UNIVERSIDADE FEDERAL DE LAVRAS

KARLA PALMIERI TAVARES BRANCHER

DETERMINING THE EFFECT OF URBANIZATION ON BEES AND ASSESSING LAND-SHARING AND LAND-SPARING AS CONSERVATION STRATEGIES

LAVRAS-MG
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Prof. Dr. Rafael Dudeque Zenni
Orientador

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DETERMINAÇÃO DO EFEITO DA URBANIZAÇÃO NAS ABELHAS E AVALIAÇÃO DE COMPARTILHAMENTO E POUPANÇA DE TERRAS COMO ESTRATÉGIAS DE CONSERVAÇÃO

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À minha filha Catarina
Dedico

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RESUMO

A urbanização é uma das mais intensas formas de mudança na paisagem, e provavelmente se tornará mais acentuada nos próximos anos, provocando mais danos à biodiversidade. Estudos tem demonstrado que as abelhas são influenciadas pela urbanização, devido à redução da vegetação natural e à alta proporção de áreas impermeáveis que substituem os recursos florais e de nidificação necessários para a sua sobrevivência. Entretanto esse conhecimento ainda é restrito, já que a maioria dos estudos foi realizada em grandes metrópoles, onde a urbanização é notoriamente mais intensa. Além disso, a região tropical está sub-representada. Diante desse cenário, o objetivo principal deste estudo foi avaliar os efeitos da urbanização na comunidade de abelhas em cidades de médio porte no Brasil. O presente estudo foi dividido em três capítulos. No primeiro capítulo, avaliamos a riqueza e abundância de abelhas, seus respectivos grupos funcionais, e a composição da comunidade ao longo de um gradiente de urbanização e em relação à comunidade de plantas. A riqueza total de abelhas diminuiu com o aumento da cobertura impermeável. A heterogeneidade da paisagem teve um efeito positivo sobre a riqueza total, de abelhas que nidificam acima do solo e de abelhas generalistas. A abundância das abelhas solitárias e que nidificam abaixo do solo foram positivamente influenciadas pelo aumento na cobertura de gramínea. O número total de plantas nativas e exóticas coletadas influenciou positivamente a abundância total de abelhas, bem como as abundâncias de abelhas altamente eussociais, que nidificam acima e abaixo do solo e generalistas. O número de plantas nativas influenciou positivamente a riqueza total e a abundância de abelhas especialistas. No segundo capítulo da tese avaliamos três formas de desenvolvimento urbano, economia de terra (“land-sparing”), compartilhamento de terra (“land-sharing”) e área totalmente ocupada (“land fully ocupied”) e seus efeitos sobre a comunidade de abelhas. Demonstramos um benefício do modelo “land-sharing”, principalmente em relação ao modelo “land fully ocupied”, tendo apresentado maior riqueza de espécies, riqueza de gêneros e número de espécies únicas. No terceiro e último capítulo da tese, avaliamos como a estrutura das redes de interação muda ao longo de um gradiente de urbanização. Avaliamos também a importância das espécies de plantas e famílias botânicas, para identificar quais delas atraem mais abelhas nos ambientes urbanos. Encontramos um aumento na conectância da rede e na uniformidade de interação com o aumento da urbanização, provavelmente devido à perda de espécies de abelhas. Algumas espécies de plantas e famílias botânicas atraíram mais espécies de abelhas, dentre elas Asteraceae, Fabaceae, Bignoniaceae, Convolvulaceae, Malvaceae, Melastomataceae, and Lythraceae. Concluímos que mesmo em cidades menores e com menores intensidades de urbanização, a comunidade de abelhas foi influenciada pela urbanização em escala local e de paisagem. Além disso, apresentamos um dos poucos estudos que avaliaram efeitos dos modelos de desenvolvimento urbano sobre a biodiversidade. Nosso estudo trouxe resultados importantes para o entendimento do efeito da urbanização na comunidade de abelhas em cidades de médio porte, contribuindo com o conhecimento sobre a proteção da biodiversidade nativa frente ao rápido crescimento urbano.

Palavras-chave: Abelhas nativas. Biodiversidade urbana. Polinizadores urbanos. Redes mutualísticas.

ABSTRACT

Urbanization is one of the most intense forms of landscape change and is likely to become more pronounced in the coming years, causing further damage to biodiversity. Studies have shown that bees are influenced by urbanization, due to the reduction of natural vegetation and the high proportion of impervious areas that replace the floral and nesting resources necessary for their survival. However, this knowledge is still limited, since most studies were carried out in large metropolises, where urbanization is notoriously more intense. In addition, the tropical region is underrepresented. Therefore, the main objective of this study was to evaluate the effects of urbanization on the bee community in medium-sized cities in Brazil. The present study was divided into three chapters. In the first chapter, we evaluated bee richness and abundance, their respective functional groups, and community composition along an urbanization gradient and concerning the plant community. Total bee richness decreased with increasing impervious cover and increased with landscape heterogeneity, which also had a positive effect on the richness of aboveground-nesting bees and generalist bees. The abundance of solitary bees and belowground-nesting bees were positively influenced by the increase in grass cover. The total number of native and exotic plants collected positively influenced the total abundance of bees, as well as the abundances of highly eusocial bees, which nest above- and belowground, and generalists. The number of native plants positively influenced the total richness and abundance of specialist bees. In the second chapter, we evaluated the effects of three forms of urban development on the bee community: land-sparing, land-sharing, and land fully occupied. We demonstrated a benefit of the land-sharing model, mainly concerning the land fully occupied model, as it presented greater species richness, genera richness, and a number of unique species. In the third and final chapter, we assess how the structure of interaction networks changes along an urbanization gradient. We also evaluated the importance of plant species and botanical families, to identify which ones attract more bees in urban environments. We found an increase in network connectance and interaction evenness with increasing urbanization, probably due to the loss of bee species. Some plant species and botanical families attracted more bee species, among them Asteraceae, Fabaceae, Bignoniaceae, Convolvulaceae, Malvaceae, Melastomataceae, and Lythraceae. We conclude that even in smaller cities with lower urbanization intensities, the bee communities were influenced by urbanization at the local and landscape scales. In addition, we present one of the few studies that have evaluated the effects of urban development models on biodiversity. Our study provides important results for understanding the effect of urbanization on bee communities in medium-sized cities, contributing to knowledge about the protection of native biodiversity in the face of rapid urban growth.

Keywords: Native bees. Urban biodiversity. Urban pollinators. Mutualistic networks.

SUMÁRIO

PRIMEIRA PARTE

1 INTRODUÇÃO GERAL

Atualmente, a urbanização é o tipo de uso da terra que mais cresce globalmente, com magnitude sem precedentes. Em 1950, a proporção global da população urbana era de 29%, e as projeções para 2050 preveem um aumento para 70%, o que significa um adicional de 2,6 bilhões de pessoas (UN, 2011; SETO, PARNELL & ELMQVIST, 2013). As projeções também mostram que a urbanização está ocorrendo mais rapidamente e em maior extensão nas cidades dos países em desenvolvimento (ANGEL et al., 2005). Essas regiões abrigam quase 90% das áreas protegidas passíveis de serem impactadas pela urbanização (MCDONALD, KAREIVA & FORMAN, 2008). Por exemplo, a maior expansão urbana em “hotspots” de biodiversidade está prevista para ocorrer na América do Sul (GÜNERALP & SETO, 2013). Portanto, à medida que as áreas urbanas aumentam, cresce o interesse em entender como as cidades devem se expandir e minimizar seus impactos ecológicos.

A relação entre urbanização e biodiversidade é controversa. Apesar de algumas áreas urbanas abrigarem alta riqueza de espécies, outras podem estar relacionadas à perda de biodiversidade (MCKINNEY, 2006). As abelhas, por exemplo, são um grupo taxonômico significativamente afetado pela urbanização, e os impactos na riqueza de espécies e na estrutura da comunidade têm sido amplamente investigados (WENZEL et al., 2020). O processo de urbanização está associado à redução da vegetação natural, à poluição do ar e ao estabelecimento de uma alta proporção de áreas impermeáveis, como concreto e asfalto. Estacionamentos, estradas e setores industriais substituem os recursos florais e de nidificação necessários para a sobrevivência das abelhas (CANE et al., 2006; MCKINNEY, 2008; CARIVEAU & WINFREE, 2015). Dentre os efeitos provocados pela urbanização sobre as abelhas estão diminuição na riqueza e abundância, mudanças na composição da comunidade e nas redes de polinização (CANE et al., 2006; GESLIN et al., 2013; FORTEL et al., 2014; BALDOCK et al., 2015; GESLIN et al., 2016; MCKINNEY, 2006; GRAF et al., 2022).

As características funcionais das abelhas, como comportamento social, comportamento de nidificação e especialização trófica, podem determinar suas respostas às modificações das paisagens urbanas (BANASZAK-CIBICKA & ŻMIHORSKI, 2012; GESLIN et al., 2016; GRAF et al., 2022; BANASZAK-CIBICKA & DYLEWSKI, 2021). Em relação à socialidade, a riqueza e abundância das espécies de abelhas sociais aumentaram em áreas urbanas, devido à maior flexibilidade comportamental e ecológica (BANASZAK-CIBICKA & ZMIHORSKI, 2012; HINNERS et al., 2012; BANASZAK-CIBICKA et al., 2018). Em relação ao comportamento de nidificação, espécies que nidificam no solo (cerca de

75% de todas as espécies de abelhas) são frequentemente influenciadas negativamente pela urbanização, enquanto aquelas que nidificam em cavidades costumam ser mais abundantes nas cidades, pois as paisagens urbanas oferecem uma grande variedade de recursos de nidificação, como prédios, cercas e muros (CANE et al., 2006; BANASZAK-CIBICKA & ZMIHORSKI, 2012; HINNERS et al., 2012). Quanto à especialização trófica, espécies com dietas restritas e estratégias de forrageamento especializadas (espécies oligoléticas) podem ser afetadas negativamente pela introdução de plantas exóticas, enquanto as espécies generalistas (poliléticas) podem ser beneficiadas (BANASZAK-CIBICKA & ZMIHORSKI, 2012; GESLIN et al., 2013). Dessa forma, a urbanização e a vegetação composta principalmente por plantas exóticas em parques e jardins podem diminuir a riqueza e abundância de abelhas nas cidades (MORÓN et al., 2009; HENRÍQUEZ-PISKULICH et al., 2018).

Os efeitos negativos da urbanização nas comunidades de polinizadores também podem impactar as redes de interação planta-polinizador (HENNIG & GHAZOUL, 2011). As interações planta-polinizador são essenciais para o funcionamento dos ecossistemas terrestres, uma vez que a maioria das plantas depende de vetores bióticos para polinização e uma grande diversidade de animais depende de recursos florais (OLLERTON et al., 2011). Consequentemente, a perda das principais interações bióticas pode ter efeitos generalizados, acelerando a extinção local de espécies e diminuindo as funções do ecossistema que prestam serviços aos seres humanos (TYLIANAKIS et al., 2010; VALIENTE-BANUET et al., 2014). Estudos mostraram que a urbanização mudou a dinâmica das interações entre plantas e polinizadores (SILVA et al., 2021, FISOGNI et al., 2022). O número e diversidade de interações, a frequência de visitas de polinizadores especialistas e abelhas solitárias, bem como o sucesso reprodutivo de espécies vegetais foram afetados negativamente pela urbanização (TONIETTO et al., 2011; VERBOVEN et al., 2012; GESLIN et al., 2013).

Apesar de todos os efeitos negativos citados, muitas espécies de abelhas persistem em áreas urbanas (WENZEL et al., 2020). Estudos recentes demonstraram que as áreas urbanas apresentam capacidades inesperadas para o fornecimento de serviços ecossistêmicos e apoio à biodiversidade (UNEP – WCMC, 2007; MCKINNEY, 2008; EDMONDSON et al., 2014). Dessa forma, é necessário um entendimento mais completo sobre como a cidade pode ser planejada para esse fim. Uma das abordagens que tem sido discutida a respeito do planejamento urbano para a conservação da biodiversidade é o compartilhamento da terra (*land-sharing*) versus economia de terra (*land-sparing*). No primeiro caso, a paisagem é gerida com menor intensidade para permitir a coexistência de vegetação e ambiente urbano num mosaico, enquanto no segundo, a preservação da terra permite a retenção de grandes, embora isolados, fragmentos de hábitat em toda a paisagem que contribuem para os objetivos de conservação (LIN & FULLER, 2013). Nesse contexto, uma das lacunas de conhecimento diz respeito a quais configurações da paisagem urbana são úteis no apoio à diversidade de abelhas nativas e ao serviço ecossistêmico de polinização, especialmente em regiões tropicais.

