GE	1,46
	<i>Augochlora sp.</i>	2	PE	AG	GE	1,13
	<i>Augochlorella Urania</i>	2	PE	GR	GE	1,15
	<i>Augochloropsis sp. 1</i>	10	PE	GR	GE	1,71
	<i>Augochloropsis sp. 2</i>	12	PE	GR	GE	1,84
	<i>Augochloropsis sp. 3</i>	2	PE	GR	GE	1,44
	<i>Augochloropsis sp. 4</i>	2	PE	GR	GE	1,75
	<i>Augochloropsis calypso</i>	4	PE	GR	GE	1,91
	<i>Augochloropsis crassiceps</i>	1	PE	GR	GE	2,11
	<i>Augochloropsis diversipennis</i>	9	PE	GR	GE	1,55
	<i>Augochloropsis hebesceus</i>	1	PE	GR	GE	2,71
	<i>Augochloropsis rotalis</i>	3	PE	GR	GE	1,89
	<i>Dialictus sp. 1</i>	4	PE	GR	GE	0,99
	<i>Dialictus sp. 2</i>	6	PE	GR	GE	0,95
	<i>Dialictus sp. 3</i>	18	PE	GR	GE	0,97
	<i>Neocorynura codion</i>	29	SO	GR	GE	1,72
	<i>Pereirapis semiaurata</i>	5	PE	GR	GE	0,87
	<i>Pseudagapostemon (Pseudagapostemon) pissisi</i>	1	SO	GR	GE	1,27
	<i>Pseudaugochlora graminea</i>	121	SO	GR	GE	2,16
Megachilinae	<i>Anthodiocetes megachiloides</i>	12	SO	AG	GE	1,99
	<i>Dartylomegachile sp. 1</i>	1	SO	AG	GE	2,89
	<i>Dicranthidium alicae</i>	10	SO	AG	GE	1,86
	<i>Epanthidium tigrinum</i>	11	SO	AG	GE	2,49
	<i>Megachile (Acentron) lentifera</i>	2	SO	AG	GE	3,42
	<i>Megachile (Acentron) sp. 1</i>	1	SO	AG	GE	4,25
	<i>Megachile (Austromegachile) sp. 1</i>	3	SO	AG	GE	3,38

	<i>Megachile (Chrysosarus) sp. 1</i>	1	SO	AG	GE	3,23
	<i>Megachile (Moureapis) sp. 1</i>	3	SO	AG	GE	3,47
	<i>Megachile (Moureapis) sp. 2</i>	6	SO	AG	GE	3,02
	<i>Megachile (Moureapis) sp. 3</i>	1	SO	AG	GE	2,81
	<i>Megachile (Ptilosarus) sp. 1</i>	3	SO	AG	GE	2,48
	<i>Megachile (Tylomegachile) orba</i>	1	SO	AG	GE	3,28

Tab. S6 Bee species (Hymenoptera: Apoidea), their total abundance and traits found along the urban gradient in Belo Horizonte city. For bee traits, the acronyms represent sociability as follows: SO = solitary, HE = highly eusocial, and PE = primitively eusocial. For nesting preferences, the acronyms are GR = ground-nesting and AG = above-ground nesting. For trophic specialization, GE = generalist and SP = specialist.

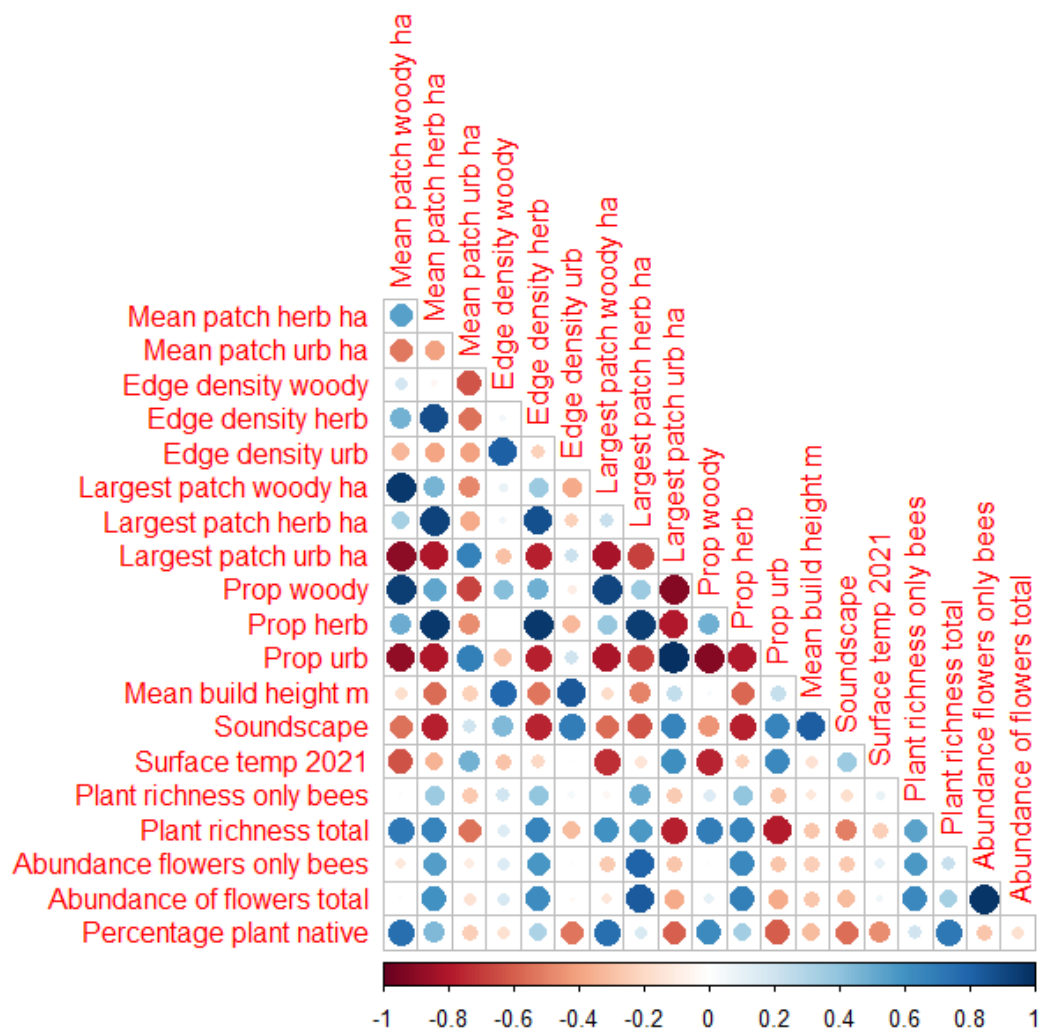
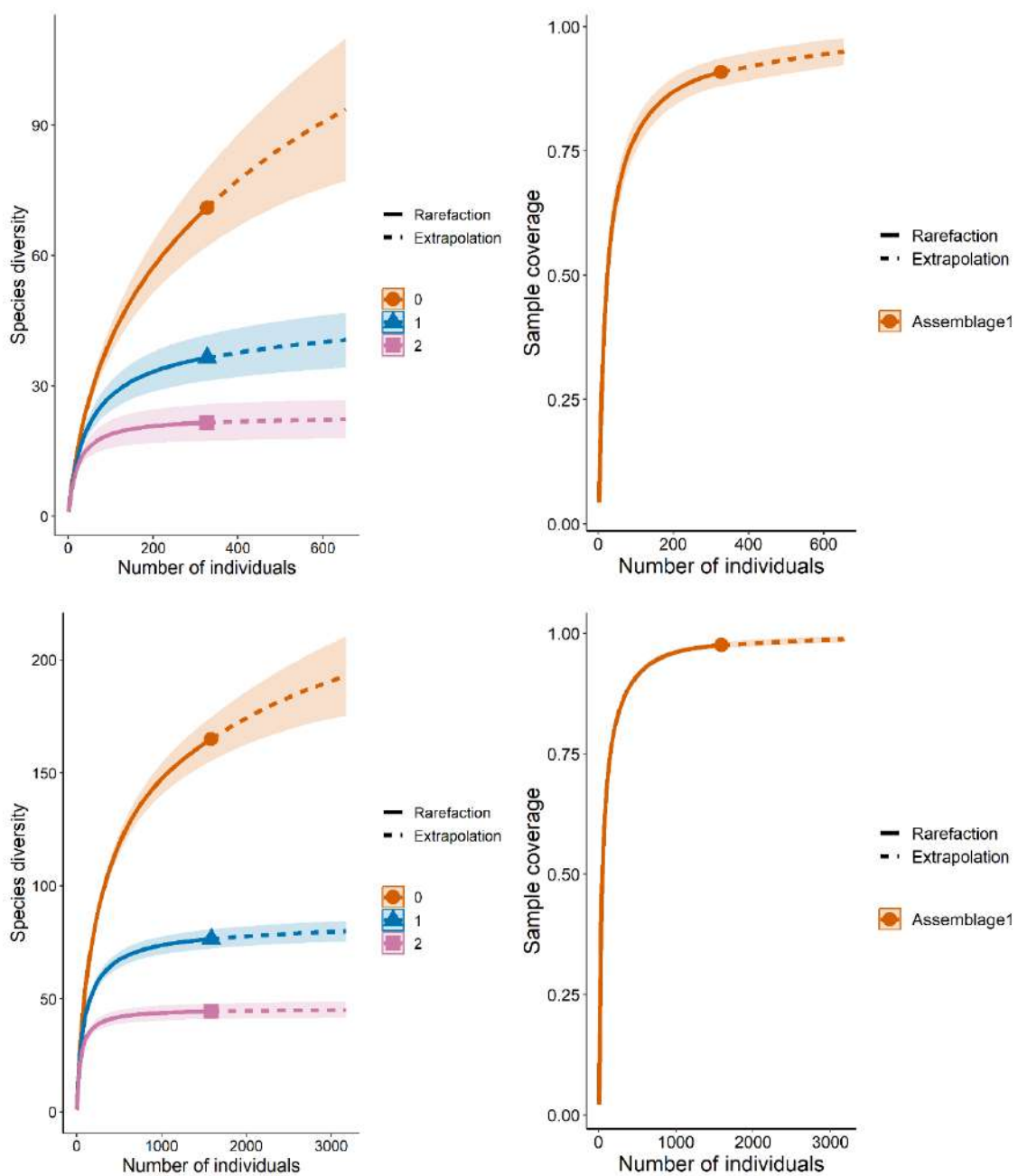
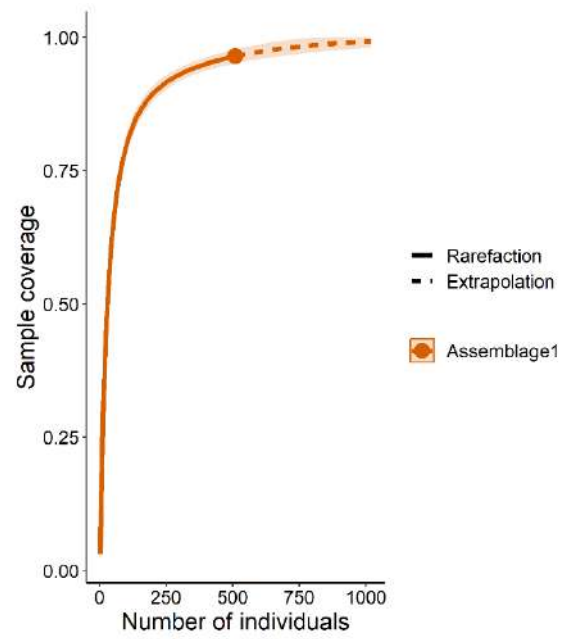
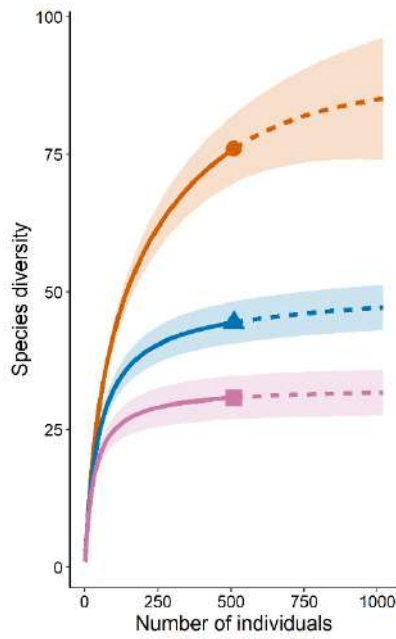
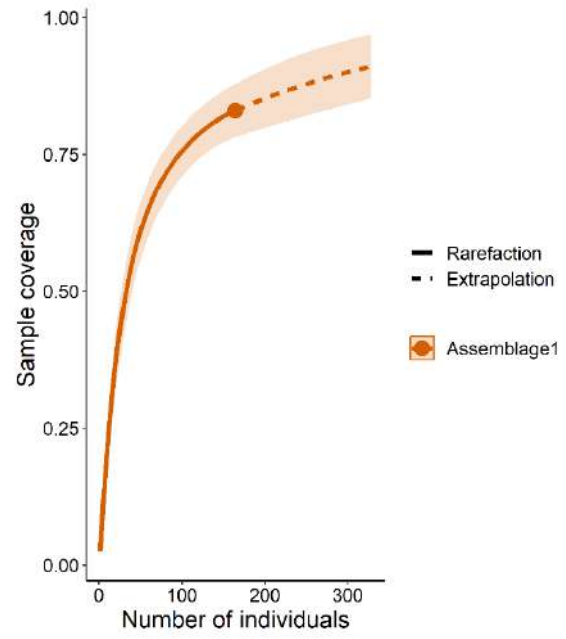
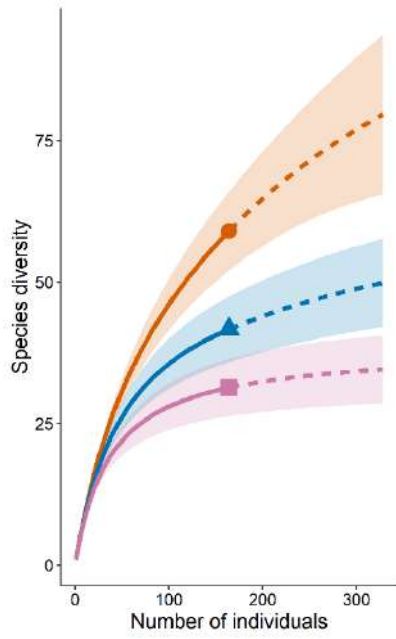
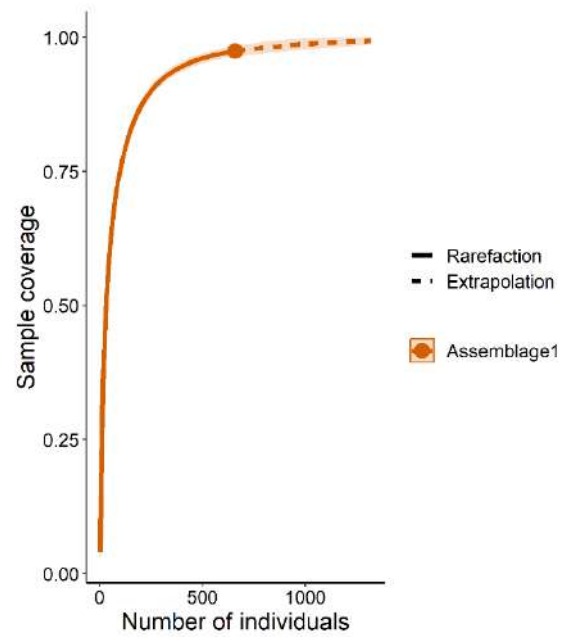
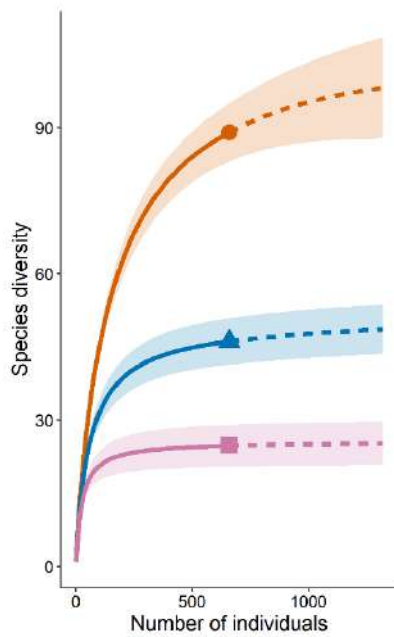
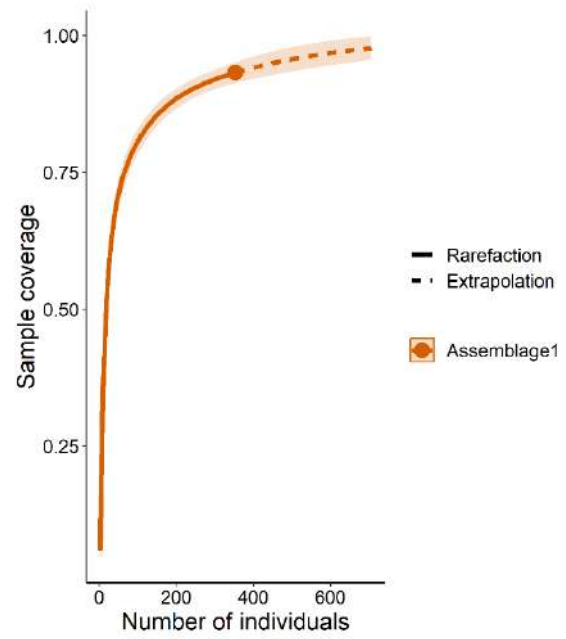
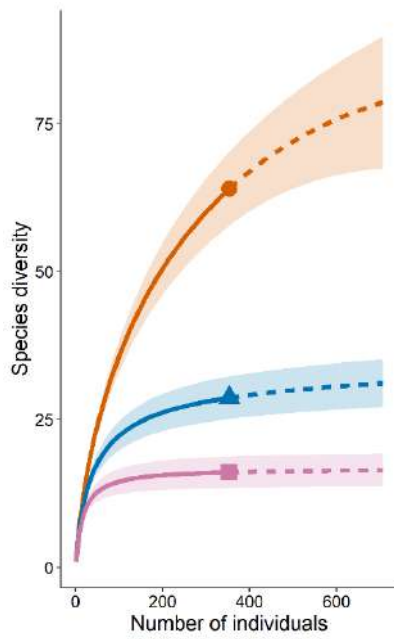
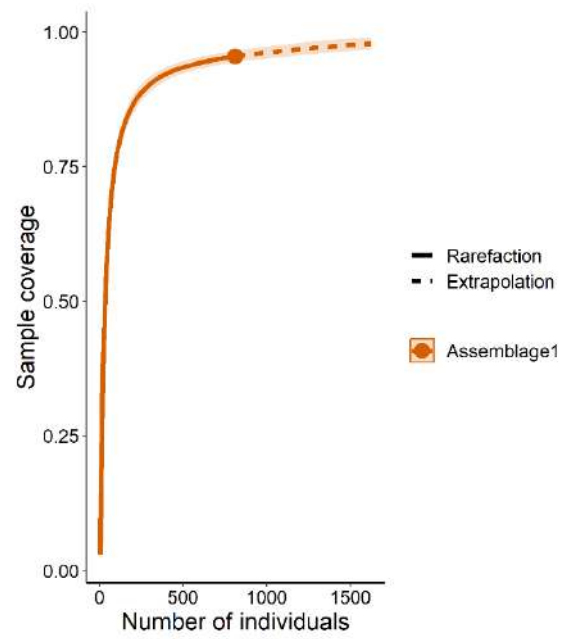
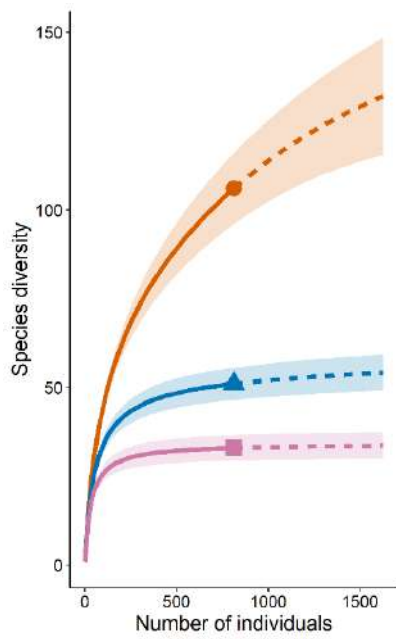
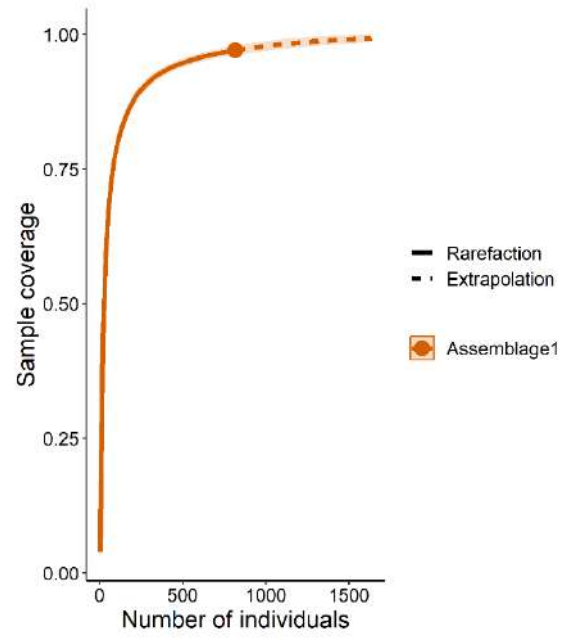
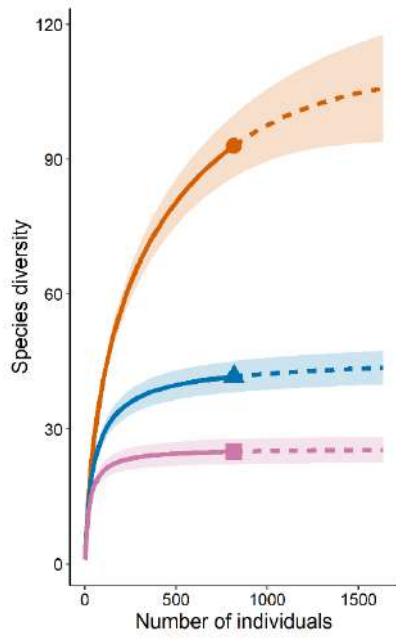


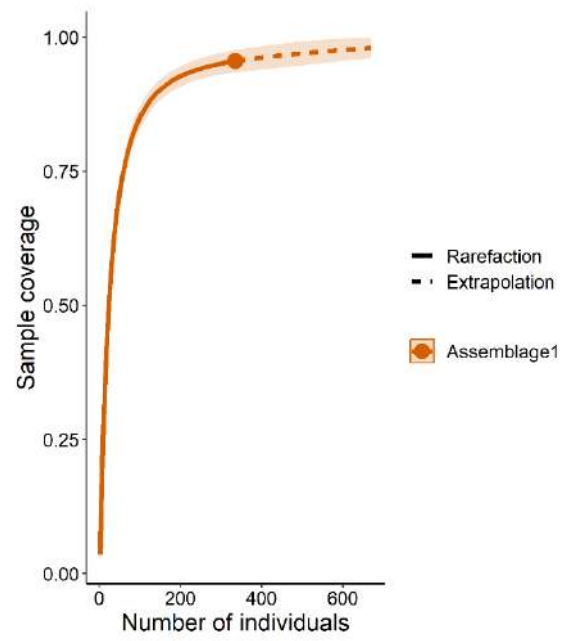
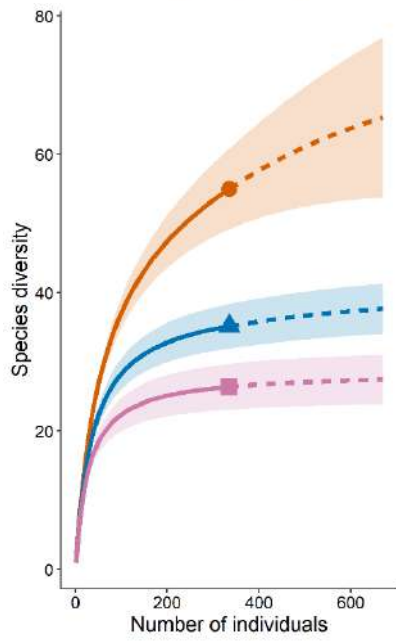
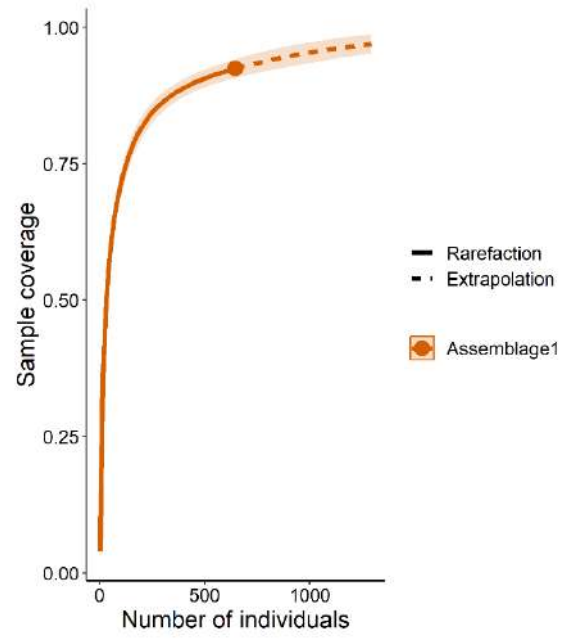
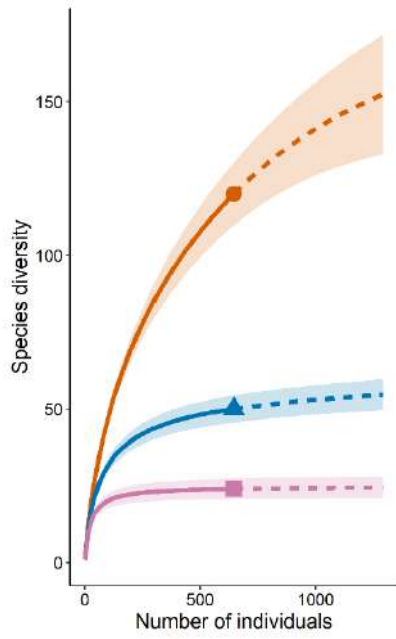
Fig. S1 Correlation analysis of the between predictor variables for diversity analysis. Red and blue colors indicate negative and positive correlations, respectively. Larger circles with more intense colors represent a high degree of correlation between the variables.

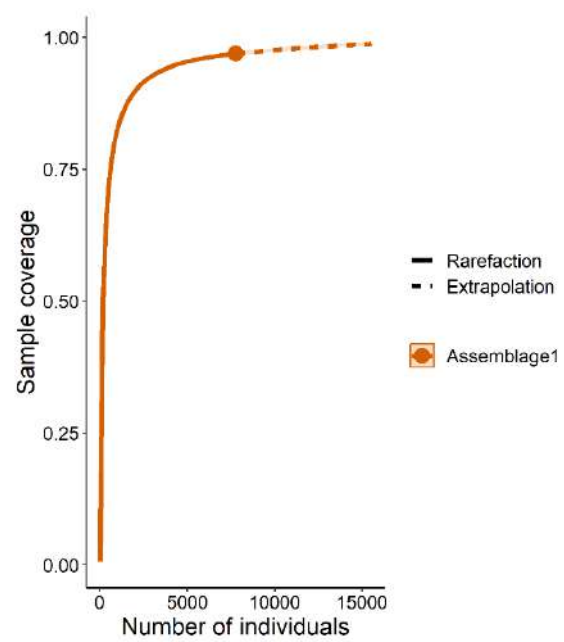
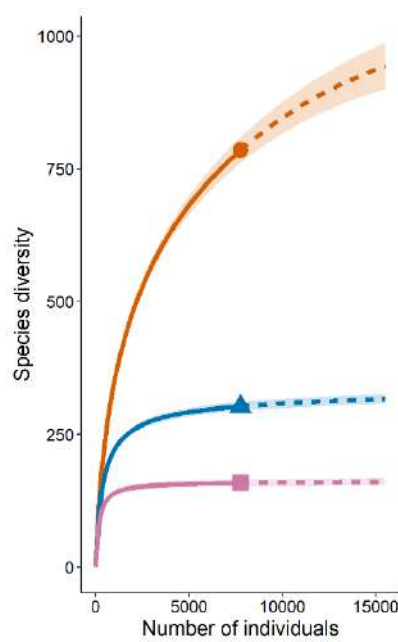
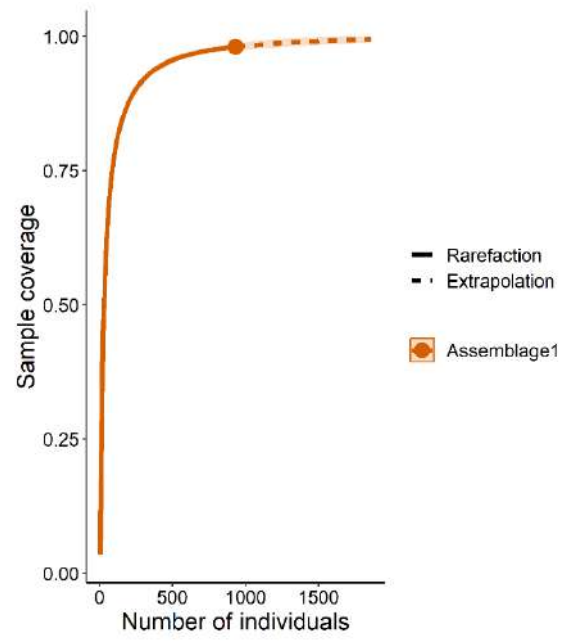
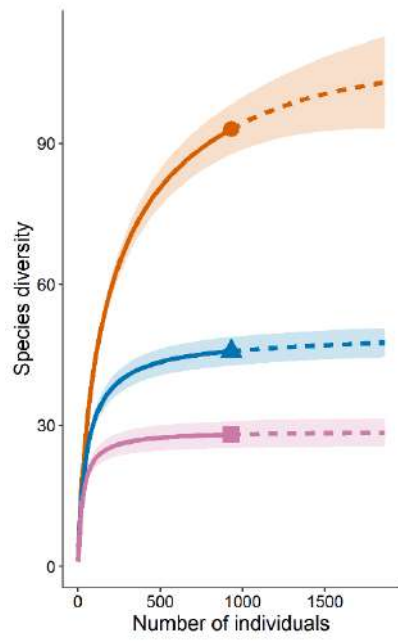