Embora nossa compreensão do impacto ecológico da urbanização tenha melhorado nas últimas décadas, ela não acompanhou o crescimento rápido e generalizado das cidades (LIN & FULLER, 2013). O conhecimento sobre o impacto da urbanização nas abelhas ainda é restrito, e grande parte dos estudos foi realizada em grandes metrópoles, onde a urbanização é notoriamente mais intensa, com maiores densidades demográficas e construção vertical (WENZEL et al., 2020). Até agora, pouca atenção tem sido dada às cidades com menos de 500 mil habitantes. Porém, cidades pequenas e médias correspondem a mais de 99% dos 5.570 municípios brasileiros, por exemplo, e correspondem às cidades nas quais vivem grande parte da população europeia e dos EUA (IBGE, 2017; GIFFINGER et al., 2007; US CENSUS BUREAU, 2010).

À medida que a ecologia urbana avança na ciência da ecologia, devemos atualizar a compreensão do papel das cidades na conservação de abelhas, como enfatizado pelo último Relatório da Plataforma Intergovernamental sobre Biodiversidade e Serviços Ecossistêmicos (IPBES) (POTTS et al., 2016), a fim de engajar os planejadores urbanos e residentes na melhoria do hábitat dos polinizadores como uma prática de conservação. Como as abelhas são um grupo-chave de polinizadores em todo o mundo tanto para as plantas nativas como para as cultivadas, elas podem ser prontamente usadas para ilustrar a importância dos serviços ecossistêmicos, funções dos ecossistemas e capital natural.

O objetivo principal deste estudo foi avaliar os impactos da urbanização na comunidade de abelhas. Para isso, a presente tese foi dividida em três capítulos, respondendo às seguintes perguntas:

1) *Como a urbanização e a disponibilidade de plantas afetam a riqueza, abundância de espécies, características funcionais e composição da comunidade de abelhas em cidades de médio porte?*

   No primeiro capítulo da tese, submetido para a *Austral Ecology*, nosso objetivo foi avaliar a riqueza e abundância de abelhas, seus respectivos grupos funcionais, e a composição da comunidade ao longo de um gradiente de urbanização em 21 localidades distribuídas entre 6 cidades brasileiras de médio porte. Avaliamos também o efeito das plantas, bem como sua origem biogeográfica (exótica ou nativa).

2) *Como os modelos de desenvolvimento urbano afetam a diversidade taxonômica e funcional, a diversidade beta e a composição de espécies das abelhas?*

   Muitos trabalhos têm dado enfoque ao efeito da composição da paisagem urbana na riqueza e diversidade de espécies. Porém, uma das lacunas de conhecimento no campo da ecologia urbana diz respeito a quais configurações da paisagem são úteis no apoio à biodiversidade. No segundo capítulo da tese avaliamos três formas de desenvolvimento urbano, economia de terra (land-sparing), compartilhamento de terra (land-sharing) e área totalmente ocupada (land fully ocupied) e seus efeitos sobre a comunidade de abelhas. Nosso estudo abordou múltiplas medidas de diversidade a fim de avaliar qual desses modelos melhor contribui para a comunidade de abelhas em áreas urbanas.

3) *Como a estrutura das redes de interação planta-polinizador mudam ao longo de um gradiente de urbanização? E quais são as plantas mais importantes para as abelhas nos ambientes urbanos?*

   Além dos efeitos sobre a comunidade de abelhas, a urbanização também pode ter efeitos negativos sobre as suas interações com as plantas. Assim, no terceiro capítulo, avaliamos como a estrutura das redes de interação muda ao longo de um gradiente de urbanização. Avaliamos também a centralidade das duas espécies generalistas mais comuns nos ambientes urbanos brasileiros, a espécie exótica *Apis mellifera* e a nativa *Trigona spinipes*. Por fim, avaliamos a importância das espécies de plantas e famílias botânicas, para identificar quais delas atraem mais abelhas nos ambientes urbanos.

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SEGUNDA PARTE – ARTIGOS

ARTIGO I

Urbanization and abundance of floral resources affect bee communities in medium-sized neotropical cities

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Urbanization and abundance of floral resources affect bee communities in medium-sized neotropical cities

Abstract

Bees are important pollinators that have been negatively impacted by anthropogenic environmental changes, such as urbanization. In addition, urban development can reduce and degrade the natural habitat of bees by increasing the proportion of impervious surfaces, decreasing green areas, and increasing the number of exotic ornamental plants. On the other hand, cities can provide refuge for bees because they provide an environment with a wide variety of nesting and foraging resources. The objective of our study was to evaluate the richness and abundance of bees, their respective functional groups, and community composition along an urbanization gradient in 21 locations distributed among 6 medium-sized Brazilian cities (with populations between 80,000 and 170,000 inhabitants). We also evaluated the effect of richness, number of plants and proportion of native plants. We collected a total of 132 species of bees. Total bee richness decreased with increasing impervious cover and increased with landscape heterogeneity, which also had a positive effect on the richness of aboveground-nesting bees and generalist bees. Regarding abundance data, solitary bees and belowground-nesting bees were positively influenced by the increase in grass cover. The total number of native and exotic plants collected positively influenced the total abundance of bees, as well as the abundances of eusocial bees, which nest above- and belowground, and generalists. The proportion of native plants positively influenced the total richness and abundance of specialist bees. Our results indicate that medium-sized urban areas may be home to a wide diversity of bee species, but species that nest in the soil and specialist species may be more sensitive to urbanization and the decrease in the supply of floral resources.

Keywords: native bees, urban biodiversity, urban landscape, urban pollinators.

1. Introduction

Bees (Hymenoptera: Apoidea) are essential for the maintenance of ecosystems, biodiversity, and food production (Biesmeijer *et al.* 2006; Klein *et al.* 2006; Potts *et al.* 2010, Brown *et al.* 2016), but increasing evidence shows that these pollinators are in decline (Goulson *et al.* 2008; Potts et al. 2010; Carvalheiro et al. 2013). This decline has occurred due to anthropogenic actions, such as the use of pesticides, introduction of pathogens, climate change, and habitat fragmentation for agricultural intensification and urban expansion (Biesmeijer *et al.* 2006; Hegland *et al.* 2009; Giannini *et al.* 2015). However, the role of urbanization in bee diversity is still poorly understood (Winfree *et al.* 2011; Martins et al. 2017).

Urbanization is one of the fastest growing types of land use globally, and it is predicted that by 2050, urban areas will need to accommodate an additional 2.6 billion people (United Nations 2011). The urbanization process is associated with the reduction of natural vegetation and air pollution and the establishment of a high proportion of impervious areas, such as concrete and asphalt (Blair and Launer 1997; Williams *et al.* 2009; Banaszak-Cibicka *et al.* 2018)). Car parks, roads, and industrial sectors replace the floral and nesting resources necessary for bee survival (Cane et al. 2006; McKinney 2008; Cariveau and Winfree 2015). The effects urbanization has on bees include changes in community composition, pollination networks and biotic homogenization (Cane *et al.* 2006; Carré *et al.* 2009; Carper *et al.* 2014; Fortel *et al.* 2014; Geslin *et al.* al. 2016; Geslin *et al.* 2013; Baldock *et al.* 2015; McKinney 2006).

The functional characteristics of bees, such as social behavior, nesting behavior and trophic specialization, can determine their responses to changes in urban landscapes (Banaszak-Cibicka & Żmihorski 2012; Geslin *et al.* 2016; Cardoso and Gonçalves 2018; Graf *et al.* 2022 Banaszak-Cibicka & Dylewski, 2021). Regarding sociality, the richness and abundance of social bee species increase in urban areas, and their survival in urbanized environments may be due to greater behavioral and ecological flexibility (Banaszak-Cibicka *et al.* 2018; Banaszak-Cibicka & Zmihorski, 2012; Hinners *et al.* 2012; Chapman and Bourke 2001; Banaszak-Cibicka & Zmihorski 2012). Concerning nesting behavior, species that nest in the soil (approximately 75% of all bee species (Antoine and Forrest 2020)) are often negatively influenced by urbanization, while those that nest in cavities are usually more abundant in cities because urban landscapes offer a large variety of nesting resources, such as buildings, fences, and walls (Banaszak-Cibicka & Zmihorski 2012; Cane *et al.* 2006; Cardoso and Gonçalves 2018; Hinners et al. 2012; Wojcik 2011; Hinners *et al.* 2012). Regarding trophic specialization, species with restricted diets and specialized foraging strategies (oligolectic species) may be negatively affected by the introduction of exotic plants, because these can display flowers specialized for pollination, and nectar and pollen rewards may not be accessible to native bee species (Stout & Morales 2009). On the other hand, generalist (polylectic) species are able to include alien plant species in their diet and may dominate urban areas (Banaszak-Cibicka & Zmihorski 2012; Geslin et al. 2013; Wray and Elle 2015). Thus, urbanization and vegetation composed mainly of exotic plants in parks and gardens can decrease the richness and abundance of bees in cities (Morón et al. 2009; Fenesi *et al.* 2015; Henríquez-Piskulich *et al.* 2018).

Knowledge about the impact of urbanization on bees is still limited. Most studies about the effects of urbanization on biodiversity have been conducted in metropolises such as Chicago (USA), Leon (France), New York City (USA), Berlim (Germany) and Curitiba (Brazil), illustrating the bias towards sampling larger cities (Kendal *et al.* 2020; Rega-Brodsky *et al.* 2022). To date, little attention has been given to cities with fewer than 500,000 inhabitants. However, small and medium-sized cities correspond to more than 99% of the 5,570 Brazilian municipalities and to the cities where a large part of the European and US population lives (IBGE 2017; Giffinger *et al.* 2007; US Census Bureau 2010) . Thus, the influence of urbanization in smaller cities with agricultural crops and with relatively lower urbanization levels remains unknown. In addition, recent reviews of pollinators in urban areas suggest that the world’s most biodiverse regions from the Global South are often understudied and underrepresented in the international literature (Wenzel *et al*. 2020; Maruyama *et al.* 2021). Brazil, for example, is one of the countries with the greatest biodiversity in the world and the Brazilian Atlantic Forest (one of the world's biodiversity hotspots) is home to more than 120 million people in urban areas (Pinto *et al*. 2014).

The objective of our study was to determine how urbanization and plant availability affect the richness, species abundance, functional characteristics, and composition of bee communities in medium-sized cities. We present the hypotheses that the richness and total abundance of bees, as well as only those that nest in the soil and are solitary, would decrease with an increase in urbanization. We also expected that the richness of native plants collected would positively influence the richness and abundance of bees, especially specialist species. Finally, we expected a change in the composition of bee species along the impervious surface gradient.

2. Methods

2.1 Study area

Our study was conducted in six cities in southern Minas Gerais, Brazil: Alfenas, Poços de Caldas, Pouso Alegre, Varginha, Três Corações, and Lavras (Fig. 1A). The region is mainly composed of urban ecosystems (80,973 to 169,838 inhabitants), intensive agricultural landscapes (mainly coffee and pasture crops), and remnants of the Atlantic Forest (IBGE 2017). According to the Köppen-Geiger system, the climate of the region is classified as Cwa (dry winters and hot summers) and Cwb (dry winters and temperate summers) (Sá-Junior 2009). The region has a predominantly mountainous relief with elevations ranging from 800 to 1,400 m (Alvares 2013).

In the six sampled cities, we selected a total of 21 locations following an increasing gradient of impervious coverage (from 20 to 70%) within a radius of 1 km from the central collection point (centroid) (Fig. 1B). How the impermeable cover was quantified is described in section 2.2.3. Sampling was performed during two campaigns: the first between February and March 2020 and the second between September and November 2020 and January 2021. Each location was visited once a month for 6 months. There was no collection in December due to the large volume of rainfall in this period. The collection schedule could not be followed continuously due to the lockdown caused by the coronavirus pandemic.

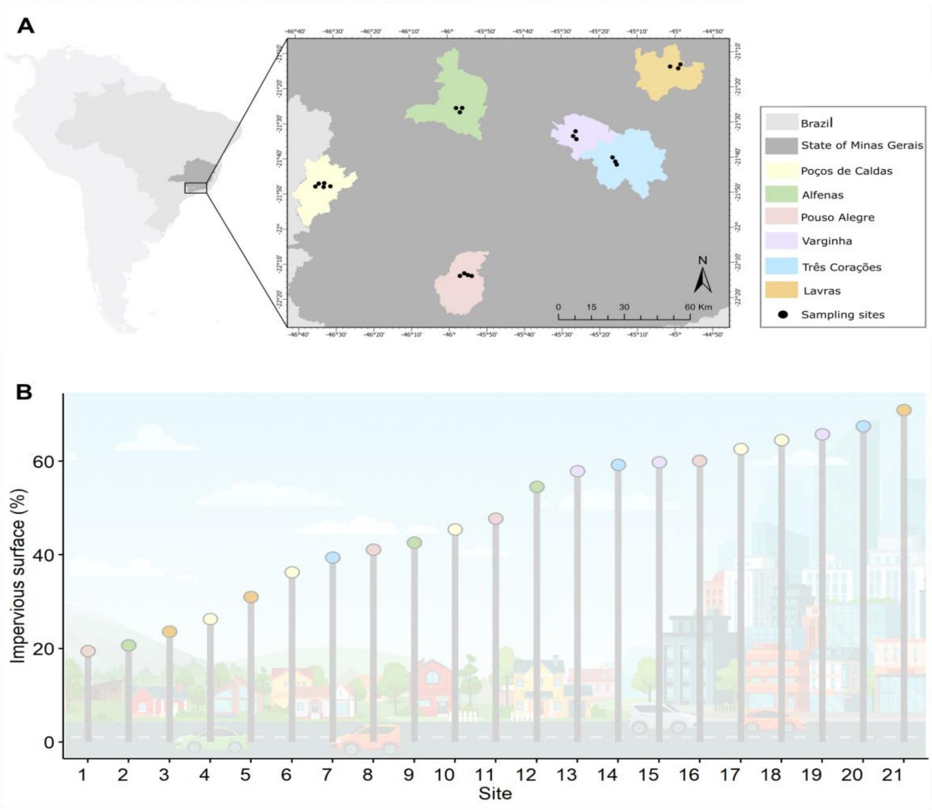

Fig. 1 (**A**) Sampling points distributed in six cities in the state of Minas Gerais, Brazil: Alfenas, Poços de Caldas, Pouso Alegre, Varginha, Três Corações, and Lavras. (**B**) Graphical representation of the urbanization gradient for the 21 sampling locations (sorted by ranking) in the six cities following an increasing gradient of impervious coverage (from 19.5 to 70.5%) within a radius of 1 km from the central collection point. The different colors of the points represent the 6 different cities. The background image was freely obtained from "www.freepik.com" (designed by tartila).

2.2 Data collection

2.2.1 Sampling of bees

To evaluate the bee community at each site for 6 months in 2020 and 2021, we used the active capture method. Sampling was performed by only one collector within a radius of 200 m from the central point of each location. We walked along sidewalks, squares, flowerbeds, and vacant lots. We observed all flowering plants (up to 3 m in height, reach of the entomological network). The bees were collected directly from flowers using an entomological net. In each plant, the bees were collected for 10 minutes. If in 5 minutes no bees were observed, then we left to observe another plant.

Active capture occurred for four hours in the morning (8:00 am - 12:00 pm) and four hours in the afternoon (1:00 pm - 5:00 pm), alternating the periods at each location to reduce bias related to the collection time. The collected specimens were processed, fixed, and identified. The determination to genus was performed using the book by Silveira *et al.* (2002) and to species level through studies of taxonomic reviews performed by experts.. Whenever there was doubt about the identification, we used the assistance of specialists (see acknowledgments).

Bees were characterized according to the following functional groups: social behavior, nesting habit, and trophic specialization. Regarding social behavior, we considered 3 groups: highly eusocial, primitively eusocial, and solitary. In highly eusocial bees, the queen differs morphologically, behaviorally, and physiologically from the workers (for example, Meliponini tribe). In primitively eusocial bees, the queen differs only in physiology and behavior, rarely with morphological differences (for example, Bombini tribe) (Michener 2007). Regarding nesting behavior, we also considered 2 groups, aboveground-nesting bees (e.g., tree cavities, preexisting cavities, human constructions, and dead wood) and belowground-nesting bees. Finally, regarding trophic specialization, we consider generalist (polylectic) or specialist (oligolectic) species. The kleptoparasite group was not included in any of the categories. Information on the functional characteristics of each species was obtained from data available in the literature (Michener 2007; Martins *et al.* 2013; Graf *et al.* 2022) and consultation with experts (see acknowledgments and supplementary material).

2.2.2 Sampling of plants

Bee sampling was performed on plants with accessible flowers up to approximately 3 m in height (reach of entomological net reach). All tree, shrub, herbaceous, and liana plants with flowers on which the bees were captured were collected to obtain the richness and number of available plants. We considered the richness to be the number of plant species collected at each location, while the number of available plants was counted independently of the species. We also calculated the proportion of native plants in relation to total plant richness and total number of plants collected.

All sampled species were identified at the species level and classified as native or exotic, according to the Flora and Fungus Project of Brazil (http://floradobrasil.jbrj.gov.br), and are available in the supplementary material. The species that occur naturally in the Atlantic Forest biome and in the study region were considered native. Nonnative plants in this biome were classified as exotic.

2.2.3 Landscape characterization

We used Sentinel-2 images of the study areas (obtained in September 2019) with a resolution of 10 m to characterize the landscape around each study site. The Semiautomatic Classification (SCP) plugin (Congedo 2016) was used to classify the images in QGIS software version 3.10.0 (QGIS Development Team 2019). Four classes of land cover were considered: water bodies, impervious surfaces, trees, and grasses. For impervious surface cover, we consider all urban areas, such as roads, buildings, and industrial areas. The tree cover class included forests, parks, and restored areas. For the grass land cover class, we included exposed soil, natural open fields, areas covered with ruderal plants, and managed grass. These sites are often used for bees to build their nests (below-ground nesting bees) and offer floral resources. The land use map resulting from the classification was manually postprocessed to correct the small errors of the semiautomatic classification.

Using the LeCos plugin (Jung 2016), we calculated the coverage percentages of each class and the Shannon diversity index of the landscape at along four radii (200 m, 500 m, 750 m and 1,000 m). The percentages of land cover represent the class cover in relation to the total landscape area, and the Shannon diversity index describes the environmental heterogeneity of the landscape, considering the number and proportion of landscape classes (Boscolo *et al.* 2017; Nery *et al.* 2017). al., 2018). The Shannon index of the landscape increases when the number of different land cover units increases and/or the proportional area of these units becomes more equitable (McGarigal *et al.* 2012). We considered the percentage of impervious surface cover, which varied between 19.5 and 70.5%, to characterize the urbanization gradient.

We did not include radii greater than 1000 m in the analyses because the study cities are medium size, and a radius greater than 1000 m extrapolates a larger urban perimeter. In addition, studies have shown that although bees can forage in a larger area (up to approximately 2 km), urban environments can offer resistance to foraging activity since the permeability of the urban matrix may change according to the availability of nesting resources and density of buildings (Boscolo *et al.* 2017). There is probably also a preference for using resources near nests, which decreases the scale of the landscape to which they respond (Araújo *et al.* 2004; Wright *et al.* 2015; Geslin *et al.* 2016). In general, a radius up to 1000 m has been a good predictor of community characteristics in urban areas (Pardee *et al.* 2014; Fortel *et al.* 2014; Geslin *et al.* 2016; Graf *et al.* 2022).

2.3 Data analysis

The diversity of bees was characterized by species richness and total abundance of individuals, as well as richness and abundance of each functional group. The species accumulation curve is available in the supplementary material.

To determine how the landscape composition and plant community variables were correlated with each other, we calculated Spearman correlation coefficients (ρ). Due to the high correlation between the measurements of the landscape in the three radii, the analyses were performed separately for each radius. For each radius, we removed the highly correlated explanatory variables ($\rho > 0.70$ or $\rho < -0.70$) with the impervious cover and the landscape heterogeneity. As the correlations between these two variables were high (< -0.70) and both are considered important for the bee community, we used them separately in the analyses (Graf *et al.* 2022). For the variables related to plants, we maintained the uncorrelated variables: “total richness”, “total number of plants”, and “proportion of native plants”. The results of the correlation analysis of the variables are available in the supplementary material.

We used generalized linear models (GLMs) to evaluate whether the richness and total abundance of bees change along an urbanization gradient (percentage of impervious cover) to other elements of the urban landscape and in relation to the plant community. We used the Poisson error distribution for species richness and negative binomials for species abundance since they showed overdispersion in the model with a Poisson distribution (O'Hara & Kotze 2010). Subsequently, we also built the models by incorporating information on the functional characteristics of the species, where we used the abundance and richness of the species in each functional group (i.e., social behavior, nesting habit, and trophic specialization) as a response variable. We also tested the categorical variable “city” in the models to determine whether the city in which the collection was performed affected the results obtained. We used raw and untransformed values for all predictor and response variables.

Before performing the statistical tests, we verified the spatial autocorrelations between the sites with reference to our tested variables using the Moran index. We found that the richness of eusocial species showed significant spatial autocorrelation ($p = 0.03$). Thus, we included the covariates latitude and longitude in the models for this group. In each radius, the models were simplified by direct selection based on the Akaike information criterion with a correction (AICc) values, a selection criterion corrected for small sample sizes (Anderson & Burnham 2004). Models with $\Delta AICc < 2$ were considered equally plausible, and no alternative model was considered when the null model was $\Delta AICc < 2$.

Finally, we examined the effect of landscape and plant community composition on bee community composition using redundancy analysis (RDA) with the *rda* function of the *vegan* package (Oksanen *et al*. 2019). Using the *decostand* function, we standardized the species matrix through the *Hellinger* transformation, appropriate for abundance data (Legendre 2005), and standardized the environmental matrix at zero due to the range of absolute values that vary naturally. We tested the same sets of noncorrelated explanatory variables for all study radii used in the GLMs, and for the 200 m radius, we combined the impervious cover and the richness and number of available plants (total and native). Before performing the ordination, the species with an abundance of only one individual (54 species) were removed from the dataset because they may reflect stochastic sampling effects and therefore add noise rather than information beyond more common species (Gauch and Gauch 1982; Poos and Jackson 2012). We added geographical coordinates to the RDA as a conditioning matrix to control the spatial effect.

3. Results

3.1 Characterization of the bee and plant communities

A total of 4,279 bee specimens belonging to the five subfamilies that occur in Brazil (Andreninae, Apinae, Colletinae, Halictinae, and Megachilinae) were collected, belonging to 55 genera and 132 species (Supplementary Material II). Apinae had the highest richness, with 85 species, followed by Halictinae (29), Megachilinae (13), Andreninae (3), and Colletinae (2). We collected 24 highly eusocial bees, 24 primitively eusocial bees, 83 solitary bees, 75 aboveground-nesting bees, 53 belowground-nesting bees, 105 generalist bees, and 22 specialist bees. Only 6 individuals of 4 species with kleptoparasitic behavior were captured. The species *Eulaema nigrita* Lepeletier, 1841, has the habit of building its nests both belowground and aboveground; thus, it was counted for species richness and abundance in both categories. We collected only one exotic bee species, *Apis mellifera* Linnaeus, 1758. The three most abundant species were *A. mellifera* (928 individuals), *Trigona spinipes* (651 individuals), and *Tetragonisca angustula* (489 individuals).

Regarding the plant community, a total of 858 plants of 190 species, 158 genera and 58 families were sampled (Supplementary Material III). A total of 123 species were classified as exotic (~ 65%), and 67 were classified as native (~ 35%).

3.2 Effects of urbanization on the diversity of the bee community

The models that best described the variation in bee richness and abundance included impervious cover, grass cover, landscape heterogeneity, and tree cover (Table I).

For the total bee richness, we found an effect of impervious cover, grass cover, and landscape heterogeneity for the radii of 750 m and 1,000 m. The impervious cover had a negative effect on the total richness in the 1,000 m radius (p = 0.02, Fig. 2A), while the landscape heterogeneity showed a positive effect for the 750 m and 1,000 m radii (p = 0.003 and p = 0.004, respectively, Fig. 2B). The grass cover was also considered important for the total richness of bees and was selected in the models. As the effects were similar for the two radii, in the graphs, we represented only the relationship between the response and predictor variables with a significant effect for the 1,000 m radius.

The richness of aboveground-nesting bees was positively influenced by the diversity of the landscape in the radii of 750 m and 1,000 m (p = 0.03 and p = 0.03, respectively, Fig. 2C), as well as the richness of generalist bees (p = 0.002 and p = 0.002, respectively, Fig. 2D). We found no effect of any of the urban landscape variables on the richness of eusocial bee, primitively eusocial bees, belowground-nesting bees, and specialist bees. The abundance of solitary bees and belowground-nesting bees was positively influenced by the increase in grass cover in the 1,000 m radius (p = 0.01, p = 0.01, Fig. 2E and 2F, respectively). The impervious cover and the grass cover were also selected in the models for these groups.

Table I Models selected to determine bee community responses to urban landscape variables. The AICc, ΔAICc, weight, and adjusted R^2 values are represented for each selected model.