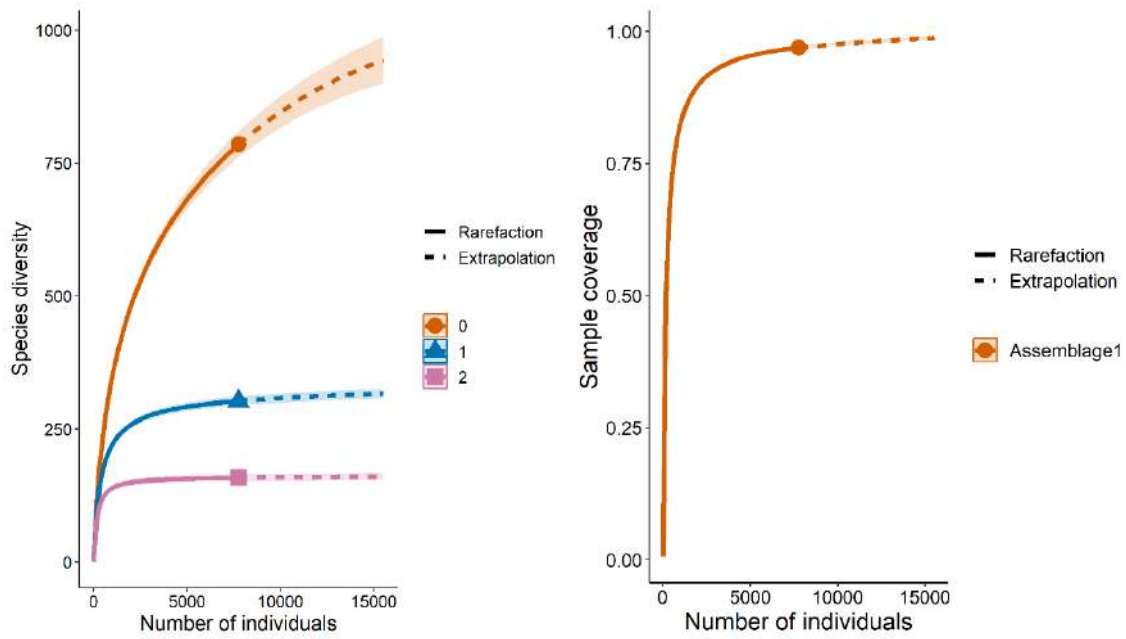


Fig. S2 Accumulation curves based on abundances in each sampling site and total (all areas) respectively.

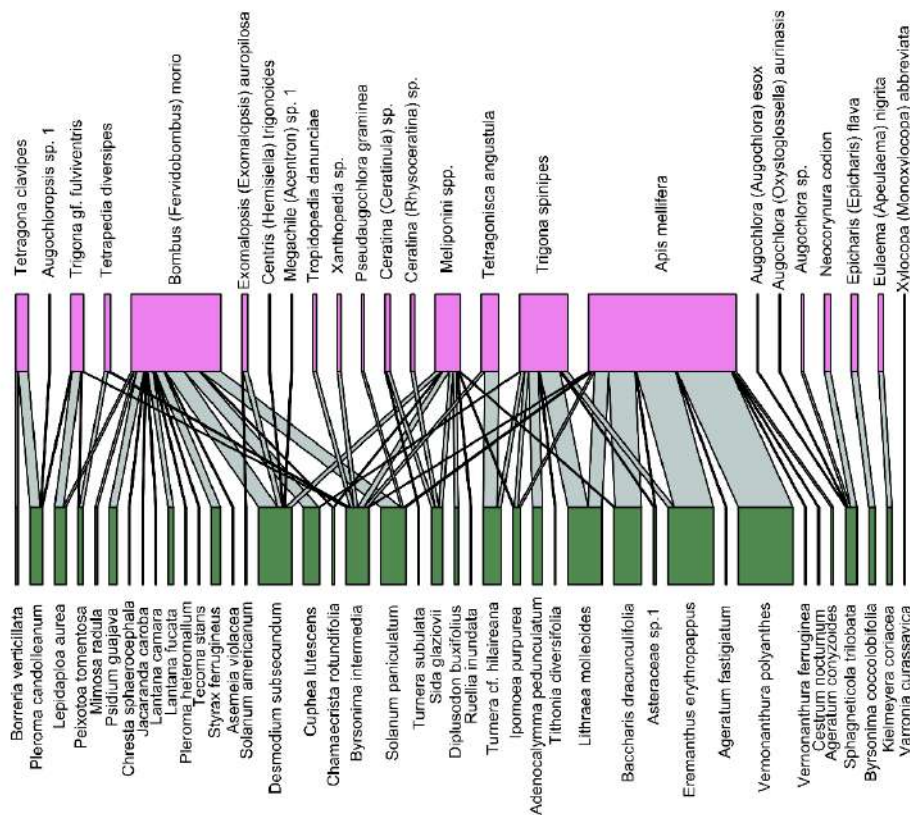
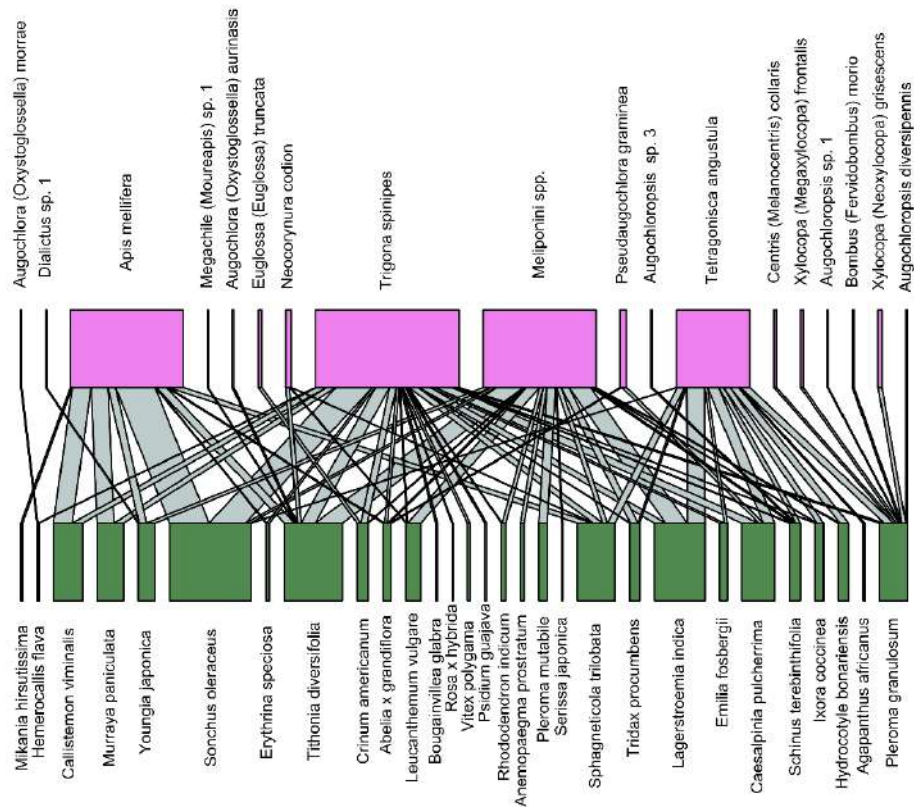


Fig. S3 Bee-plant interaction networks in serra do curral with 16.38% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

**Fig.**

S6 Bee-plant interaction networks in aggeio pio with 50.96% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

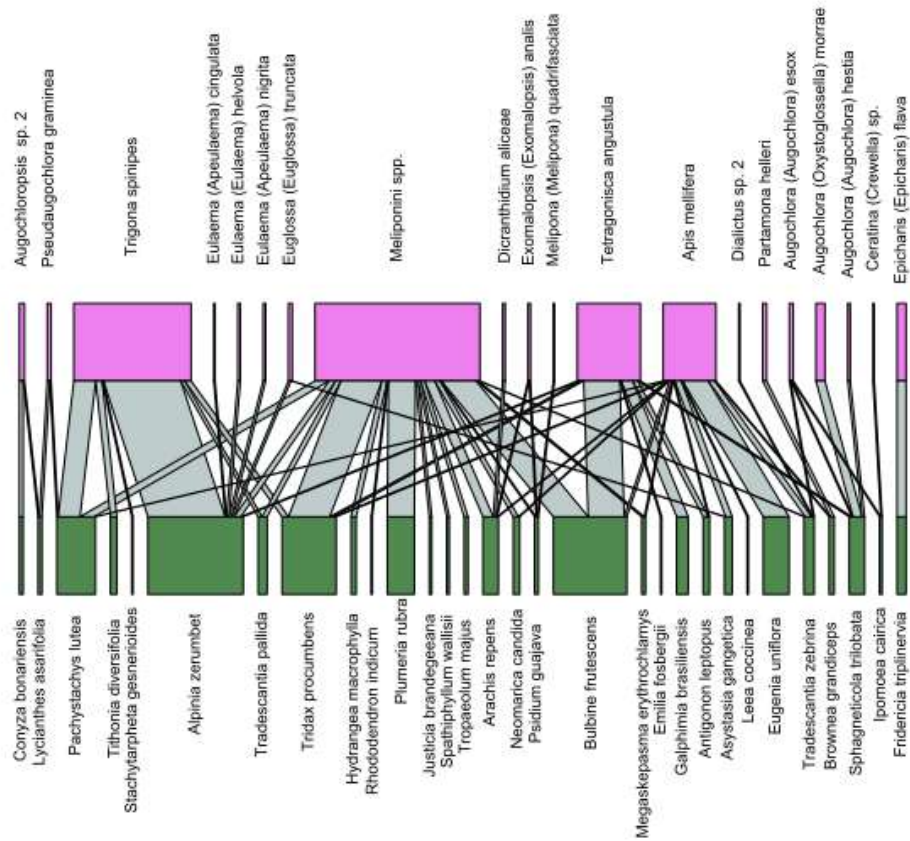


Fig.

S7 Bee-plant interaction networks in museu with 53.63% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

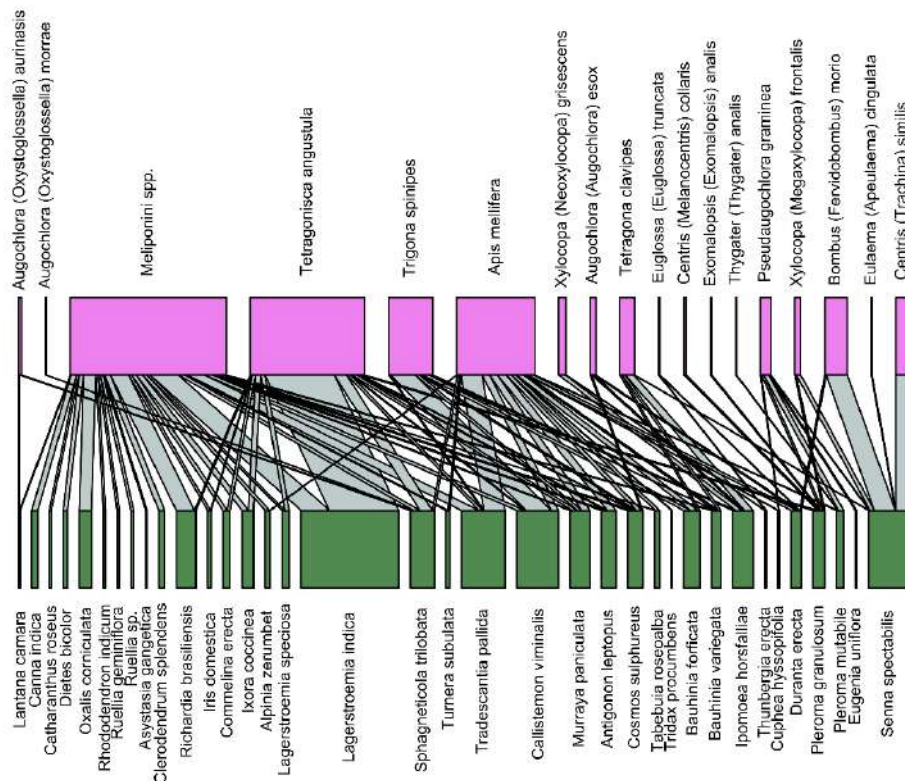


Fig.