Dependent variable	**Radius (m)**	**Model**	**AICc**	**ΔAICc**	**Weight (w_i)**	**Intercept (α)**	**p-value**	**R^2_{aj}**
Bee richness	1000	Impervious cover + Grass cover	133.2	0	0.31	-0.71 | 0.51	0.008 | 0.08	0.22
	1000	Impervious cover	133.3	0.16	0.29	-0.6	0.02	0.15
	1000	Landscape heterogeneity	130.2	0	0.95	1.21	0.004	0.30
	750	Landscape heterogeneity	129.8	0	0.96	1.15	0.003	0.31
Richness of aboveground-nesting bees	1000	Landscape heterogeneity	117.2	0	0.74	1.16	0.03	0.19
	750	Landscape heterogeneity	117.1	0	0.75	1.08	0.03	0.20
Richness of generalist bees	1000	Landscape heterogeneity	121.7	0	0.97	1.4	0.002	0.40
	750	Landscape heterogeneity	121.4	0	0.97	1.3	0.002	0.40
Abundance of solitary bees	1000	Grass cover	171.4	0	0.39	1.95	0.01	0.15
	1000	Impervious cover + Grass cover	172.6	1.20	0.21	-0.99 | 2.27	0.15 | 0.003	0.03
Abundance of belowground-nesting bees	1000	Grass cover	183.0	0	0.32	1.41	0.01	0.17
	1000	Tree cover + Grass cover	183.6	0.57	0.24	1.25 | 1.26	0.09 | 0.02	0.15

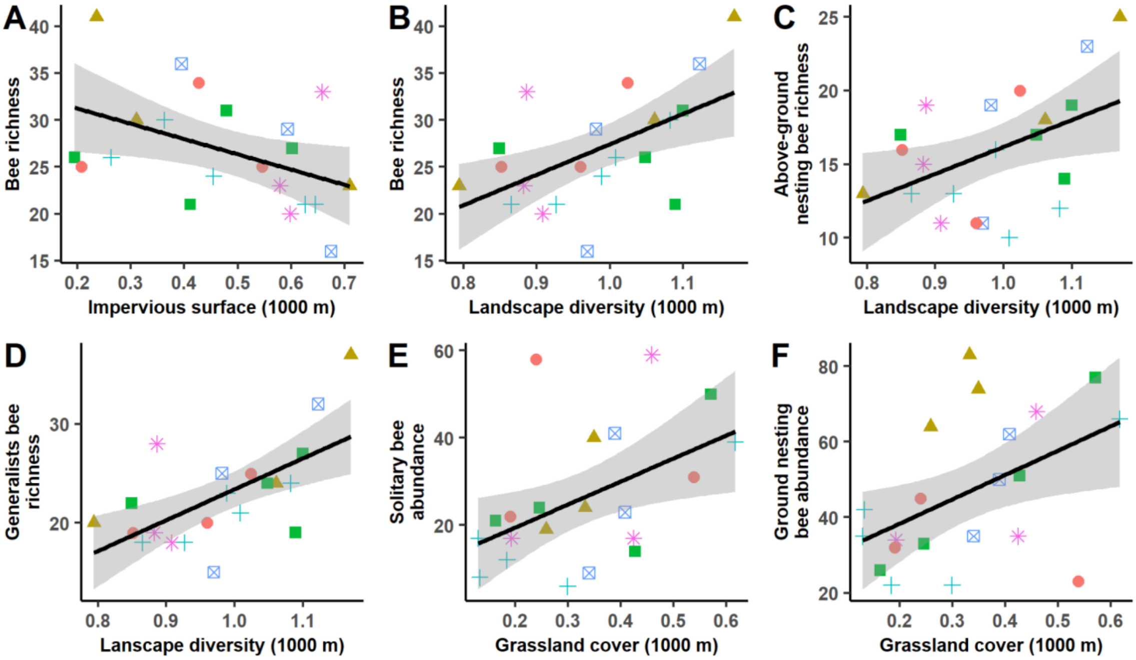

Fig. 2 (A) Total richness x impervious cover in a radius of 1,000 m; (B) total richness x Shannon index of the landscape in a radius of 1,000 m. (C) Richness of aboveground-nesting bees in relation to the diversity of the landscape in a radius of 1,000 m; (D) richness of polylectic bees in relation to landscape diversity in a radius of 1,000 m; (E) abundance of solitary bees in relation to grass cover in a radius of 1,000 m; (F) abundance of soil nesting bees in relation to grass cover in a radius of 1000 m. The solid line represents the fit of the model, the shaded area represents the 95% confidence interval, and the points represent the 6 different cities (red circle: Alfenas; brown triangle: Lavras; green square: Pouso Alegre; blue square: Três Corações; blue cross: Poços de Caldas; and pink asterisk: Varginha).

The total abundance of eusocial bees, primitively eusocial bees, aboveground-nesting bees, generalist bees, and specialist bees was not influenced by the urban landscape variables for any of the evaluated radii. We did not find any significant effect of the cities on the total richness and abundance of bees or on the bee functional groups.

3.3 Responses of bee community diversity to plants

The models that best explained the variation in bee richness and abundance included the total number of plants and the proportion of native plants (Table II). We found that total bee richness increased with an increasing proportion of native plants (p = 0.05, Fig. 3A). The total number of plants was also important for the total richness of bees and was selected in the models. The total abundance of bees increased with the total number of available plants (p <0.001, Fig. 3B), and the proportion of native plants was also selected in the models.

When we evaluated the responses of the bee functional groups in relation to the plants, we found a positive effect of the total number of plants on the abundance of eusocial bees ($p < 0.001$, Fig. 3C), as we observed for the total abundance of bees. The abundance of aboveground-nesting bees increased with the increase in the total number of plants collected ($p < 0.001$, Fig. 3D), as well as the number of belowground-nesting bees ($p = 0.03$, Fig. 3E). The proportion of native plants was considered important for the abundance of belowground-nesting bees because it was selected in the models.

Regarding trophic specialization, we found that as the total number of plants increased, the abundance of generalist species also increased ($p < 0.001$, Fig. 3F), while the proportion of native plants had a positive effect on the abundance of specialist bees ($p = 0.03$, Fig. 3G). For these two groups, the proportion of native plants and the total number of plants were also considered important predictors. For richness and abundance of primitively eusocial and solitary bees, we did not find any effect of richness and number of plants (total and native).

Table II Models selected to determine bee community responses to plants. The AICc, ΔAICc, weight, and adjusted R^2 values are represented for each selected model.

Dependent variable	Model	AICc	ΔAICc	Weight (w_i)	Intercept (α)	p-value	R^2_{aj}
Species richness	Total number of plants + Proportion of native plants	132.9	0	0.58	0.02 | 0.01	0.03 | 0.01	0.28
	Proportion of native plants	134.8	1.9	0.18	0.008	0.05	0.10
Total abundance	Total number of plants	207.0	0	0.41	0.04	< 0.001	0.51
	Total number of plants + Proportion of native plants	207.5	0.47	0.32	0.04 | 0.004	< 0.001 | 0.1	0.60
Abundance of eusocial bees	Total number of plants	204.2	0	0.60	0.05	< 0.001	0.57
Abundance of aboveground-nesting bees	Total number of plants	211.4	0	0.64	0.04	< 0.001	0.26
Abundance of belowground-nesting bees	Total number of plants + Proportion of native plants	183.3	0	0.38	0.04 | 0.01	0.004 | 0.04	0.30
	Total number of plants	184.0	0.71	0.27	0.03	0.03	0.21
Abundance of generalist bees	Total number of plants	203.0	0	0.52	0.04	< 0.001	0.57
	Total number of plants + Proportion of native plants	204.7	1.69	0.22	0.04 | 0.003	< 0.001 | 0.23	0.61
Abundance of specialist bees	Total number of plants + Proportion of native plants	126	0	0.65	0.08 | 0.04	0.004 | 0.0007	0.20

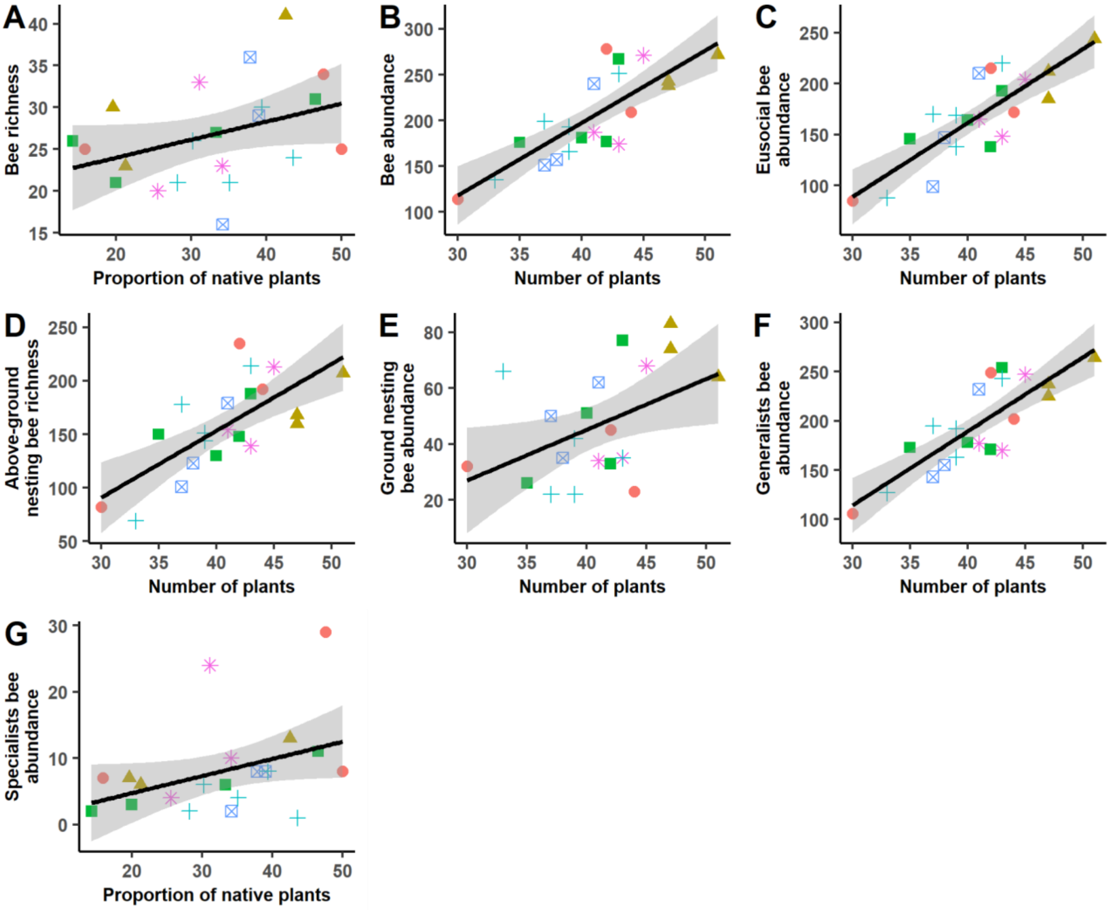

Fig. 3 Graphical representation of total bee richness and abundance for plant-related variables with significant effects. (A) Total bee richness in relation to the proportion of native plants. (B) Total bee abundance in relation to the total number of plants. (C) Abundance of eusocial bees in relation to the total number of plants; (D) abundance of aboveground-nesting bees x total number of plants; (E) abundance of belowground-nesting bees in relation to the total number of plants; (F) abundance of generalist bees in relation to total number of plants; (G) abundance of specialist bees in relation to the proportion of native plants. The solid line represents the fit of the model, the shaded area represents the 95% confidence interval, and the colors and shapes of the points represent the 6 different cities (red circle: Alfenas; brown triangle: Lavras; green square: Pouso Alegre; square blue: Três Corações; blue cross: Poços de Caldas; and pink asterisk: Varginha).

3.4 Response of the bee community composition

The RDA showed that the composition of the bee community was not influenced by the urban landscape and plant variables in any of the evaluated radii ($p > 0.05$).

4 Discussion

As we predicted in our hypothesis, the increase in the percentage of impervious cover, i.e., the increase in urbanized areas, with buildings and streets, resulted in a decrease in the total richness of the bees in our study. This result is consistent with the findings of previous studies conducted along urbanization gradients in different cities. These studies found significant decreases in the richness and abundance of generalist bees and soil nesting bees with the increase in the proportion of impervious surfaces in urban areas (Geslin *et al.* 2016; Ahrné *et al.* 2009; Matteson *et al.* 2008; Bates *et al.* 2011; Fortel *et al.* 2014). The decrease in bee richness with the increase in impervious cover can be explained by the fact that approximately 40% of the bee species we collected nest belowground, and impervious surfaces reduce the availability of resources and nesting sites and can prevent these species from reproducing in cities (Hostel and McIntyre 2001; Ahrné *et al.* 2009). Although the richness of bees that nest in the soil was not directly affected by the impervious cover, its abundance increased with the increase in grass cover, as did the abundance of solitary bees. Half of the collected solitary bee species nest in the soil, and these species are especially sensitive to urbanization because they require good-quality soil surfaces to establish their nests, such as uncompacted soils (Cane *et al.* 2006). We emphasize the importance of maintaining areas with permeable surfaces to provide nesting resources for these bee species in urban environments.

In contrast to the total richness of bees, we did not find an effect of impervious cover on richness and abundance per functional group, as demonstrated in other studies (Fortel *et al.* 2014; Geslin *et al.* 2016). However, studies that evaluated this effect are more common in metropolitan areas and cities with more than 500,000 inhabitants (Kendal *et al.* 2020), where urbanization is notoriously more intense, with higher population densities and more vertical construction (Saure 1996; Zapparoli 1997; Cane 2005; Banaszak-Cibicka and Żmihorski 2012). In our study, we did not find urban sites with more than 70% impermeable surface as reported in other cities in the world, which could explain this result. In addition, some studies demonstrated that cities can often contain greater bee species diversity than rural or natural areas, considering urban areas as a refuge for pollinators (Hall *et al.* 2016).

As bees form a diverse group with different requirements for nesting and feeding, a greater diversity of landscape elements in urban areas can support greater species richness (Aguirre-Gutiérrez *et al.* 2015; Boscolo et al. 2017; Nery *et al.* 2018). Aboveground-nesting bees, for example, may be favored in more heterogeneous cities due to numerous nesting opportunities, such as holes in building walls, vacant lots, garden fences, and tree hollows present in impervious and vegetated areas (Cane *et al.* 2006; Pardee *et al.* 2014; Geslin *et al.* 2016). Our study reinforces this hypothesis because we observed that a more heterogeneous urban landscape, represented by the Shannon index of the landscape, had a positive effect on the total bee richness, as well as on several functional groups, such as solitary bees, aboveground-nesting bees, and generalist bees. In Curitiba, a Brazilian metropolitan area, positive relationships were also observed between the heterogeneity of the urban landscape and the total richness of bee species, as well as of its various bee functional groups (Graf *et al.* 2022).

Regarding the collected plants, our results showed that the richness of plant species had no effect on the richness and abundance of bees, which was surprising, given the importance of floral diversity to bee diversity. However, the increase in the total number of available plants had a positive effect on the total abundance of eusocial bees, aboveground-nesting bees, belowground-nesting bees, and generalist bees. Thus, for these groups, the origin of the plants where they were found was not important, as several studies have shown that exotic flowers are not necessarily less attractive to urban pollinators (Garbuzov *et al.* 2015; Garbuzov and Ratnieks 2014; Hinners and Hjelmroos- Koski 2009; Majewska *et al.* 2018; Martins *et al.* 2017; Matteson and Langellotto 2011; Frankie *et al.* 2019; Wenzel et al. 2020). On the other hand, some highly specialized bee species may be at a disadvantage and become scarce in cities due to the prevalence of exotic flowers, such as those used in landscaping and those from ruderal invasions (Cane 2005; Frankie et al. 2005; Cane et al. 2006; McFrederick and Le Buhn 2006; Chrobock *et al.* 2013; Fukase and Simons 2016; Rocha-Filho *et al.* 2018; Jain *et al.* 2016; Wenzel *et al.* 2020). Our results corroborate this scenario because the total bee richness and the abundance of specialist bees increased with the increase in the proportion of native plants present in the urban areas in this study (i.e., decrease in the proportion of exotic plants).

We found no effect of urbanization and plant community on the composition of the bee community. This result probably occurred because we collected bees in different cities, and therefore, the geographic factors may have been more the determinants in the composition of the bee species than the variables measured in our study. Geppert *et al.* (2022) found that the temperature was the key driver of wild bee composition and functional diversity, regardless of the cover of the open habitat and the distance from the city center. Therefore, it is likely that the composition of bee species is also determined by variables that act at a broader scale.

Our study provides important results for understanding the effect of urbanization on bee communities in medium-sized cities in a tropical region. We contributed to reducing the geographical and environmental bias of studies with bees and urbanization since most were conducted in the northern hemisphere and in gardens, which often have high species richness levels and ornamental species abundance and therefore different compositions of vegetation. (Buchholz and Egerer 2020). Even in smaller cities with lower urbanization intensities, the bee communities were influenced by urbanization at the local and landscape scales. Therefore, efforts aimed at the conservation of bees in cities should focus both on landscape factors, such as promoting a greater diversity of habitats for bees, and on local factors, such as incorporating native plants into the urban flora.

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Supplementary material

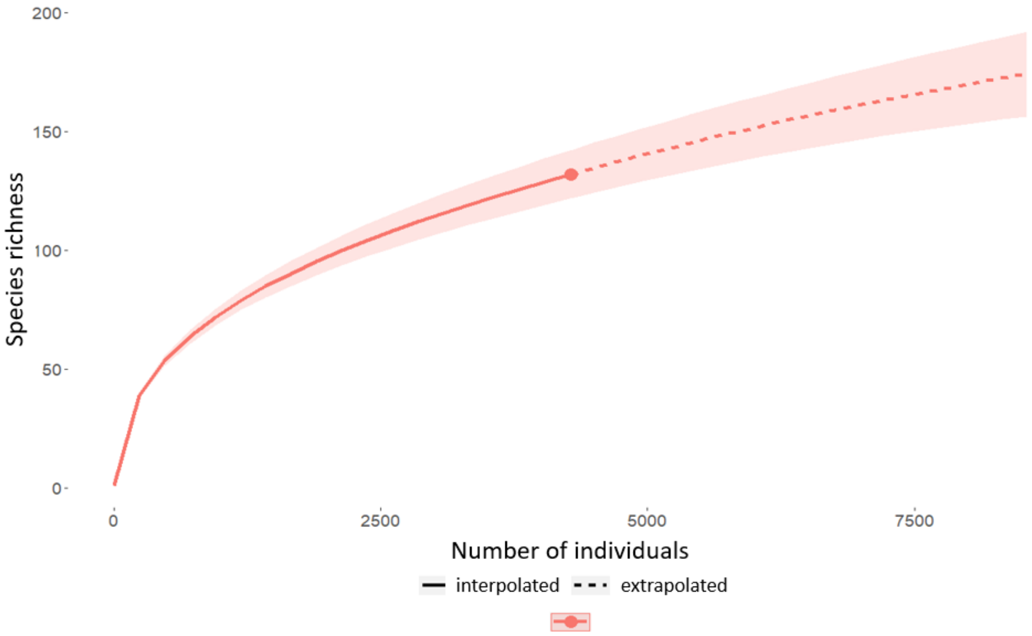

Fig. S1 Interpolated (continuous line) and extrapolated (dashed line) richness accumulation curves estimated based on the number of individuals collected in the 21 sample areas calculated using the iNEXT package version 2.0.9 (Hsieh et al. 2016) in the R 3.3.1 program (Main Development Team R 2016). The point represents the number of individuals collected on the X axis and the number of species on the Y axis, and the shaded area represents the 95% confidence interval.

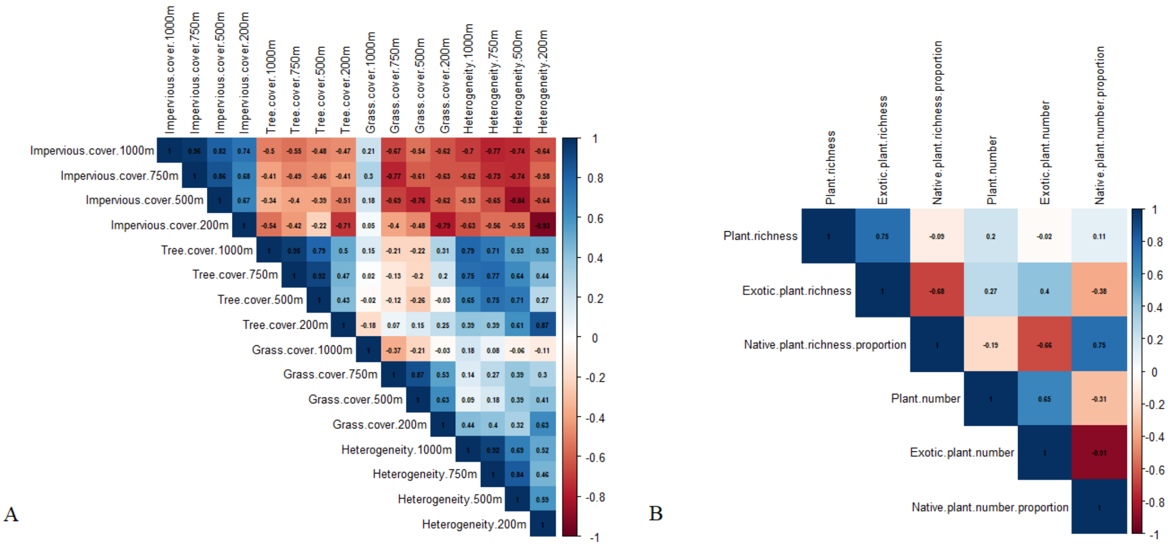

Fig. S2 Spearman correlation matrix. A: landscape variables for all radii; B: plant variables.

Table S1. Species of bees and their functional characteristics. Social behavior: (So) solitary, (Pe) primarily eusocial, (He) highly eusocial. Nesting location: (G) soil, (A) aboveground, (Cl) kleptoparasite. Trophic specialization: (S) specialist, (EG) generalist. (NA) not specified.

Bee species	**Abundance**	**Social behavior**	**Nesting site**	**Trophic specialization**
Andreninae				
Calliopsini				
Acamptopoeum prinii Holmberg, 1884	2	So	G	Ge
Protandrenini				
Cephalurgus anomalus Moure & Lucas de Oliveira, 1962	12	So	G	S
Oxaeini				
Oxaea flavescens Klug, 1807	15	So	G	Ge
Apinae				
Emphorini				
Melitoma segmentaria Fabricius, 1804	17	So	G	S
Apini				
Apis mellifera Linnaeus, 1758	928	He	A	Ge
Bombini				
Bombus brasiliensis Lepeletier, 1836	7	Pe	A	Ge
Bombus morio Swederus, 1787	75	Pe	A	Ge
Bombus pauloensis Friese, 1913	24	Pe	A	Ge
Centridini				
Centris aenea Lepeletier, 1841	9	So	G	S
Centris analis Fabricius, 1804	19	So	A	S
Centris collaris Lepeletier, 1841	13	So	G	S
Centris discolor Smith, 1874	4	So	G	S
Centris fuscata Lepeletier, 1841	3	So	G	S
Centris mocsaryi Smith, 1874	1	So	G	S
Centris sp1	2	So	G	S
Centris tarsata Smith, 1874	12	So	A	S
Centris trigonoides Lepeletier, 1841	12	So	A	S

Epicharis albofasciata Smith, 1874	1	So	G	S
Epicharis analis Lepeletier, 1841	9	So	G	S
Epicharis flava Friese, 1900	41	So	G	S
Eucerini				
Melissodes nigroaenea Smith, 1854	4	So	G	Ge
Melissoptila cnecomala Moure, 1944	1	So	G	S
Melissoptila similis Urban, 1988	1	So	G	S
Peponapis fervens Smith, 1879	2	So	G	S
Thygater analis Lepeletier, 1841	40	So	G	Ge
Thygater palliventris Friese, 1908	1	So	G	Ge
Euglossini				
Euglossa cordata Linnaeus, 1758	4	Pe	A	Ge
Euglossa securigera Dressler, 1982	1	Pe	A	Ge
Euglossa townsendi Cockerell, 1904	2	Pe	A	Ge
Euglossa truncata Rebêlo & Moure, 1996	3	Pe	A	Ge
Eulaema nigrita Lepeletier, 1841	31	So	A/G	Ge
Exaerete smaragdina Guérin, 1844	2	So	Cl	NA
Exomalopsini				
Exomalopsis analis Spinola, 1853	7	So	G	Ge
Exomalopsis auropilosa Spinola, 1853	75	So	G	Ge
Exomalopsis collaris Friese, 1899	1	So	G	Ge
Exomalopsis fernandoi Moure, 1990	1	So	G	Ge
Exomalopsis fulvofasciata Smith, 1879	6	So	G	Ge
Exomalopsis sp1	4	So	G	Ge
Exomalopsis sp2	1	So	G	Ge
Exomalopsis sp3	1	So	G	Ge
Meliponini				
Cephalotrigona capitata Smith, 1854	16	He	A	Ge
Friesella schrottkyi Friese, 1900	16	He	A	Ge
Geotrigona subterranea Friese, 1901	139	He	G	Ge
Melipona marginata Moure, 1971	1	He	A	Ge
Melipona quadrifasciata Lepeletier, 1836	6	He	A	Ge