S8 Bee-plant interaction networks in ruas with 56.59% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

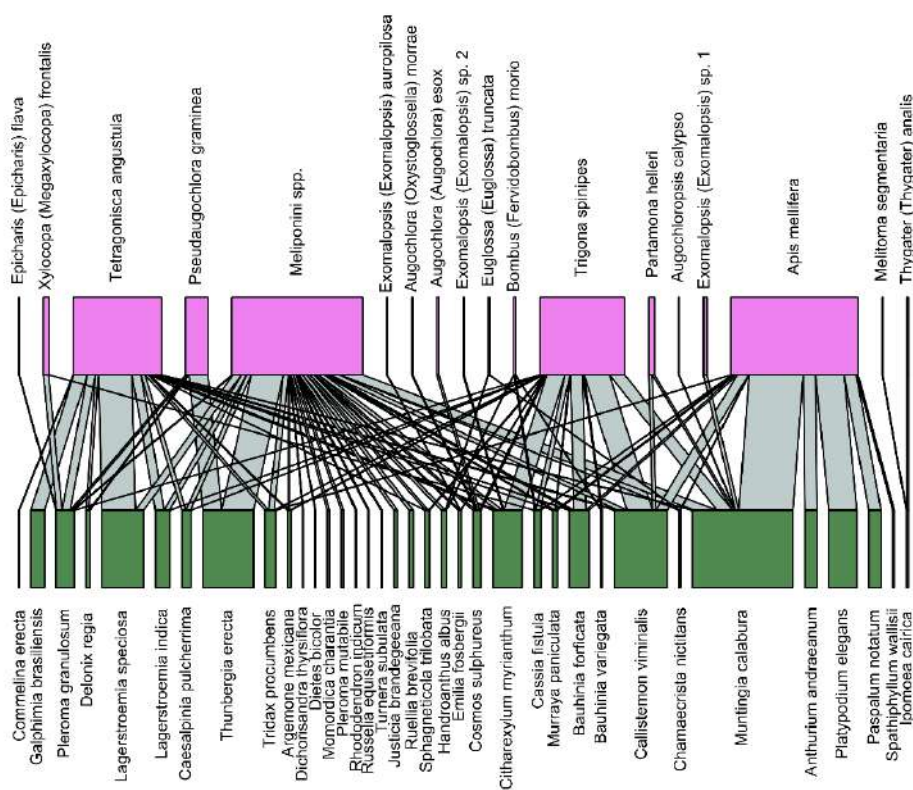


Fig. S9 Bee-plant interaction networks in Eduardo Couri with 64.30% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

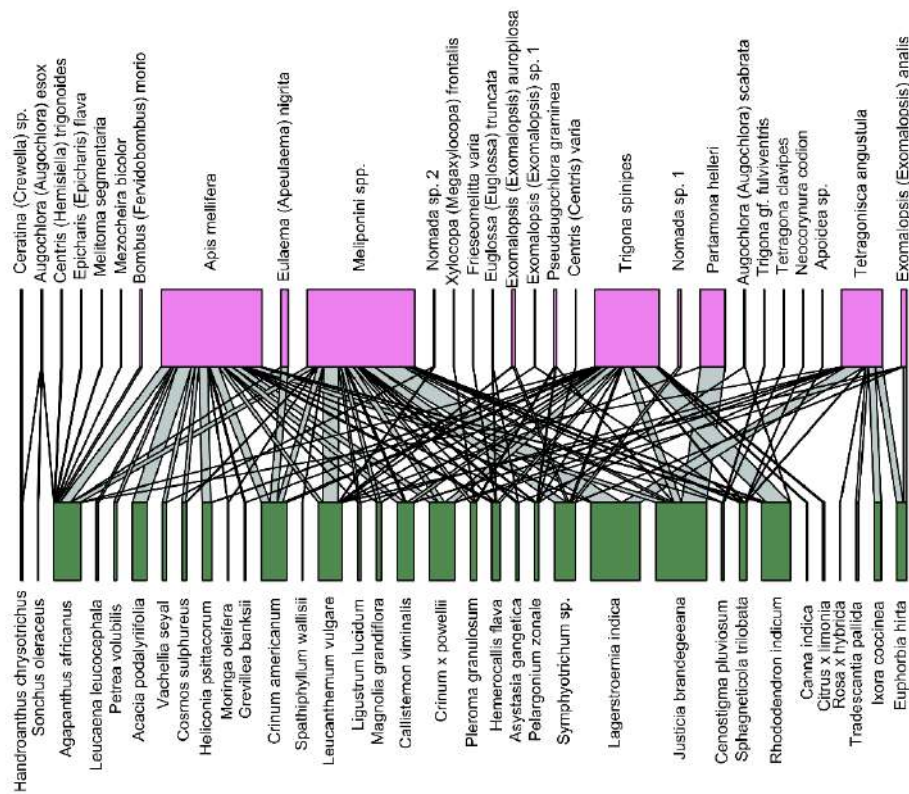


Fig.

S10 Bee-plant interaction networks in praça da liberdade with 65.21% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

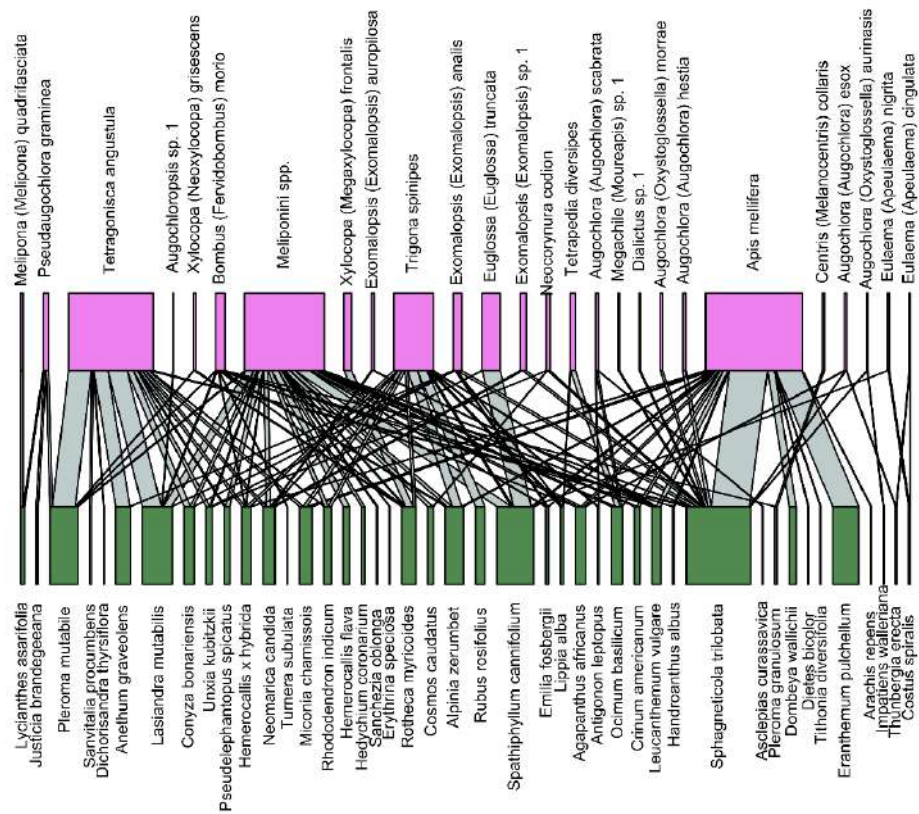


Fig.

S11 Bee-plant interaction networks in p. municipal with 68.73% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

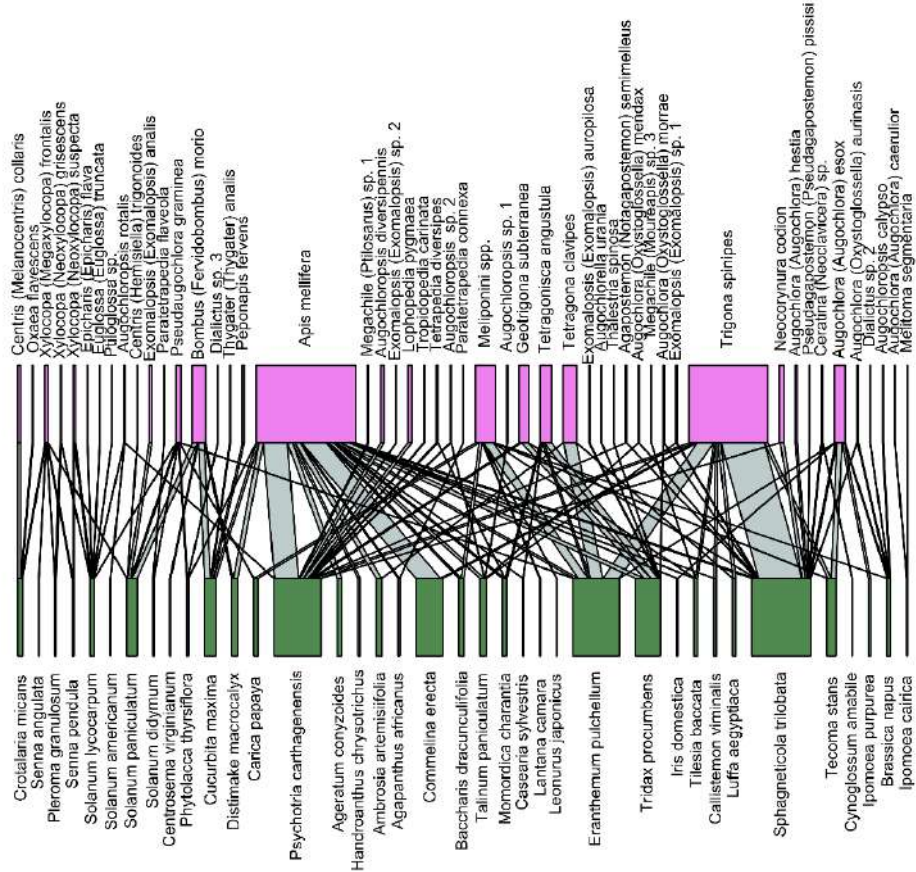


Fig.

S12 Bee-plant interaction networks in p. ursulina area with 72.14% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

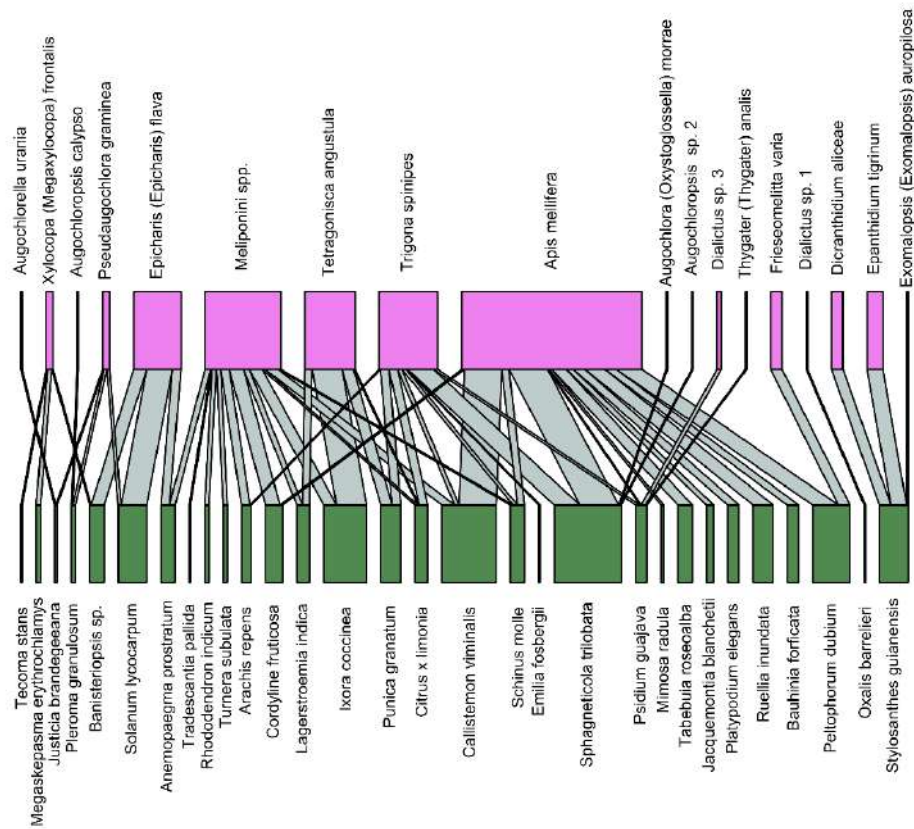


Fig.

S13 Bee-plant interaction networks in p. Renato Azeredo area with 83.80% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

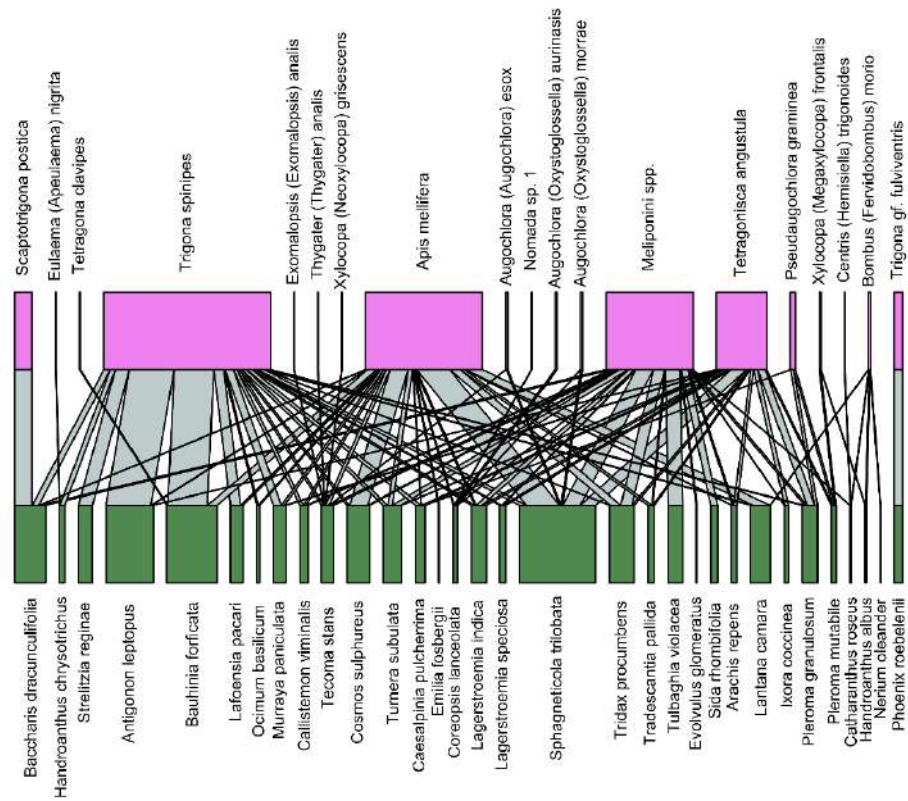


Fig.