Melipona quinquefasciata Lepeletier, 1836	7	He	G	Ge
Melipona rufiventris Lepeletier, 1836	1	He	A	Ge
Nannotrigona testaceicornis Lepeletier, 1836	225	He	A	Ge
Oxytrigona tataira Smith, 1863	1	He	A	Ge
Paratrigona lineata Lepeletier, 1836	323	He	G	Ge
Paratrigona subnuda Moure, 1947	72	He	G	Ge
Partamona cupira Smith, 1863	1	He	A	Ge
Partamona helleri Friese, 1900	13	He	A	Ge
Partamona rustica Pedro & Camargo, 2003	4	He	A	Ge
Plebeia droryana Friese, 1900	378	He	A	Ge
Plebeia remota Holmberg, 1903	1	He	A	Ge
Scaptotrigona bipunctata Lepeletier, 1836	111	He	A	Ge
Scaptotrigona postica Latreille, 1807	27	He	A	Ge
Schwarziana quadripunctata Lepeletier, 1836	7	He	G	Ge
Tetragona clavipes Fabricius, 1804	49	He	A	Ge
Tetragonisca angustula Latreille, 1811	489	He	A	Ge
Trigona fuscipennis Friese, 1900	46	He	A	Ge
Trigona spinipes Fabricius, 1793	651	He	A	Ge
Protepeolini				
Leiopodus lacertinus Smith, 1854	2	So	Cl	NA
Tapinotaspidini				
Lophopedia minor Aguiar, 2009	1	So	A	S
Lophopedia nigrispinis Vachal, 1909	1	So	A	S
Monoeca sp1	1	So	G	S
Paratetrapedia conexa Vachal, 1909	3	So	A	S
Paratetrapedia flaveola Aguiar & Melo, 2011	4	So	A	S
Tetrapediini				
Tetrapedia diversipes Klug, 1810	1	So	A	Ge
Xylocopini				

Ceratina (Ceratinula) sp1	2	So	A	Ge
Ceratina (Ceratinula) sp2	2	So	A	Ge
Ceratina (Ceratinula) sp3	4	So	A	Ge
Ceratina (Ceratinula) sp4	1	So	A	Ge
Ceratina (Crewella) sp1	1	So	A	Ge
Ceratina (Crewella) sp2	1	So	A	Ge
Ceratina (Crewella) sp3	7	So	A	Ge
Ceratina canaliculata Roig-Alsina, 2016	2	So	A	Ge
Ceratina oxalidis Schrottky, 1907	2	So	A	Ge
Ceratina richardsoniae Schrottky, 1909	2	So	A	Ge
Ceratina sclerops Schrottky, 1907	1	So	A	Ge
Xylocopa frontalis Olivier, 1789	9	So	A	Ge
Xylocopa grisescens Lepeletier, 1841	1	So	A	Ge
Xylocopa hirsutissima Maidl, 1912	3	So	A	Ge
Xylocopa macrops Lepeletier, 1841	1	So	A	Ge
Xylocopa ordinaria Smith, 1874	1	So	A	Ge
Xylocopa subcyanea Pérez, 1901	1	So	A	Ge
Xylocopa suspecta Moure & Camargo, 1988	27	So	A	Ge
Colletinae				
Hylaeini				
Hylaeus sp1	1	So	A	Ge
Hylaeus sp2	1	So	A	Ge
Halictinae				
Augochlorini				
Augochlora (Augochlora) sp1	1	Pe	A	Ge
Augochlora (Augochlora) sp2	3	Pe	A	Ge
Augochlora (Augochlora) sp3	1	Pe	A	Ge
Augochlora (Augochlora) sp4	4	Pe	A	Ge
Augochlora (Oxystoglossella) sp1	7	Pe	A	Ge
Augochlora (Oxystoglossella) sp2	2	Pe	A	Ge
Augochlora (Oxystoglossella) sp3	1	Pe	A	Ge

Augochlora morrae Strand, 1910	5	Pe	A	Ge
Augochlora esox Vachal, 1911	44	Pe	A	Ge
Augochlorella ephyra Schrottky, 1910	10	Pe	G	Ge
Augochloropsis (Augochloropsis) sp1	1	So	G	Ge
Augochloropsis (Paraugochloropsis) sp1	3	So	G	Ge
Augochloropsis (Paraugochloropsis) sp2	4	So	G	Ge
Augochloropsis (Paraugochloropsis) sp3	1	So	G	Ge
Augochloropsis (Paraugochloropsis) sp4	8	So	G	Ge
Dialictus sp1	14	Pe	G	Ge
Dialictus sp2	1	Pe	G	Ge
Dialictus sp3	2	Pe	G	Ge
Dialictus sp4	1	Pe	G	Ge
Dialictus sp5	1	Pe	G	Ge
Dialictus sp6	1	Pe	G	Ge
Dialictus sp7	1	Pe	G	Ge
Habralictus sp	1	So	G	Ge
Neocorynura codion Vachal, 1904	5	So	G	Ge
Paroxystoglossa crossotos Vachal, 1904	1	So	G	Ge
Paroxystoglossa seabrai Moure, 1960	1	So	G	Ge
Pseudaugochlora graminea Fabricius, 1804	67	So	G	Ge
Temnosoma sp1	1	So	Cl	NA
Halictini				
Pseudagapostemon arenarius Schrottky, 1902	2	So	G	Ge
Megachilinae				
Megachilini				
Coelioxys sp1	1	So	Cl	NA
Megachile (Austromegachile) sp1	1	So	A	Ge
Megachile (Dactylomegachile) sp1	1	So	A	Ge
Megachile (Ptilosarus) sp1	1	So	A	Ge
Megachile apicipennis Schrottky, 1902	3	So	A	Ge

Megachile orba Schrottky, 1913	1	So	A	Ge
Megachile pseudanthidioides Moure, 1943	1	So	A	Ge
Megachile susurrans Haliday, 1836	1	So	A	Ge
Anthidiini				
Anthidiini sp1	1	NA	NA	NA
Anthodioctes megachiloides Holmberg, 1903	1	So	A	Ge
Dicranthidium gregarium Schrottky, 1905	1	So	A	Ge
Epanthidium sp1	1	So	A	Ge
Epanthidium tigrinum Schrottky, 1905	10	So	A	Ge

Table S2. List of plants used by the bees found in this study. Origin E (exotic) and N (native).

Plant species	**Origin**
Asphodelaceae	
Bulbine frutescens (L.) Willd.	E
Plantaginaceae	
Penstemon grandiflorus Nutt.	E
Acanthaceae	
Justicia brandegeeana Wassh. & L.B.Sm.	E
Odontonema tubaeforme (Bertol.) Kuntze	E
Ruellia simplex C.Wright	E
Thunbergia erecta (Benth.) T. Anderson	E
Thunbergia grandiflora Roxb.	E
Odontonema cuspidatum (Nees) Kuntze	E
Pachystachys lutea Nees	E
Adoxaceae	
Sambucus nigra L.	E
Aizoaceae	
Mesembryanthemum cordifolium L.f.	E
Amaranthaceae	
Alternanthera brasiliana (L.) Kuntze	N
Amaranthus spinosus L.	E
Celosia argentea L.	E
Amaryllidaceae	
Agapanthus africanus (L.) Hoffmanns.	E
Anacardiaceae	
Mangifera indica L.	E
Schinus molle L.	E
Schinus terebinthifolia Raddi	N
Apiaceae	
Pimpinella anisum L.	E
Apocynaceae	
Allamanda blanchetii A.DC.	E
Allamanda cathartica L.	N
Catharanthus roseus (L.) Don	E
Nerium oleander L.	E
Thevetia peruviana (Pers.) K.Schum.	E
Arecaceae	
Washingtonia robusta H.Wendl.	E
Asparagaceae	
Asparagus aethiopicus L.	E
Chlorophytum comosum (Thunb.) Jacques	E
Asteraceae	
Acmella ciliata (Kunth) Cass.	N
Ageratum conyzoides L.	N

Aldama robusta (Gardner) E.E.Schill. & Panero	E
Aspilia camporum Chodat	E
Aspilia reflexa (Sch.Bip. ex Baker) Baker	E
Bidens pilosa L.	E
Chrysolaena obovata (Less.) Dematt.	E
Chrysolaena platensis (Spreng.) H.Rob.	N
Conyza bonariensis (L.) Cronquist	N
Cosmos sulphureus Cav.	E
Emilia fosbergii Nicolson	E
Emilia sonchifolia (L.) DC.	E
Galinsoga parviflora Cav.	E
Gutenbergia boranensis (S.Moore) M.G.Gilbert	E
Helianthus annuus L.	E
Hypochaeris radicata L.	E
Lepidaploa hagei (H.Rob.) H.Rob.	E
Leucanthemum vulgare Lam.	E
Mikania microdonta DC.	N
Parthenium hysterophorus L.	E
Senecio brasiliensis (Spreng.) Less.	N
Sonchus oleraceus L.	N
Sphagneticola trilobata (L.) Pruski	N
Symphyopappus decemflorus H.Rob.	E
Tanacetum parthenium (L.) Sch.Bip.	E
Tridax procumbens L.	E
Vernonanthura polyanthes (Sprengel) Vega & Dematteis	N
Youngia japonica (L.) DC.	E
Berberidaceae	
Nandina domestica Thunb.	E
Bignoniaceae	
Cybistax antisyphilitica (Mart.) Mart.	N
Fridericia platyphylla (Cham.) L.G.Lohmann	N
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	N
Handroanthus serratifolius (Vahl) S.Grose	N
Jacaranda mimosifolia D. Don	E
Pandorea jasminoides (Lindl.) K.Schum.	E
Podranea ricasoliana (Tanfani) Sprague	E
Tabebuia rosea (Bertol.) Bertero ex A.DC.	E
Tecoma stans (L.) Juss. ex Kunth	E
Boraginaceae	
Cordia superba Cham.	N
Brassicaceae	
Brassica napus L.	E
Brassica nigra (L.) W.D.J.Koch	E
Raphanus raphanistrum L.	E
Sinapis arvensis L.	E
Cactaceae	
Nopalea cochenillifera (L.) Salm-Dyck	E
Caprifoliaceae	

Abelia × grandiflora (Ravelli ex André) Rehder	E
Caricaceae	
Carica papaya L.	E
Caryocaraceae	
Caryocar brasiliense Cambess.	N
Clusiaceae	
Clusia rosea Jacq.	E
Combretaceae	
Combretum indicum (L.) Jongkind	E
Terminalia catappa L.	E
Commelinaceae	
Commelina erecta L.	N
Tradescantia pallida (Rose) D.R.Hunt	E
Convolvulaceae	
Ipomoea cairica (L.) Sweet	N
Ipomoea carnea Jacq.	N
Ipomoea purpurea (L.) Roth	N
Cucurbitaceae	
Bryonia alba L.	E
Cucurbita máxima Duchesne ex Lam.	E
Luffa cylindrica (L.) M.Roem.	E
Momordica charantia L.	E
Ericaceae	
Rhododendron indicum var. simsii (Planch.) Maxim.	E
Euphorbiaceae	
Euphorbia hirta L.	N
Euphorbia hypericifolia L.	N
Euphorbia milii Des Moul.	E
Euphorbia pulcherrima Willd. ex Klotzsch	E
Jatropha podagrica Hook.	E
Ricinus communis L.	E
Fabaceae	
Bauhinia purpurea L.	E
Bauhinia variegata L.	E
Caesalpinia pulcherrima (L.) Sw.	E
Calliandra brevipes Benth.	N
Calliandra tweedii Benth.	N
Cassia ferruginea (Schrad.) Schrad. ex DC.	N
Cassia fistula L.	E
Cassia grandis L.f.	N
Cenostigma pluviosum (DC.) Gagnon & G.P.Lewis	N
Chamaecrista neesiana (Mart. ex Benth.) H.S.Irwin & Barneby	E
Crotalaria micans Link	N
Delonix regia (Bojer ex Hook.) Raf.	E
Leucaena leucocephala (Lam.) de Wit	E
Macroptilium lathyroides (L.) Urb.	N
Peltophorum dubium (Spreng.) Taub.	N
Senna macranthera (DC. ex Collad.) H.S.Irwin & Barneby	N

Senna pendula (Humb.& Bonpl.ex Willd.) H.S.Irwin & Barneby	N
Tara spinosa (Molina) Britton & Rose	E
Tipuana tipu (Benth.) Kuntze	E
Hydrangeaceae	
Philadelphus coronarius L.	E
Iridaceae	
Dietes bicolor (Steud.) Klatt ex Sweet	E
Neomarica caerulea (Ker Gawl.) Sprague	N
Lamiaceae	
Callicarpa nudiflora Hook. & Arn.	E
Clerodendrum × *speciosum* Dombrain	E
Gmelina arborea Roxb.	E
Lavandula dentata L.	E
Mesosphaerum suaveolens (L.) Kuntze	N
Ocimum gratissimum L.	E
Plectranthus scutellarioides (L.) R. Br.	E
Loranthaceae	
Struthanthus flexicaulis	N
Lythraceae	
Cuphea hyssopifolia Kunth	E
Cuphea racemosa (L.f.) Spreng.	N
Lafoensia pacari A.St.-Hil.	N
Lagerstroemia indica L.	E
Lagerstroemia speciosa Pers.	E
Punica granatum L.	E
Malpighiaceae	
Banisteriopsis argyrophylla (A.Juss.) B.Gates	E
Banisteriopsis campestris (A.Juss.) Little	E
Heteropterys tomentosa A.Juss.	E
Lophanthera lactescens Ducke	E
Malpighia coccigera L.	E
Malvaceae	
Callianthe striata (Dicks. ex Lindl.) Donnel	N
Hibiscus rosa-sinensis L.	E
Hibiscus syriacus L.	E
Malvastrum coromandelianum (L.) Garcke	N
Malvaviscus arboreus Cav.	E
Sida acuta Burm.f.	N
Sida rhombifolia L.	N
Waltheria indica L.	N
Melastomataceae	
Chaetogastra herbacea (DC.) P.J.F.Guim. & Michelang.	N
Pleroma granulosum (Desr.) D. Don	N
Pleroma mutabile (Vell.) Triana	N
Meliaceae	
Azadirachta indica A.Juss.	E
Cabralea canjerana (Vell.) Mart.	N
Muntingiaceae	

Muntingia calabura L.	E
Myrtaceae	
Callistemon rigidus R.Br.	E
Eugenia involucrata DC.	N
Eugenia uniflora L.	N
Melaleuca linariifolia Sm.	E
Psidium guajava L.	E
Nyctaginaceae	
Bougainvillea spectabilis Willd.	N
Mirabilis jalapa L.	E
Oleaceae	
Ligustrum lucidum W.T.Aiton	E
Pittosporaceae	
Pittosporum tobira (Thunb.) W.T.Aiton	E
Plantaginaceae	
Russelia equisetiformis Schltdl. & Cham.	E
Plumbaginaceae	
Plumbago auriculata Lam.	E
Poaceae	
Urochloa decumbens (Stapf) R.D.Webster	E
Polygalaceae	
Asemeia violacea (Aubl.) J.F.B.Pastore & J.R.Abbott	N
Polygonaceae	
Antigonon leptopus Hook. & Arn.	E
Polygonum capitatum Buch.-Ham. ex D.Don	E
Portulacaceae	
Portulaca grandiflora Hook.	N
Portulaca oleracea L.	E
Proteaceae	
Grevillea banksii R.Br.	E
Grevillea robusta A.Cunn. ex R.Br.	E
Rosaceae	
Rosa chinensis Jacq.	E
Rubiaceae	
Borreria verticillata (L.) G.Mey.	N
Ixora coccinea L.	E
Mussaenda philippica A.Rich.	E
Richardia scabra L.	N
Rutaceae	
Citrus × *limon* (L.) Osbeck	E
Murraya paniculata (L.) Jack	E
Solanaceae	
Brugmansia suaveolens (Willd.) Sweet	E
Brunfelsia uni*flora* (Pohl) D.Don	N
Iochroma arborescens (L.) J.M.H. Shaw	N
Solanum americanum Mill.	N
Solanum lycocarpum A.St.-Hil.	N
Solanum palinacanthum Dunal	N

Turneraceae	
Turnera subulata Sm.	N
Turnera ulmifolia L.	E
Verbenaceae	
Duranta erecta L.	E
Lantana camara L.	E
Lippia alba (Mill.) N.E.Br. ex Britton & P.Wilson	N
Petrea volubilis L.	N
Stachytarpheta cayennensis (Rich.) Vahl	N
Verbena bonariensis L.	N
Verbena officinalis L.	E
Vitaceae	
Cissus verticillata (L.) Nicolson & C.E.Jarvis	N

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ARTIGO II

Sharing or sparing? Effects of the urban development on bees

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Sharing or sparing? Effects of the urban development on bees

Abstract

Urbanization is one of the most intensive and rapidly expanding forms of landscape change, resulting in consequences for biodiversity and thus ecosystem health and functioning. Understanding the mechanisms behind the loss of biodiversity is crucial to develop evidence-based sustainable solutions to preserve biodiversity in urban landscapes. Urban areas can be developed in many ways, but there are two urban development types with recent focus of debates, land-sparing (large, continuous green areas and high-density housing) and land-sharing (small, fragmented green areas and low-density housing). There are still few empirical examinations of the preferred strategy in urban landscapes for biodiversity or maintenance of ecosystem processes. Here we evaluated how these urban development models impact bee communities. We also evaluated a third model characterized by the low or absence of green areas, the land fully occupied areas. We found a higher richness of species (total, below-ground nesting bees, and generalist species), and richness of genera in the land-sharing model compared to land fully occupied model. The number of unique species was also higher in land-sharing areas compared to land-sparing areas and land fully occupied. The functional uniformity (Feve) found in land-sharing was lower compared to land fully occupied, indicating that the distributions of functional traits were less uniformly distributed in these areas. We present one of the few studies that evaluated the effects of urban development models on fauna, and we demonstrated a remarkable conservation benefit of land-sharing on bee community. The application of the land-sparing and land-sharing concept to urban planning is a significant advance over studies applied across simple urban gradients.

Keywords: urban landscape, urban biodiversity, land-sharing, land-sparing, pollinators.

1 Introduction

Urbanization is one of the fastest growing land use types globally with unprecedented magnitude. The global proportion of the urban population was 29% in 1950 and projections for 2050 predict an increase to 70%, almost doubling the 3.5 billion urban inhabitants worldwide in 2010 (UN, 2010; Seto et al., 2013). In addition, urban land is growing at rates at least twice as fast as the urban population worldwide (Angel et al., 2011). Projections also show that urbanization is occurring faster and to a greater extent in developing-country cities (Angel et al., 2005). These regions harbor almost 90% of the protected areas likely to be impacted by urbanization (McDonald et al., 2008). For instance, the largest urban expansion in biodiversity hotspots is predicted to occur in South America (Güneralp & Seto, 2013). Therefore, as urban areas increase, interest in understanding how cities should expand and minimize their ecological impacts grows.

The relationship between urbanization and biodiversity is controversial, as while some urban areas harbor high species richness, others may be related to biodiversity loss. (McKinney, 2006). Urban sprawl can lead to habitat fragmentation, harming species movement. Therefore, it is not just the size of urban areas that impacts biodiversity but also their spatial configuration and environmental heterogeneity (Ricketts, 2001; Tratalos et al., 2007). In this regard, stimulating urban development forms that support a wide range of ecological functions will be essential to future cities to prevent further biodiversity loss.

Urban areas can be developed in many ways, but a long-standing debate about urbanization regards the land-sharing or land-sparing development models (Lin & Fuller, 2013, Stott et al., 2015). Land-sharing urban areas consist of low-density built areas (e.g., family houses) with small and fragmented green areas, usually in the form of backyards and street vegetation. In contrast, land-sparing urban areas are characterized by high-density built areas (e.g., multi-story buildings) with large-sized continuous green areas (Lin & Fuller, 2013). Promoting any of these pro-biodiversity urban development strategies requires strong evidence of their benefits (Caryl et al., 2016). The urban landscape configuration, which differs between development-urban models, can act as an environmental filter for a range of species. Some evidence suggests that characteristics such as habitat specificity and individual mobility may predispose species to differently tolerate land-sparing or land-sharing strategies. Species that depend on large areas of natural habitat are likely to benefit from land-sparing scenarios (Gagné & Fahrig, 2010; Sushinsky et al., 2013; Soga et al., 2014). For instance, a study in Brisbane (Australia) showed that the richness of urban birds was higher in this urban development model (Sushinsky et al., 2013). On the other hand, species that persist in urbanized landscapes without large patches of natural habitat and that use resources from the urban matrix may benefit from land sharing, as has been demonstrated for butterflies (Soga et al., 2014).

Bees are a taxonomic group significantly affected by urbanization and impacts on species richness and community structure have been extensively investigated (Wenzel et al., 2020). At the landscape scale, bees were mainly influenced by the intensity of urbanization, often quantified as the proportion of impervious surface, and by the proportion of green areas (Fortel et al., 2014; Geslin et al., 2016; Sivakoff et al., 2018; Stewart et al., 2018; Buchholz & Egerer 2020; Banaszak-Cibicka & Dylewski 2021; Graf et al., 2022). The configuration of green areas is an important factor in patterns in the diversity of pollinators, in addition to their proportional coverage. For example, green areas that extend from the city edges towards the center can act as corridors that promote pollinator diversity in central urban areas (Banaszak-Cibicka, Ratyńska & Dylewski 2016; Wenzel et al., 2020). In this context, urban areas have the potential to provide an important contribution to bee conservation, yet large knowledge gaps remain. The aspects of urban development have been rarely investigated, and studies focus on the composition of urban matrices while neglecting the spatial configuration (Wenzel et al., 2020). Additionally, tropical regions are underrepresented in surveys.

Previous studies investigating the effects of land-sharing/land-sparing on biodiversity have focused exclusively on taxonomic diversity (e.g., Sushinsky et al., 2013; Soga et al., 2014; Villaseñor et al., 2017). However, recent trends in biodiversity studies strongly recommend the use of multiple measures to investigate several components of biodiversity simultaneously because they can be affected differently by the same process (Devictor et al., 2010; Hanspach et al., 2015; Buchholz et al., 2020). In this research, focused on bees in urban areas, we evaluated the effect of urban development models on taxonomic and functional diversity, beta diversity, and species composition. Our first prediction was that land-sharing areas would harbor greater taxonomic and functional diversity of bees compared to land-sparing and land fully occupied, as they provide greater diversity and proximity between different habitats, besides nesting and foraging resources. The second prediction was that land-sparing areas would harbor a different set of bee species, which are more specialized and less tolerant of environmental changes, representing a high ecological uniqueness compared to land-sharing and land fully occupied areas.

2 Method

2.1 Study area and classification of urban areas

Our study was conducted in six cities in southern Minas Gerais, Brazil (Fig. 1). These cities are classified as medium-sized cities (80,973 to 169,838 inhabitants), inside a non-metropolitan region. The demographic density of these cities varies from 86.7 to 311.3 inhabitants/km^2. Outside the urban areas, the region is characterized by intensive agricultural landscapes and remnants of the Atlantic Forest (IBGE, 2017). In the six sampled cities, we selected a total of 20 sites with different development urban models (land-sparing, land-sharing and land fully occupied).

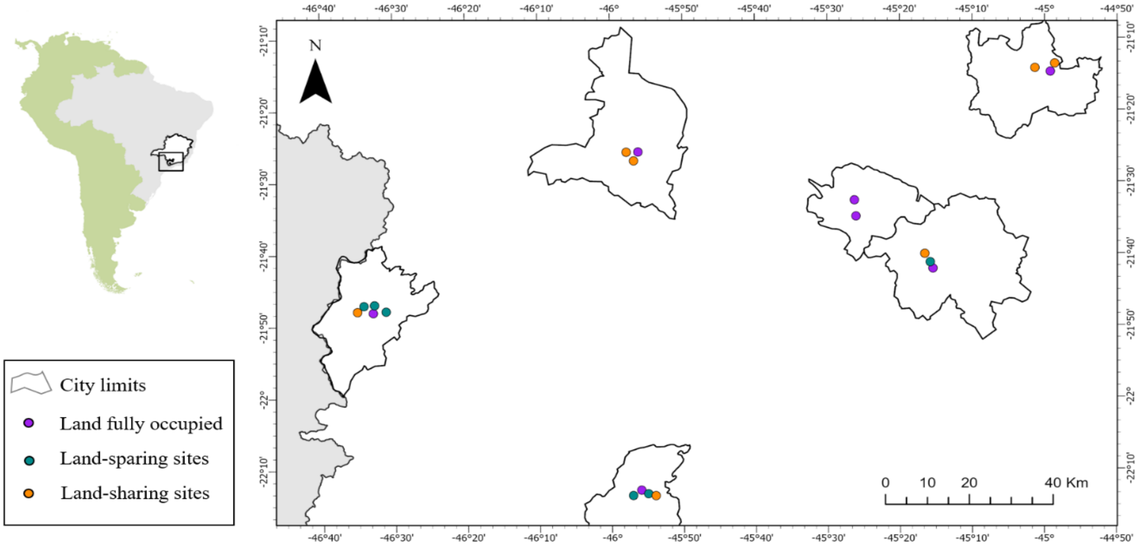

Fig. 1 Sampling design and location of the 20 sites distributed across 6 Brazilian cities. The panel on the left represents South America (light green), Brazil (light gray), and the state of Minas Gerais (white) with the delimitation of the study region (black line square). Each dot color represents an urban development model (orange = land-sharing, green = land-sparing, and purple = land fully occupied).