S14 Bee-plant interaction networks in p. Ismael de Oliveira with 89.74% of impermeable surface in Belo Horizonte Minas Gerais, Brazil.

CHAPTER 3

Jardins para Polinizadores

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RESUMO

O livro "Jardins para Polinizadores" tem como objetivo conscientizar a população sobre a importância dos polinizadores para os ecossistemas e sobre as práticas sustentáveis que podem contribuir com a conservação desse grupo nas cidades. Esta proposta surgiu da ideia de combinar os resultados dos capítulos anteriores com informações sobre Conservação e Biologia da Polinização, a fim de dialogar com a comunidade sobre esses temas. O livro foi dividido em duas partes: a primeira discute a importância dos polinizadores e das áreas verdes urbanas na sua conservação, enquanto a segunda apresenta uma lista de plantas atrativas para diferentes grupos de polinizadores, acompanhada de curiosidades sobre sua biologia e uso. A seleção das plantas foi realizada considerando sua atratividade para diferentes espécies e em sua diversidade morfológica e especialização floral, a fim de manter uma comunidade de polinizadores mais diversa, incluindo espécies especialistas. A participação das comunidades em projetos de conservação da biodiversidade é fundamental. Quando as pessoas locais se envolvem e compartilham seu conhecimento, isso ajuda a garantir que as ações de proteção sejam amplamente aceitas e apoiadas. Esse engajamento comunitário aumenta a probabilidade de que as práticas de conservação adotadas perdurem a longo prazo. Dessa forma, esperamos que este livro, juntamente com outras iniciativas, contribua a longo prazo para o aumento da diversidade de polinizadores por meio de um paisagismo mais ecológico, possibilitando uma maior disponibilidade de recursos e tornando a matriz urbana mais permeável para diferentes espécies.

GENERAL CONCLUSIONS

The results found in the thesis suggest that different functional groups of pollinators may experience the effects of urbanization differently, given that the availability of resources from urban trees is limited for most groups of pollinators evaluated. Furthermore, urban environmental factors shaped the distribution of bee species based on their functional characteristics. We found that generalist bees were positively related to a higher proportion of impervious surfaces, suggesting a greater adaptation of these species to urban conditions. In contrast, specialist bees were negatively related, which indicates a simplification of the community with a predominance of ecologically similar species in more urban areas.

Plant species richness was a key factor in increasing the overall richness and abundance of bees and species with some specific traits such as larger body size and species that nesting on the ground. These results emphasize the need for adequate planning of urban landscapes to assist in the conservation of pollinators in tropical cities. We highlight the need for a greater and equitable spatial distribution of resources used by pollinators across landscapes and the importance of diversifying attractive plant species to support a more diverse pollinator community. Using accessible language our aim with the scientific dissemination book is to support these practices, sparking curiosity, engagement, and interest not only among the public but also among park managers and professionals in the seedling and seed production sectors. We hope that the selection of plant species based on their attractiveness, and their different floral morphologies and types of resources offered contribute to more pollinator-friendly landscaping practices. The diversification of resources through collaborative efforts among the population will be crucial for preserving a wider range of pollinator species and groups, including those less favored by current landscaping practices. Nonetheless, it is important to highlight that the attractive plants were selected based on the resources available in our study area. However, it is essential to explore other plants that are not usually used in urban landscaping, but that have the potential to support pollinators.

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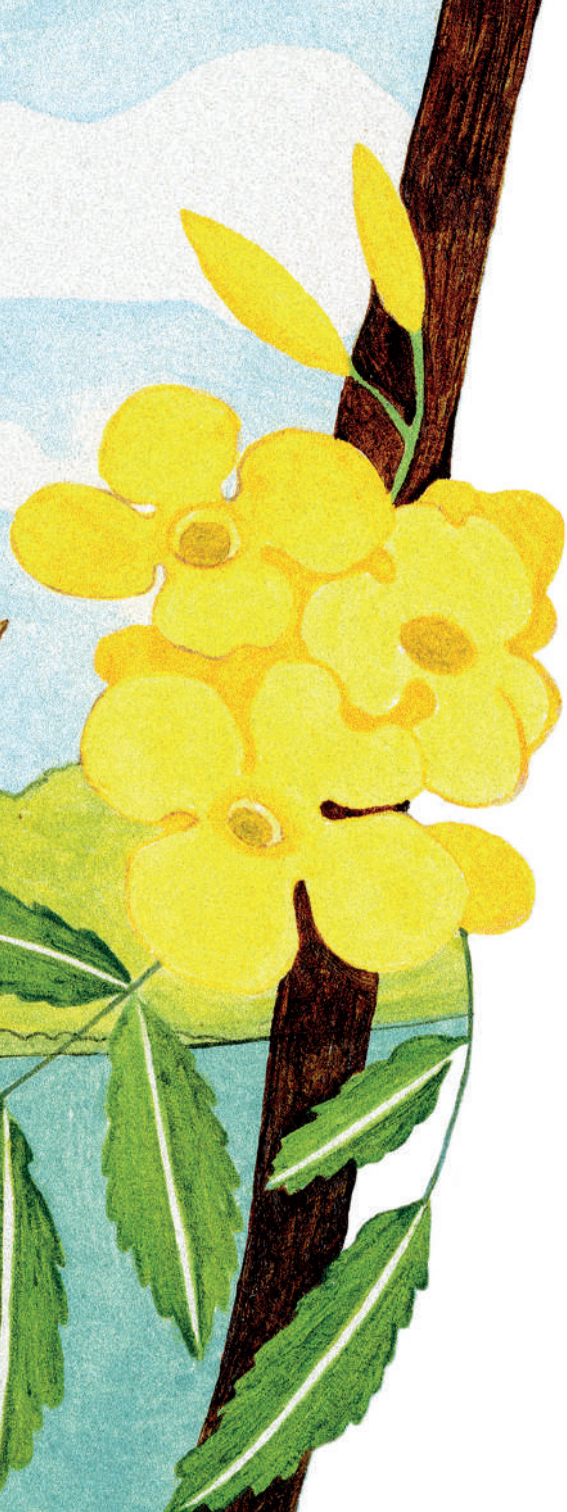
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JARDINS PARA POLINIZADORES







JARDINS PARA POLINIZADORES

Ingrid
N. Gomes

2024. Jardins para polinizadores.

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PARQUES E
ZOOBOTÂNICA





“

Dou respeito às coisas desimportantes
e aos seres desimportantes.
Prezo insetos mais que aviões.
Prezo a velocidade
das tartarugas mais que a dos mísseis.
Tenho em mim um atraso de nascença.
Eu fui aparelhado
para gostar de passarinhos.
Tenho abundância de ser feliz por isso.
Meu quintal é maior do que o mundo.”

Trecho de *O apanhador de desperdícios*
Manuel de Barros



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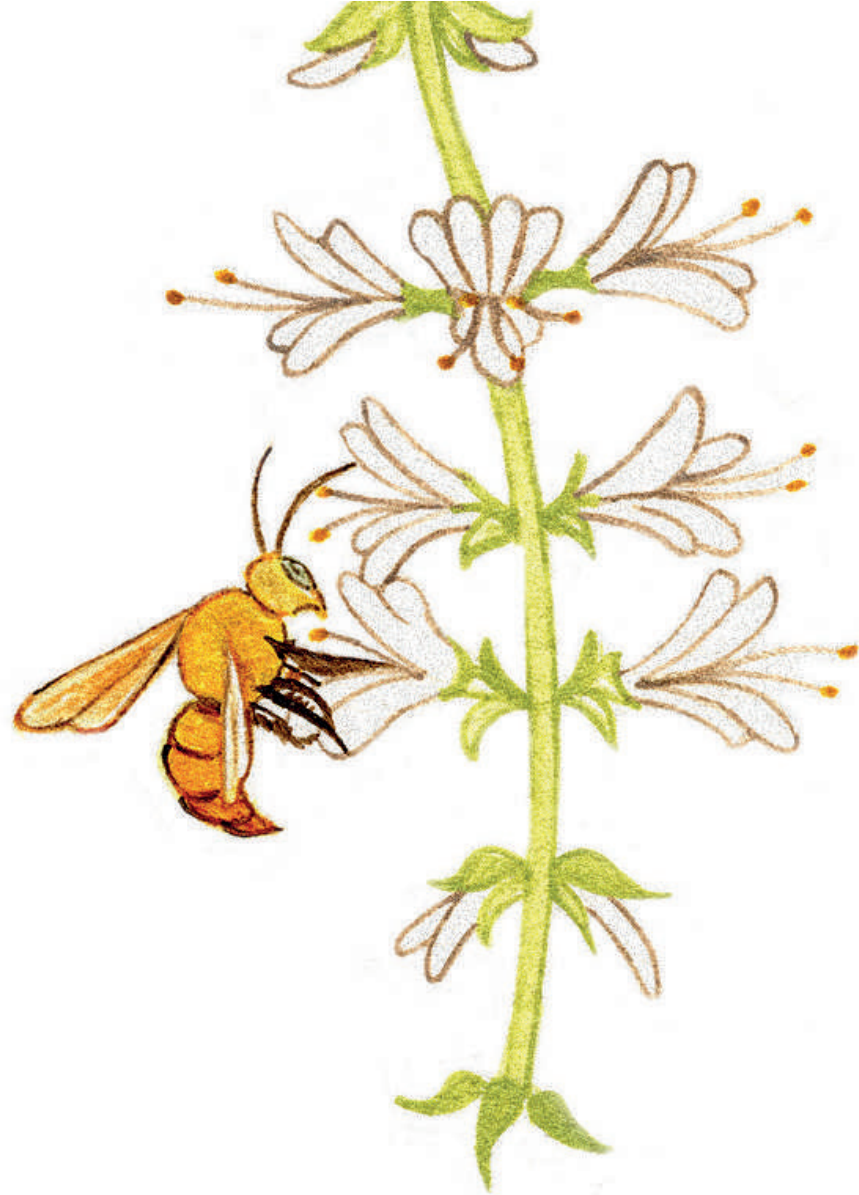
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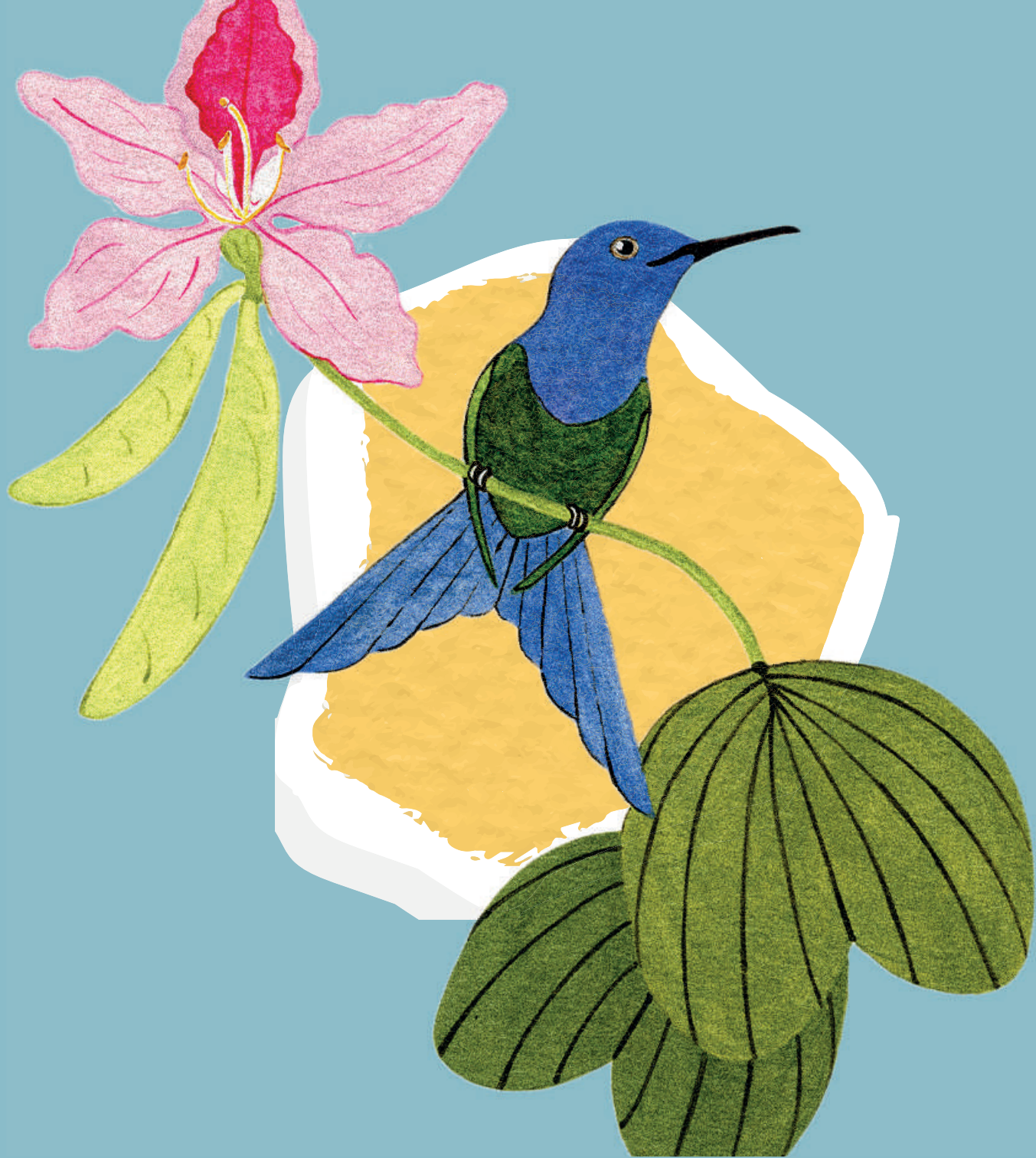
04

**Referências &
autoria das imagens**



Querido leitor, esse livro é dedicado a você que sempre gostou de jardins, quintais e flores. Já considerou que, além de sua beleza, muitas vidas podem existir nesses espaços? Muitas vezes essas vidas passam despercebidas diante de nossos olhos cansados pelas demandas do cotidiano. Aqui, você é convidado a experimentar uma nova perspectiva sobre os jardins, se apegar nos detalhes e vivenciar a felicidade de celebrar a vida em suas infinitas formas. Espero que este livro te ajude a redescobrir a diversidade que existe nos pequenos detalhes da natureza ao nosso redor. Boa leitura!





01 Prefácio

O livro 'Jardim para Polinizadores' nasceu da nossa intenção em integrar o conhecimento acadêmico em Conservação e Biologia da Polinização com o engajamento da comunidade, visando tornar as áreas verdes urbanas mais amigáveis para os polinizadores. Este livro foi idealizado no início do meu doutorado em 2019 no Centro de Síntese Ecológica e Conservação (CSEC) da Universidade Federal de Minas Gerais (UFMG) e faz parte de um dos capítulos da minha tese, sob a orientação dos Professores Pietro Kiyoshi Maruyama e João Carlos Pena. O desenvolvimento desse livro foi resultado de um trabalho em equipe e contou com a colaboração de mais dois amigos que atualmente também são doutorandos do CSEC-UFMG, Victor H. D. Silva, e Camila Bosenbecker com quem tive o prazer de fazer a coleta dos dados durante esse período.

Em linhas gerais, nossos objetivos principais com as coletas dos dados foram avaliar o impacto da urbanização em diferentes grupos de polinizadores e suas interações com as plantas, além de compreender quais espécies vegetais poderiam oferecer um suporte mais significativo para esses grupos nas áreas verdes urbanas. Para alcançarmos esses propósitos, coletamos dados sobre os polinizadores e realizamos diversas análises, que resultaram em artigos científicos, teses de doutorado e neste livro. Agradeço a nossa colaboração e parceria ao longo desses anos. Este livro é fruto do esforço conjunto de toda a equipe.

O livro está dividido em duas partes. Na primeira parte, discutimos a importância dos polinizadores, as ameaças que enfrentam e o papel fundamental das áreas verdes urbanas na sua conservação. Na segunda parte, fornecemos uma

lista das espécies mais atrativas para abelhas, borboletas, moscas, mariposas, vespas, beija-flores e morcegos, compiladas a partir dos levantamentos realizados ao longo de diferentes regiões das paisagens urbanas de Belo Horizonte. Esta lista é complementada com curiosidades sobre a biologia floral, bem como informações sobre o uso medicinal e culinário de algumas plantas, com o objetivo de tornar as visitas às áreas verdes, o plantio, e as observações dos leitores mais interessantes.

Esse livro foi idealizado para despertar curiosidades daqueles apaixonados por plantas e animais, bem como dos entusiastas que gostam de passar um tempo nos parques, nas praças ou cuidando de jardins e hortas. Além disso, tem como objetivo incentivar os setores produtivos e os gestores de parques a disponibilizarem espécies atrativas e diversificar o plantio de flores





nesses espaços. A lista de plantas é um convite para tornar o paisagismo urbano mais ecológico e mais amigável para os polinizadores, através de uma forma mais sustentável de urbanizar. É importante ressaltar que nossa lista de plantas se limita às espécies encontradas nos espaços verdes da cidade. Por isso, incentivamos fortemente e destacamos a importância de pesquisas voltadas para a seleção de plantas nativas que geralmente não são comercializadas e manejadas no paisagismo urbano para potencializar ainda mais a capacidade das áreas verdes em manter e conservar a biodiversidade local.

Espero que, ao final desta leitura, você possa apreciar as interações entre os polinizadores e as flores sob uma nova perspectiva.

Ingrid N. Gomes



02 Introdução

Quem são os
polinizadores
e por que
são tão
importantes?

Você já parou para pensar na importância dos polinizadores em nosso mundo? Ao longo deste livro, convidamos você a explorar o papel desses animais importantes para a natureza e sua relevância para a vida em nosso planeta. Os polinizadores desempenham um papel fundamental na reprodução das plantas e na manutenção da biodiversidade através da polinização. Entre os grupos principais de polinizadores estão as abelhas, os beija-flores, as borboletas, as mariposas, as moscas, as vespas e os morcegos.

Em ambientes naturais, os polinizadores garantem a reprodução de diversas plantas, através da mediação para fecundação das flores o que gera a produção de frutos e sementes, que também são fontes de recursos essenciais para a sobrevivência de vários organismos. Portanto, essas interações entre polinizadores e plantas são essenciais não apenas para a flora, mas também para a fauna que depende diretamente ou indiretamente das plantas para sua alimentação. Mas você sabia que muitas frutas, legumes e sementes consumidos por nós também dependem de polinizadores para a sua produção? Isso porque os polinizadores desempenham um papel crucial nos sistemas agrícolas, aumentando a produtividade e a qualidade de diversas culturas. Para você ter uma ideia, aproximadamente 75% das culturas de uso comum por humanos, dependem em algum grau da polinização por animais, incluindo açaí, acerola, abacate, caju, cacau, kiwi, manga, melão, maracujá e pêssgo, ufa! A lista é grande e não termina por aí. Além disso, várias culturas amplamente consumidas no nosso país, embora não sejam totalmente dependentes, se beneficiam da polinização animal, especialmente em termos de qualidade das sementes e produtividade. Exemplos incluem o café, o feijão e a soja. Imagina então como seria a nossa alimentação sem os polinizadores? Bem triste, não é mesmo? Portanto, os polinizadores são fundamentais para a conservação da vida na terra e para a garantia da segurança alimentar através dos seus serviços de polinização.

A foto abaixo ilustra como poderia ser o nosso café da manhã na ausência dos polinizadores. Certamente menos diverso, mais restrito e com uma redução significativa de nutrientes e sabores.

Café da manhã



Com polinizadores

Sem polinizadores

Por que as flores são importantes para os polinizadores e quais os recursos que estes coletam?

Considerando que os polinizadores desempenham um papel crucial na reprodução das flores quando as visitam, é natural pensarmos que estejam em busca de algo específico. Para atrair seus polinizadores, as flores disponibilizam recursos que são essenciais, como néctar, pólen, óleos e fragrâncias. Cada grupo de polinizadores tem suas preferências e necessidades específicas, o que influencia os recursos que coletam e as flores que visitam. As abelhas, no geral precisam de pólen e néctar, que são fontes de proteína e energia essenciais para sua sobrevivência e para a alimentação das crias. Além disso, algumas espécies de abelhas coletam óleo em flores, como por exemplo, nas plantas pertencentes a uma família botânica conhecida como Malpighiaceae. O óleo coletado pelas abelhas serve como alimento para as larvas em crescimento e para a impermeabilização dos ninhos. Algumas espécies de abelhas também coletam fragrâncias, especialmente nas orquídeas, e os machos dessas abelhas utilizam desse “perfume” para atrair as fêmeas. Os beija-flores, morcegos, borboletas, mariposas, moscas e vespas, por outro lado, quando interagem com as flores, vão em busca especialmente do néctar. Portanto, as flores desempenham um papel essencial na sobrevivência e desenvolvimento desses polinizadores.

Todas as interações entre os polinizadores e as flores resultam em polinização?

Então, vimos que grande parte das plantas com flores dependem de animais para reprodução, em um processo vital: a polinização. Além disso, os polinizadores interagem com as flores para coletar recursos necessários para sua sobrevivência. Mas será que todas essas interações resultam em polinização? Na verdade, não. Os desdobramentos dessas relações seriam suficientes para uma conversa em um outro momento mas, por agora, podemos dizer que para a polinização ocorrer de fato, é necessário que haja a transferência dos grãos de pólen produzidos pelas anteras (parte masculina da flor) para o estigma (parte feminina) das flores da mesma espécie. Para que isso ocorra, os polinizadores precisam tocar tanto a parte masculina quanto a parte feminina da flor ao coletar recursos. Mas, durante esse processo, podem ocorrer eventos inesperados, como abelhas transportando pólen de uma espécie para outra, o que não leva a reprodução e formação de frutos. Além disso, algumas flores têm formas que não permitem que alguns

animais que as visitam consigam realizar a polinização, como, por exemplo, as flores tubulares, que limitam a ação dos insetos de língua curta, exigindo polinizadores de línguas bastante longas como alguns grupos de abelhas em particular. Nestes casos, as abelhas podem acessar os recursos perfurando as flores na base, sem realizar a polinização, sendo chamadas de “pilhadoras” ou “ladras”. Já deu para perceber que essas interações são mais complexas do que imaginamos, não é mesmo? Portanto, na próxima vez que você observar uma flor, preste atenção nos detalhes dessas interações fascinantes.

Quais são os desafios e ameaças enfrentados pelos polinizadores?

Apesar da sua grande importância, os polinizadores enfrentam diversas ameaças decorrentes da atividade humana, que contribuem significativamente para o declínio desse grupo. Uma dessas ameaças são as mudanças climáticas e a perda de áreas naturais, impulsionadas principalmente pelos processos de expansão da atividade humana. Outro fator é o uso indiscriminado de pesticidas agrícolas, que não apenas causa mortalidade direta, mas também pode resultar em danos neurológicos e alterações comportamentais nos polinizadores. Por fim, a introdução de espécies exóticas invasoras representa outra ameaça, pois essas espécies podem competir pelos recursos de alimentação e nidifi-

cação com os polinizadores nativos, assim como transmitir diferentes patógenos. Como já podemos imaginar, após falarmos sobre a importância do grupo, a redução na diversidade de polinizadores terá impactos negativos para a biodiversidade e os seres humanos, levando a diversos problemas ambientais e econômicos.

Como as cidades podem ajudar os polinizadores?

O desenvolvimento urbano é uma das principais ameaças para os polinizadores, mas você sabia que dentro das cidades também existem soluções para amenizar esse problema? Uma delas é a presença e proximidade de espaços verdes como

parques, praças e áreas naturais. Além disso, outros ambientes menos prováveis de se pensar são os lotes vagos, os jardins e hortas residenciais e até mesmo as ruas, desde que esses espaços sejam repletos de flores atrativas e locais de nidificação para os polinizadores. Para tornar esses espaços mais atrativos, um fator muito importante é promover a diversidade de espécies com flores. Nas cidades, é comum encontrarmos uma predominância de poucas espécies no paisagismo, o que limita os recursos disponíveis para os polinizadores. Como resultado, a diversidade de polinizadores encontrados também é reduzida, sendo geralmente composta por espécies adaptadas aos ambientes urbanos. Mas, nós podemos mudar isso a partir da seleção de flores com diferentes morfologias, cores e tipos de recursos ofertados. Essa prática pode tornar as cidades mais amigáveis e atrativas para os dife-

rentes grupos de polinizadores, incluindo para espécies que têm preferências por certos tipos de flores, conhecidas como especialistas e que são mais ameaçadas pela urbanização. Então, vamos juntos tornar as paisagens urbanas mais sustentáveis e coloridas? A seguir, apresentamos uma seleção das plantas mais atrativas para os diferentes grupos de polinizadores, levando em consideração, principalmente, o número de espécies que interagiram com estas flores. Nessa seleção, incluímos o nome científico da espécie, seu nome popular, a família botânica à qual pertence, sua origem (se é nativa ou exótica no Brasil) e sua forma de vida, como árvore, erva, entre outros. Essas informações podem auxiliar na seleção das plantas que melhor se adaptam ao seu espaço. A nossa lista está baseada nos estudos conduzidos em Belo Horizonte (Minas Gerais), mas, acreditamos que muitas das plantas também poderiam ser utilizadas em outras localidades. Além disso, apresentamos curiosidades sobre





a biologia floral, sistemas de polinização, assim como informações sobre uso medicinal e culinário de algumas plantas, convidando você a explorar os conhecimentos relacionados à biologia enquanto observa as interações entre polinizadores e flores. Depois disso, escolha as suas flores favoritas pensando nos polinizadores que você gostaria de atrair, e mãos à obra jardineiras e jardineiros!





Plantas para os polinizadores

Plantas que atraem diferentes grupos

Embora algumas espécies de plantas tenham uma relação mais especializada com um grupo específico de polinizadores, muitas outras são generalistas atraindo diferentes grupos de polinizadores simultaneamente. Nesses sistemas, tanto as plantas quanto os polinizadores têm adaptações morfológicas, fisiológicas e comportamentais que lhes permitem interagir com uma variedade de parceiros. Por exemplo, as plantas podem produzir flores com néctar acessível a uma gama de polinizadores, enquanto os polinizadores podem ter comportamentos variados para acessar o néctar de diferentes tipos de flores. A seguir listamos algumas dessas plantinhas e os grupos funcionais de polinizadores atraídos por elas. Se você deseja um jardim repleto de biodiversidade, selecionar algumas dessas espécies para plantar pode ser uma ótima escolha!

ÍCONES



Abelhas



Beija-flores



Borboletas



Mariposas



Morcegos



Moscas



Vespas

Margaridão

Sphagneticola trilobata



Família: Asteraceae

Origem: nativa

Forma de vida: erva

CURIOSIDADES

Quantas flores você consegue contar na foto ao lado? Muitos de nós responderíamos apenas uma, mas na verdade, essa espécie apresenta várias flores bem pequenas localizadas no centro, conhecidas como flósculos. Cada flósculo contém todas as estruturas de uma flor completa. E aquilo que tendemos a pensar ser pétalas, na verdade são brácteas, folhas modificadas. As brácteas podem assumir uma variedade impressionante de formas, cores e tamanhos nas diferentes espécies de plantas encontradas na natureza, e suas funções principais incluem proteger as flores em desenvolvimento, atrair polinizadores e auxiliar na dispersão das sementes.

Goiabeira

Psidium guajava



Família: Myrtaceae
Origem: exótica
Forma de vida: árvore

Bem-me-quer

Leucanthemum vulgare



Família: Asteraceae
Origem: exótica
Forma de vida: erva

Embiruçu

Pseudobombax longiflorum



Família: Malvaceae
Origem: nativa
Forma de vida: árvore

Erva de touro

Tridax procumbens



Família: Asteraceae
Origem: exótica
Forma de vida: erva

Camarão azul

Eranthemum pulchellum



Família: Acanthaceae
Origem: exótica
Forma de vida: arbusto

Sanhaçaiba

Psychotria carthagenensis



Família: Rubiaceae
Origem: nativa
Forma de vida: arbusto

Lantana

Lantana camara



Família: Verbenaceae

Origem: exótica

Forma de vida: arbusto



Plantas atrativas para abelhas

As abelhas, pertencente à ordem dos Hymenoptera, são conhecidas como o principal grupo de polinizadores devido à sua eficiência na polinização de uma ampla variedade de espécies florais. Mas por que essas pequeninas desempenham um papel tão importante nesse processo? Podemos começar destacando que as abelhas dependem dos recursos florais em todas as fases de sua vida, desde o estágio larval até a fase adulta, quando estão prontas para assumir as múltiplas responsabilidades que as aguardam. Além de coletar néctar, como fazem outros polinizadores, as abelhas também buscam diferentes recursos florais, como pólen, óleo, resina, perfume e até mesmo pétalas, para sua alimentação, construção de ninhos ou atração de parceiros. Essa dependência estreita faz com que as abelhas se tornem visitantes frequentes das flores. Além disso, esses insetos possuem estruturas especializadas, como pelos altamente ramificados e pernas modificadas, que facilitam a fixação e o armazenamento eficiente dos grãos de pólen em seus corpos, contribuindo para estreitar a relação com as flores.

Também é importante destacar a grande diversidade desse grupo. Frequentemente, quando imaginamos abelhas, vem à mente a imagem da abelha listrada de preto e amarelo, com ferrão e produtora de mel. Entretanto, essa é apenas uma entre inúmeras espécies existentes. Além disso, nem todas as abelhas se encaixam nesse estereótipo, pelo contrário, nem todas produzem mel, nem todas possuem ferrão, e nem todas vivem em colônias. No Brasil, por exemplo, existem aproximadamente 1.700 espécies de abelhas nativas já conhecidas, que apresentam uma infinidade de tamanhos, formas, cores e comportamentos. Aposto que você ficou curioso né? Que tal pesquisar um pouco mais sobre essas pequenas notáveis?



Quaresmeira

Pleroma granulosum



Família: Melastomataceae
Origem: nativa
Forma de vida: arbusto

Agapanto

Agapanthus africanus



Família: Amaryllidaceae
Origem: exótica
Forma de vida: erva

Chocalho de cascavel

Crotalaria micans



Família: Fabaceae

Origem: nativa

Forma de vida: arbusto

CURIOSIDADES

Em muitas espécies de plantas, os polinizadores conseguem acessar facilmente o pólen, mas esse não é o caso de *Crotalaria micans*. Nesta espécie, o acesso dos visitantes florais ao pólen é limitado devido à configuração da flor. As pétalas se diferenciam em estandarte, duas alas e uma quilha, formada por duas pétalas, que restringe o acesso direto dos visitantes ao pólen. Durante a visita dos principais polinizadores, essas quilhas funcionam como mecanismos de alavanca. Ao pousar na flor em busca de néctar, o inseto acaba pressionando essas estruturas. Esse movimento aciona a liberação de pólen ou direciona o inseto para as partes reprodutivas da flor, contribuindo com a polinização dessa espécie. Ao lado você pode observar o comportamento de um de seus polinizadores, a abelha *Centris (melanocentris) collaris*.

Falso cardamomo

Alpinia zerumbet



Família: Zingiberaceae

Origem: exótica

Forma de vida: erva

Ipê mirim

Tecoma stans



Família: Bignoniaceae

Origem: exótica

Forma de vida: árvore

Pau cigarra

Senna multijuga



Família: Fabaceae

Origem: nativa

Forma de vida: árvore

CURIOSIDADES

Além das flores serem muito atrativas para diversas espécies de polinizadores, dentre eles, diversos grupos de abelhas, essa erva aromática também é conhecida por ser amplamente utilizada na culinária ao redor do mundo, sendo uma excelente combinação em receitas a base de tomate. Mas, você sabia que essa combinação vai além da cozinha? O manjericão e o tomate são conhecidos como plantas companheiras, uma vez que o plantio em conjunto dessas espécies permite uma interação biológica benéfica. A presença do manjericão atrai insetos através do aroma liberado pelas plantas que combatem algumas das principais pragas do tomateiro. Isso reduz a necessidade de inseticidas e promove um ambiente mais saudável para o crescimento do tomateiro, influenciando positivamente sua produtividade. Uma associação incrível não é mesmo?

Manjericão

Ocimum basilicum



Família: Lamiaceae

Origem: exótica

Forma de vida: erva

CURIOSIDADES

Aqui podemos observar uma condição interessante da flor conhecida como heteranteria, na qual diferentes tipos de estames (órgãos masculinos das flores) ocorrem em uma mesma flor. Nas flores desta espécie em particular, encontramos três conjuntos de estames: dois longos, um médio e quatro curtos. Esta peculiaridade desperta naturalmente nossa curiosidade sobre sua funcionalidade. Uma das explicações sugere que esses estames desempenham funções distintas para diminuir o conflito entre a demanda dos polinizadores por alimento (pólen) e a necessidade das plantas de reprodução. Os estames curtos, também conhecidos como estames de alimentação, são atrativos e facilmente acessíveis aos polinizadores, enquanto os estames longos, chamados de estames de polinização, são menos atrativos e posicionados próximos ao estigma (órgão feminino das flores) de forma a permitir a deposição dos grãos de pólen na região dorsal das abelhas, onde estas não conseguem realizar a limpeza com as pernas. Portanto, nesta espécie, a heteranteria garante o fornecimento de recursos ao polinizador sem comprometer a disponibilidade de grãos de pólen para o sucesso reprodutivo da planta.

Fedegoso

Senna pendula



Família: Fabaceae

Origem: nativa

Forma de vida: árvore

Urucum

Bixa orellana



Família: Bixaceae

Origem: nativa

Forma de vida: erva

CURIOSIDADES

O nome popular urucum vem da língua tupi-guarani e significa vermelho. As sementes dessa espécie têm sido historicamente utilizadas por comunidades indígenas como fonte natural de corante para diversas finalidades. Esses corantes são conhecidos como "urucum" ou "colorau" e também são amplamente utilizados na culinária tradicional, não apenas por sua capacidade de colorir alimentos, mas também por seus potenciais benefícios à saúde, como propriedades antioxidantes e anti-inflamatórias. Além disso, suas flores atraem diversas espécies de abelhas como a *Euglossa (Euglossa) truncata* Rebêlo & Moure, 1996 (família Apidae, tribo Euglossini - grupo das abelhas das orquídeas), na foto ao lado.

Manacá da serra

Pleroma mutabile



Família: Melastomataceae

Origem: nativa

Forma de vida: árvore

CURIOSIDADES

As flores dessa espécie produzem um belo padrão de cores brancas e rosas que adornam a copa das árvores durante o período de floração. No entanto, essa mudança vai além da estética, desempenhando um papel fundamental na interação com as abelhas, seus principais polinizadores. As flores de *P. mutabile* passam por uma transformação de cor durante seus quatro dias de floração, mudando de branco para rosa. Através da retenção das flores velhas na copa das árvores, as abelhas conseguem detectar os recursos a longas distâncias. Além disso, à medida que se aproximam das flores, as abelhas conseguem distinguir as flores brancas recém-abertas, que oferecem uma quantidade maior de pólen, em comparação com as flores rosas velhas, que já foram visitadas e possuem pouco ou nenhum recurso restante. Essa característica não apenas otimiza a busca por pólen, mas também aumenta a eficiência da polinização dessa espécie.

CURIOSIDADES

Essa espécie possui anteras (órgão masculino da flor) poricidas em formato de cone, limitando o acesso dos polinizadores ao pólen contido dentro dessa estrutura. Para que ocorra a liberação do pólen através dos pequenos poros terminais dessas anteras, as abelhas, seus principais polinizadores, precisam adotar um comportamento de vibração durante suas visitas. Esse comportamento se inicia quando as abelhas pousam sobre as anteras da flor, curvam-se em volta ou no ápice das anteras e se agarram fortemente. Em seguida, elas contraem os músculos torácicos, gerando vibrações que resultam na liberação do pólen, permitindo sua coleta. Testemunhar esse processo é uma experiência fascinante, por isso, na sua próxima visita a um jardim ou horta, busque por flores com anteras poricidas (por exemplo nas plantas de tomate, berinjela, jiló) e aprecie essa interessante interação.

Lobeira

Solanum lycocarpum



Família: Solanaceae

Origem: nativa

Forma de vida: árvore

Jurubeba

Solanum paniculatum



Família: Solanaceae

Origem: nativa

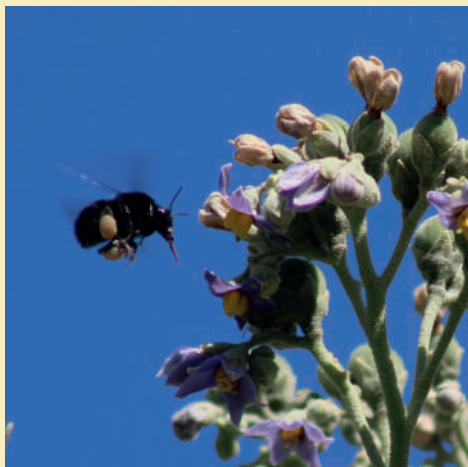
Forma de vida: arbusto

CURIOSIDADES

Essa espécie é popularmente conhecida como jurubeba e seus frutos fazem parte da tradição gastronômica de várias regiões do nosso país. Seu uso está muitas vezes associado a memórias afetivas e a pratos tradicionais transmitidos de geração em geração. Seus frutos são principalmente utilizados na preparação de conservas e produção de licores, mas também são valorizados por suas propriedades medicinais. As flores dessa espécie também apresentam anteras poricidas, assim como outras plantas utilizadas para o nosso consumo, como por exemplo, tomate, berinjela, jiló e pimentão. Então, para que ocorra a produção desses frutos, são necessárias visitas de abelhas que vibram. Algumas dessas abelhas são mostradas nas próximas páginas.

Espécies que vibram e suas interações

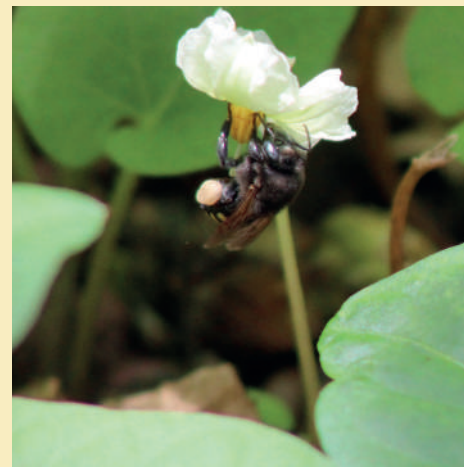




Bombus morio
em flor de jurubeba.



Pseudaugochlora graminea
em flor de jiló.



Melipona quadrifasciata
em flor de *Lyciantes asarifolia*



Plantas atrativas para abelhas especialistas e que coletam outros recursos

As abelhas especialistas, também conhecidas como oligoléticas, são abelhas que se especializaram na coleta de recursos de um número limitado de espécies de plantas. Ao contrário das abelhas generalistas, que visitam uma ampla variedade de flores de diversas espécies. A especialização das abelhas em determinadas plantas muitas vezes é essencial para a polinização de suas plantas parceiras, sendo geralmente os polinizadores mais eficazes para essas espécies. No entanto, a perda dessas plantas pode colocar em risco as populações de abelhas especialistas, tornando-as mais vulneráveis a mudanças ambientais e perda de habitat. As abelhas que coletam outros tipos de recursos como óleo e perfume de plantas específicas também podem estar mais ameaçadas devido a sua dependência desses recursos durante o seu ciclo de vida. Portanto, é essencial aumentar esses recursos nas áreas verdes urbanas para garantir a sobrevivência dessas abelhas. Algumas dessas espécies de plantas são descritas nas próximas páginas.

Ipomeia

Ipomoea cairica



Família: Convolvulaceae

Origem: nativa

Forma de vida: liana

Espécie que interage



Melitoma segmentaria

Abóbora menina

Cucurbita maxima



Família: Cucurbitaceae

Origem: exótica

Forma de vida: liana

Espécie que interage



Peponapis fervens

Rosedá amarelo

Galphimia brasiliensis

Espécie que interage



Centris (Centris) varia



Família: Malpighiaceae

Origem: nativa

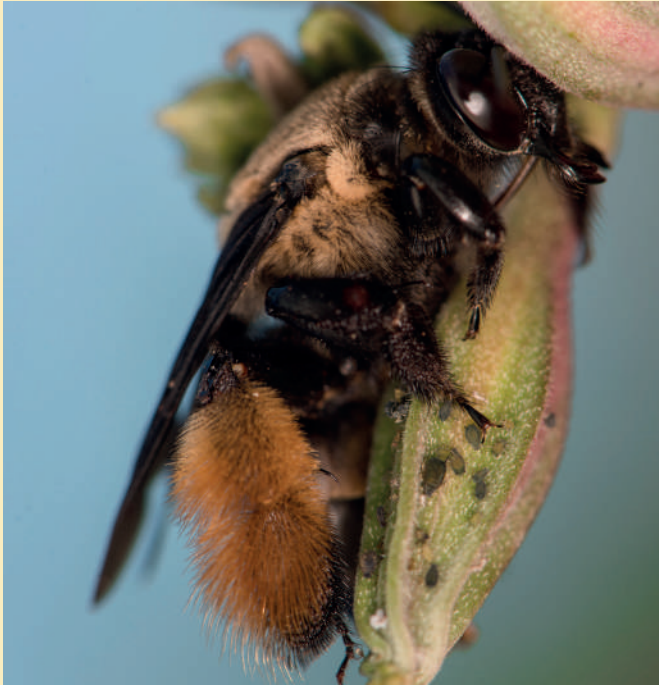
Forma de vida: erva

Recurso: óleo

Muricí anão do campo

Byrsonima intermedia

Espécie que interage



Epicharis (Epicharis) flava



Família: Malpighiaceae

Origem: nativa

Forma de vida: arbusto

Recurso: óleo

Aceroleira

Malpighia emarginata



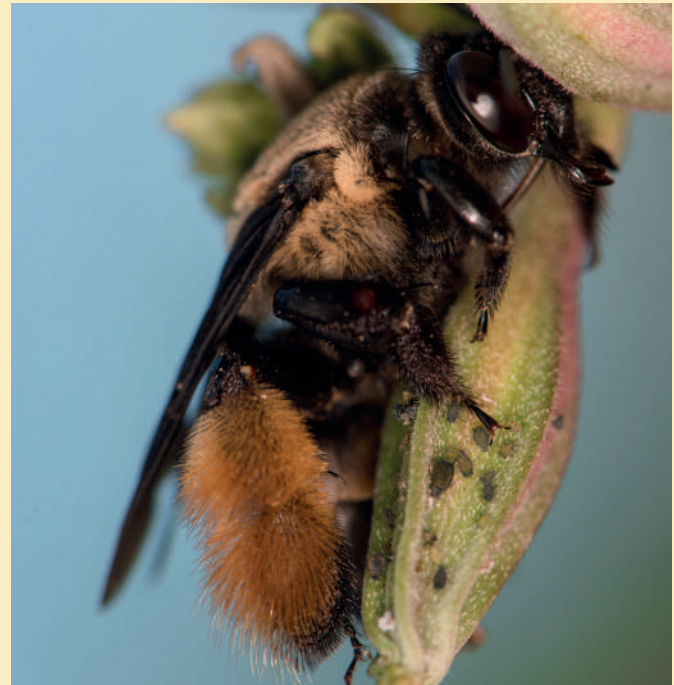
Família: Malpighiaceae

Origem: exótica

Forma de vida: árvore

Recurso: óleo

Espécie que interage



Epicharis (Epicharis) flava

Lírio da paz gigante

Spathiphyllum cannifolium



Família: Araceae

Origem: nativa

Forma de vida: erva

Recurso: fragrância/"perfume"

Espécie que interage



Euglossa truncata



Plantas atrativas para borboletas

As borboletas fazem parte da ordem de insetos conhecida como Lepidoptera, e são visitantes frequentes em nossos jardins, sempre encantando com suas belas cores e com o característico bater de suas asas. As borboletas são conhecidas por seus hábitos diurnos, e muitas espécies desse grupo dependem do néctar fornecido pelas flores para se alimentar durante sua fase adulta, desempenhando assim um papel crucial na polinização das flores que se abrem durante o dia. Durante suas visitas às flores, as borboletas usam sua espirotromba, um aparelho bucal semelhante a um canudo retrátil, para coletar o néctar. Esse órgão é particularmente adaptado para alcançar flores com estruturas em tubo, acessíveis apenas para espécies com aparelho bucal especializado. Da próxima vez que estiver no jardim, reserve um momento para observar um desses insetos desenrolando suas espirotrombas e explorando as flores com uma destreza incrível! Vale destacar também que os insetos da ordem Lepidoptera, como as borboletas e mariposas (sobre as quais falaremos em seguida), passam por uma fase de lagarta em seu ciclo de vida, durante a qual dependem de plantas hospedeiras para se alimentar. Portanto, na próxima vez que você encontrar uma lagartinha em seu jardim, talvez seja gentil deixá-la onde está, permitindo que um dia ela se transforme em uma linda adulta voadora.

Mentrasto

Ageratum conyzoides



Família: Asteraceae

Origem: nativa

Forma de vida: erva

Coromandel

Asystasia gangetica



Família: Acanthaceae
Origem: exótica
Forma de vida: erva

Lantana

Lantana montevidensis



Família: Verbenaceae
Origem: nativa
Forma de vida: subarbusto

Violeteira

Duranta erecta



Família: Verbenaceae
Origem: exótica
Forma de vida: arbusto

Margaridinha de fruta

Tilesia baccata



Família: Asteraceae
Origem: exótica
Forma de vida: arbusto



Plantas atrativas para mariposas

Apesar de serem “parentes” das borboletas, as mariposas têm hábitos normalmente noturnos. Entre elas, destacam-se os esfingídeos, conhecidos pela sua espirotromba muito longa, especialmente adaptada para alcançar o néctar de flores tubulares e que se abrem à noite. Além disso, as flores polinizadas por mariposas compartilham outras características como, coloração pálida e néctar rico em açúcar para suprir as necessidades energéticas desses visitantes que podem voar por quilômetros de distância em busca de flores. Outro fator importante na seleção de flores por esse grupo é a liberação de voláteis florais, que são aromas específicos que ajudam na atração das mariposas em noites escuras. Quando você estiver passeando à noite em uma praça, fique atento ao perfume adocicado que permeia o ar. Esse aroma pode ser um sinal da presença de flores polinizadas por mariposas. Um exemplo interessante é a planta conhecida como dama da noite (*Cestrum nocturnum*), cuja fragrância noturna é uma verdadeira maravilha para os que passeiam nas ruas de muitas cidades.

CURIOSIDADES

Essa espécie tem características florais específicas como a abertura floral noturna, coloração branca, forma mais estreita, e liberação de perfume adocicado. Todas essas características as tornam atrativas para espécies de mariposas com hábitos noturnos. A abertura floral inicia-se por volta das 18h da tarde e se encerra por volta das 6h da manhã. Durante a interação com essa espécie, as mariposas pairam em frente à flor introduzindo sua probóscide (aparelho bucal) muito longa no interior do tubo da flor para obter néctar, encostando, assim, nas estruturas reprodutivas e aumentando a probabilidade de polinização.

Boa noite

Ipomoea alba



Família: Convolvulaceae

Origem: nativa

Forma de vida: liana/trepadeira

Trombeta de anjo

Brugmansia suaveolens



Família: Solanaceae
Origem: exótica
Forma de vida: arbusto

Dama da noite

Cestrum nocturnum



Família: Solanaceae
Origem: exótica
Forma de vida: arbusto



Plantas atrativas para moscas

O papel das moscas na polinização é muitas vezes negligenciado. Entretanto esse grupo que pertence à ordem Diptera, representa um dos grupos mais importantes de insetos polinizadores, contribuindo para a reprodução de muitas plantas, incluindo culturas agrícolas como abacate, manga e kiwi. Uma das características que diferencia as moscas de outros insetos é ter apenas um par de asas na fase adulta, devido à redução das asas posteriores em estruturas em forma de halteres. Essas estruturas promovem agilidade e habilidade durante o voo e o pouso, permitindo movimentos em várias direções, além da capacidade de pairar, que é incomum entre os insetos. Similarmente às abelhas, as moscas podem se alimentar de pólen e néctar. No entanto, devido à ausência de cuidado parental, as moscas buscam esses recursos exclusivamente para seu próprio sustento. Algumas espécies de plantas adotam estratégias peculiares para atrair as mosquinhas, emitindo odores semelhantes aos de matéria orgânica em decomposição, mesmo que as flores sejam lindas. Essa tática tem tudo a ver com a expressão “não é flor que se cheire” não é mesmo?

Vassourinha de botão

Borreria verticillata



Família: Rubiaceae

Origem: nativa

Forma de vida: subarbusto

Alecrim do campo

Baccharis dracunculifolia



Família: Asteraceae

Origem: nativa

Forma de vida: arbusto

CURIOSIDADES

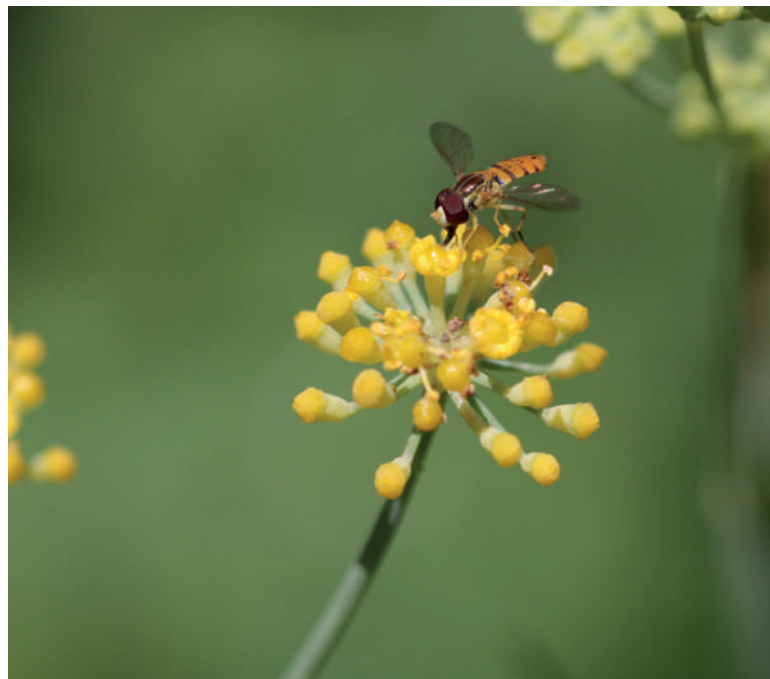
Alecrim do campo é o nome pelo qual é conhecida em muitas regiões a espécie *Baccharis dracunculifolia*. Um fato interessante sobre a biologia floral é que essa espécie apresenta indivíduos que produzem exclusivamente flores masculinas e outros que produzem apenas flores femininas, além de emitirem um leve aroma de mel durante sua florada. Além disso, é uma planta de grande importância ecológica, desempenhando um papel crucial na biorremediação de solos contaminados com metais pesados e na restauração ambiental. Além dessas contribuições, a espécie possui diversas propriedades farmacológicas, incluindo atividades antimicrobiana, anti-inflamatória e de controle da hipertensão arterial, apresentando também ação repelente.

CURIOSIDADES

O endro é uma erva aromática que apresenta uma inflorescência conhecida na botânica como umbela, onde todas as flores surgem do mesmo ponto no caule, formando uma conformação que lembra a copa de uma árvore ou um guarda-chuva. Essa espécie é amplamente utilizada na culinária devido ao seu sabor fresco e é conhecida por suas propriedades medicinais, sendo utilizada para aliviar problemas digestivos e como expectorante para tosses leves. Além disso, atua como repelente natural de pragas e atrai diversos insetos polinizadores, tornando-se uma excelente planta para ter pertinho de casa, não é mesmo?

Endro

Anethum graveolens



Família: Apiaceae

Origem: exótica

Forma de vida: erva



Plantas atrativas para vespas

As vespas, assim como as abelhas, fazem parte da ordem Hymenoptera, embora sejam consideradas menos eficientes como polinizadoras quando comparadas com suas parentes próximas. Uma das explicações para essa diferença está na presença de pelinhos no corpo. Vespas tendem a possuir menos pelos em comparação com as abelhas, refletindo em uma quantidade menor de pólen aderido e transportado de flor em flor. Na fase larval, a maioria das espécies de vespas é carnívora, alimentando-se de outros artrópodes ou parasitando insetos. Quando adultas, as vespas frequentemente visitam flores em busca de néctar para se alimentarem ou, no caso das espécies sociais, para manterem a colônia. Durante esse processo, as vespas transportam pólen em seus corpos, contribuindo também para a polinização das plantas. Elas também podem ser excelentes para controlar algumas pragas no seu jardim, sendo importantes inimigas naturais.

Pata de vaca

Bauhinia forficata



Família: Fabaceae

Origem: nativa

Forma de vida: árvore



Plantas atrativas para beija-flores

Nos jardins e áreas verdes urbanas, é comum avistarmos os beija-flores, membros da família Trochilidae. Essas aves compartilham algumas características específicas, como pequeno porte, bico alongado e asas longas e estreitas. Essas características das asas associadas a outros fatores como uma alta capacidade pulmonar e um sistema circulatório eficiente permitem que os beija-flores sejam capazes de voar em altas velocidades e realizar manobras aéreas incríveis, como por exemplo, pairar no ar enquanto se alimentam. Isso resulta em um metabolismo muito acelerado, tornando-os dependentes do néctar das flores, uma fonte alimentar altamente energética. Este estilo de vida agitado e especializado torna os beija-flores essenciais para a polinização de muitas espécies de plantas. Essas plantas normalmente possuem flores grandes e com uma coloração chamativa aos olhos humanos, com uma alta produção de néctar, geralmente sem odor e que se abrem durante o período diurno. Da próxima vez que avistar um beija-flor, não deixe de observar os movimentos desses apressadinhos nas flores e as lindas cores brilhantes de suas plumagens.

CURIOSIDADES

Muitas espécies de plantas polinizadas por beija-flores exibem uma adaptação morfológica notável, onde o tamanho e a forma de seus bicos correspondem às características das flores que visitam. Um exemplo são as flores de *Russelia equisetiformis*, que tem um formato tubular alongado. Além disso, como muitas flores atrativas aos beija-flores, essas flores apresentam a coloração vermelha. Essa faixa de cor é menos visível para as abelhas, que são muito mais numerosas em campo, o que implica mais néctar disponível para os beija-flores, que não precisam dividir esse recurso com as “abelhudas”.

Planta coral ou Russelia

Russelia equisetiformis



Família: Plantaginaceae

Origem: exótica

Forma de vida: herbácea

Escova de garrafa

Callistemon viminalis



Família: Myrtaceae
Origem: exótica
Forma de vida: árvore

Bico de papagaio

Heliconia rostrata



Família: Heliconiaceae
Origem: nativa
Forma de vida: erva

Chapéu chinês

Holmskioldia sanguinea



Família: Verbenaceae
Origem: exótica
Forma de vida: arbusto

Camarão vermelho

Justicia brandegeana



Família: Acanthaceae
Origem: exótica
Forma de vida: herbácea

Sanquésia

Sanchezia oblonga



Família: Acanthaceae
Origem: exótica
Forma de vida: arbusto

Justicia vermelha

Megaskepasma erythrochlamys



Família: Acanthaceae
Origem: exótica
Forma de vida: arbusto



Plantas atrativas para morcegos

Os morcegos, pertencentes à ordem Chiroptera, nem sempre são lembrados como polinizadores importantes e de fato a maioria das espécies se alimentam predominantemente de insetos. No entanto, duas das dezoito famílias que compõem essa ordem são especializadas na alimentação de néctar, desempenhando um papel essencial como polinizadores de muitas espécies de plantas. Esses morcegos nectarívoros compartilham algumas características morfológicas, como rostos alongados, dentição reduzida em tamanho e número de dentes e uma língua longa com cerdas que é usada para auxiliar na coleta eficiente de néctar durante as visitas às flores. As características florais associadas à polinização por morcegos incluem uma coloração mais discreta como, por exemplo, branca ou verde, frequentemente acompanhada pela abertura floral noturna, coincidindo com o período de atividade dos morcegos. Além disso, essas flores produzem uma grande quantidade de néctar que atende às demandas energéticas dos morcegos. Esse grupo é muito importante na conservação de diversas espécies de plantas, uma vez que seu tamanho e alcance de voo permitem que eles depositem grandes quantidades de pólen nos estigmas das plantas e sejam eficientes dispersores de pólen a longas distâncias, além de sementes. Portanto é importante mudar a percepção negativa comumente relacionada aos morceguinhos que desempenham um papel importante na conservação dos nossos ecossistemas.

Cuieira

Crescentia cujete



Família: Bignoniaceae

Origem: exótica

Forma de vida: árvore

Pequizeiro

Caryocar brasiliense



Família: Caryocaraceae

Origem: nativa

Forma de vida: árvore

CURIOSIDADES

O pequizeiro destaca-se pelo seu potencial econômico, pois seus frutos são amplamente empregados na alimentação humana, sendo utilizados na elaboração de pratos típicos, condimentos, óleos e sorvetes. A flor dessa espécie, possui morfologia em forma de pincel, corola aberta, pétalas reduzidas e estruturas reprodutivas externadas maiores que as pétalas oferecendo, portanto, livre acesso dos polinizadores aos recursos florais. Apesar dos morcegos serem considerados os principais polinizadores do pequizeiro, essas características florais fazem com que essa espécie receba também visitas de outros grupos funcionais, como aves, mariposas e abelhas, que podem atuar como polinizadores secundários dessa espécie.



04 Referências

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