We used Sentinel-2 images of the study areas (obtained in September 2019) with a resolution of 10 m to characterize the landscape around each study site. The Semiautomatic Classification (SCP) plugin (Congedo, 2016) was used to classify the images in QGIS software version 3.10.0 (QGIS Development Team, 2019). Using the LeCos plugin (Jung 2016), we calculated the proportion of impervious surface, the proportion of green surface (forest remnants and parks), and the largest patch index (LPI) within a 1 km radius. LPI represents the proportion of green space in a given locality that comprises a single contiguous patch. High values, therefore, represent increasingly large (i.e., spared) patches relative to overall cover by green space (Dennis et al., 2019). We did not include pastures and grasses in the green areas because they are areas that are constantly changing in the urban environment, such as vacant lots quickly converted into built-up areas.

We performed a principal component analysis (PCA) to identify patterns and categorize the 20 urban areas according to their LPI and impervious surface values. We did not incorporate the proportion of green coverage as it was highly correlated with LPI ($\rho = 0.9$). The analysis was performed in R Software using "FactorMineR" package (Husson et al., 2016).

2.2 Bee survey

We sampled bees at each site one day per month, four hours per day, for six months in 2020 and 2021. We sampled floral visitors in all plant species in a radius of 200 m around the center point of each location. We only collected in urban areas adjacent to green areas. For each plant species, we captured bees for ten minutes with an entomological net. Bees were kept in bottles with ethyl acetate, processed, fixed, and identified. The determination to genus was performed using the book by Silveira et al. (2002) and even species through studies of taxonomic reviews performed by experts.

2.3 Data analysis

We evaluated the changes in alpha, beta and functional diversity of the community to assess how urban development models influence the bee community. Bee richness, bee abundance, and richness and abundance of each functional group (eusocial, solitary, primitively eusocial, above-ground nesting, below-ground nesting, generalist, and specialist), genera richness, number of unique species (abundance equal to 1), and Shannon's diversity index were selected as alpha diversity metrics. We calculated these metrics using the package "vegan" (Oksanen et al., 2019). Information on the functional characteristics of each species was obtained from data available in the literature (Michener 2007; Martins et al., 2013; Graf et al., 2022) and consultation with experts.

We also calculated the main components of functional diversity: functional richness (Fric), functional divergence (Fdiv) and functional evenness (Feve), calculated as described by Mason et al. (2005) and Villéger et al. (2008). Functional richness is a representation of the species richness (and its functional attributes) of a community and measures the amount of functional space filled by the species (Mason et al., 2013). Functional divergence is a measure that describes the irregularity in the distribution of attribute values in the volume of functional space occupied by all species in a certain community (Garnier & Navas, 2012). Functional evenness measures how uniform is the distribution of the abundance of functional attribute values in the functional space (Villéger et al., 2008). We used information about bee functional traits (social behavior, nesting habit, and trophic specialization) to calculate feature distances between species based on the Gower distance coefficient using the *gowdis* function from the FD package (Laliberté et al., 2014).

We calculated total beta diversity (BDtotal) and considered the local contribution to beta diversity (LCBD) following the approach proposed by Legendre and De Cáceres (2013). LCBD represents the ecological singularity of a local, providing a measure of the relative contribution of a given sampling unit to beta diversity. Following Legendre & De Cáceres (2013), the abundance matrix is transformed by the "hellinger" method and, subsequently, the total beta diversity (total BD) and the LCBD value for each location are calculated using *beta.div* function in "adespatial" package (Dray et al., 2018). High values of LCBD indicate the high importance of a given site for overall beta diversity (i.e., variation in species composition between sites).

The differences in alpha diversity, functional diversity, and LCBD indices among urban development models were assessed by one-way ANOVA followed by Tukey's post hoc tests. When the assumptions of normality and homogeneity of variance were not met, we used the Kruskall-Wallis test with subsequent paired Wilcoxon test with Bonferroni correction. All statistical tests were considered significant at $p < 0.05$. We considered models that were significantly different ($p<0.05$) compared to the null models tested. Effect sizes for ANOVASs and Kruskall-Wallis test were reported as Eta Squared (η) using *eta_squared* and *kruskal_effsize* functions, respectively, in "rstatix" package (Kassambara et al., 2020).

To compare the species composition within each urban development model, we performed a principal coordinate analysis (PCOA) of the presence/absence and abundance data, using the Jaccard and Bray-Curtis dissimilarity index, respectively. We removed species whose abundance was equal to 1 (Legendre & Gallagher, 2001). We performed a logarithmic transformation on the species matrix, calculated the distance matrix (*vegdist* function, "vegan" package) and performed the PCOA with the *caillidez* correction (*pcoa* function, "ape" package (Paradis et al., 2019). As we capture many low-abundance bee species, whose probability of being caught in all locations may be low, we repeated the same procedure for the eusocial bees, which are naturally more abundant and therefore more likely to be collected. Furthermore, as the study locations were distributed among six different cities, we also analyzed the set of species that were collected in at least four cities (37 species). Clusters were evaluated using permutational analysis of variance (PERMANOVA) (Anderson, 2001) with 9,999 permutations to test for significant differences in species composition (Anderson & Walsh 2013). All statistical analyzes were performed in R (R Core Team, 2019).

3 Results

We collected 4,279 individuals from 132 bee species and 55 genera. Of the total, 54 species were represented by only one individual, 37 species were sampled in the three urban development models, while 16 species were found only in the land-sparing model, 37 in land-sharing, and 14 in the land fully occupied model (Fig.2). The list of species found in each model is available in the supplementary material.

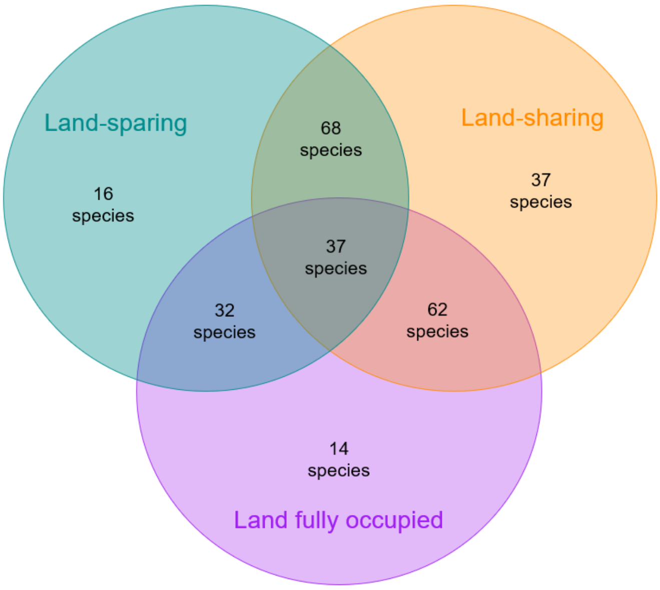

Fig.2 Venn diagram representing the number of species found in each model of urban development.

Through the analysis of PCA, which presented 56.6% variation on the first axis and 43.4% on the second axis, we obtained the grouping of the three urban development models (Fig. 3). Six areas were classified as land-sparing, seven areas as land-sharing and seven areas as land fully occupied. The models classified as "land fully occupied" had a percentage of tree cover lower than 10% within a 1 km radius. The land-sharing sites had patches of green areas inserted and sprawled in the urban matrix, while the land-sparing sites had large and continuous patches but were isolated from the urbanized area.

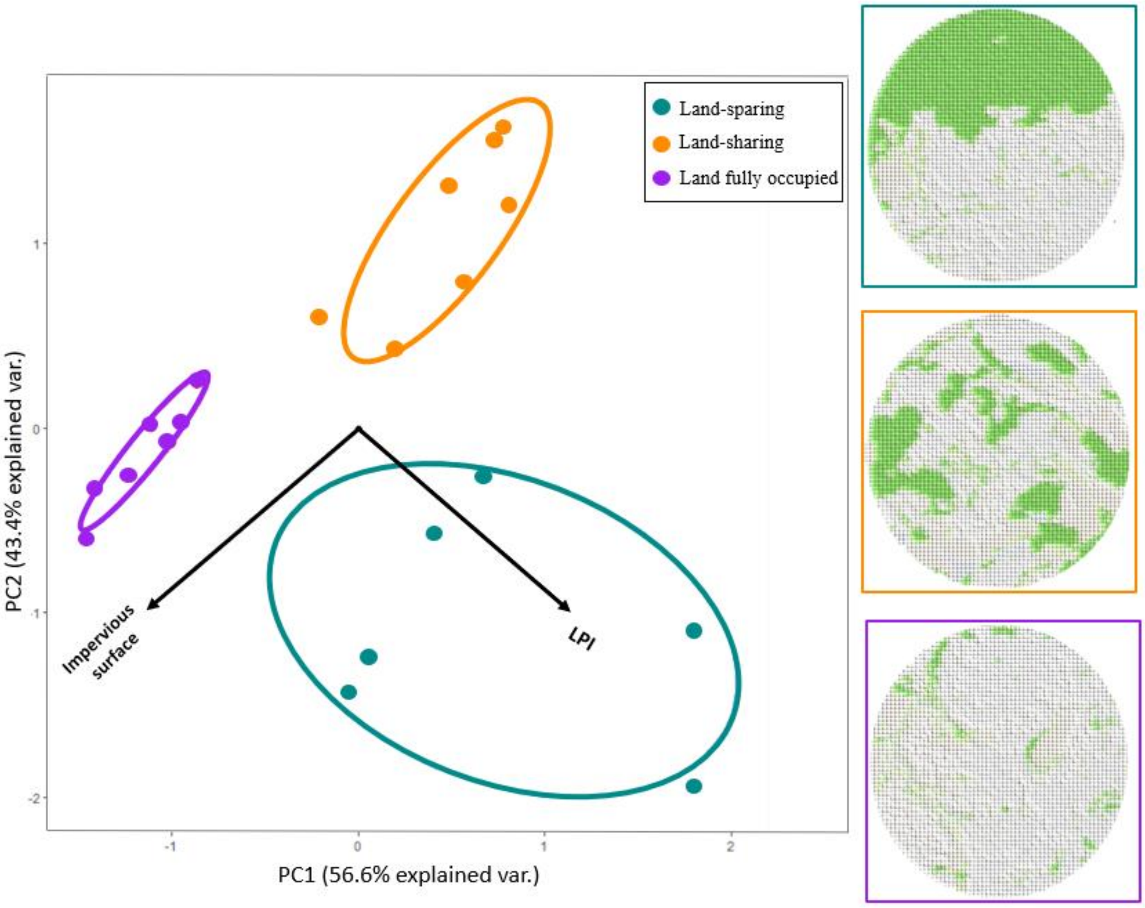

Fig. 3 Results of a principal component analysis (PCA) analysis showing the clustering of urban development models (land-sparing, land-sharing, and land fully occupied). Next to the PCA plot are schematic illustrations with examples of three study areas within a 1 km radius (land-sparing, land-sharing, and land fully occupied sites). Green and gray cells indicate arboreal vegetation and urbanized areas, respectively.

Total bee richness, genera richness, number of unique species, below-ground nesting bee richness and generalist bee richness were higher in the land-sharing model compared to land fully occupied (Table 1, Fig. 4). The number of unique species in land-sharing was about twice compared to those of land-sparing and land fully occupied. Regarding the functional diversity metrics, we found a difference only for the functional regularity (Feve), which was lower in the land-sharing compared to land fully occupied (Table 1, Fig. 4). The effect size for these metrics revealed a large difference between the three models (η = 0.33 to 0.44) (Cohen, 1992). In general, land-sparing and land fully occupied did not differ for the evaluated metrics.

Eusocial, primitively eusocial, solitary, above-ground, and specialist bee richness, as well as total abundance and functional groups abundance, did not show differences between the three urban development models. The Shannon diversity index and the other functional diversity indices were also no different between land-sharing, land-sparing, and land fully occupied.

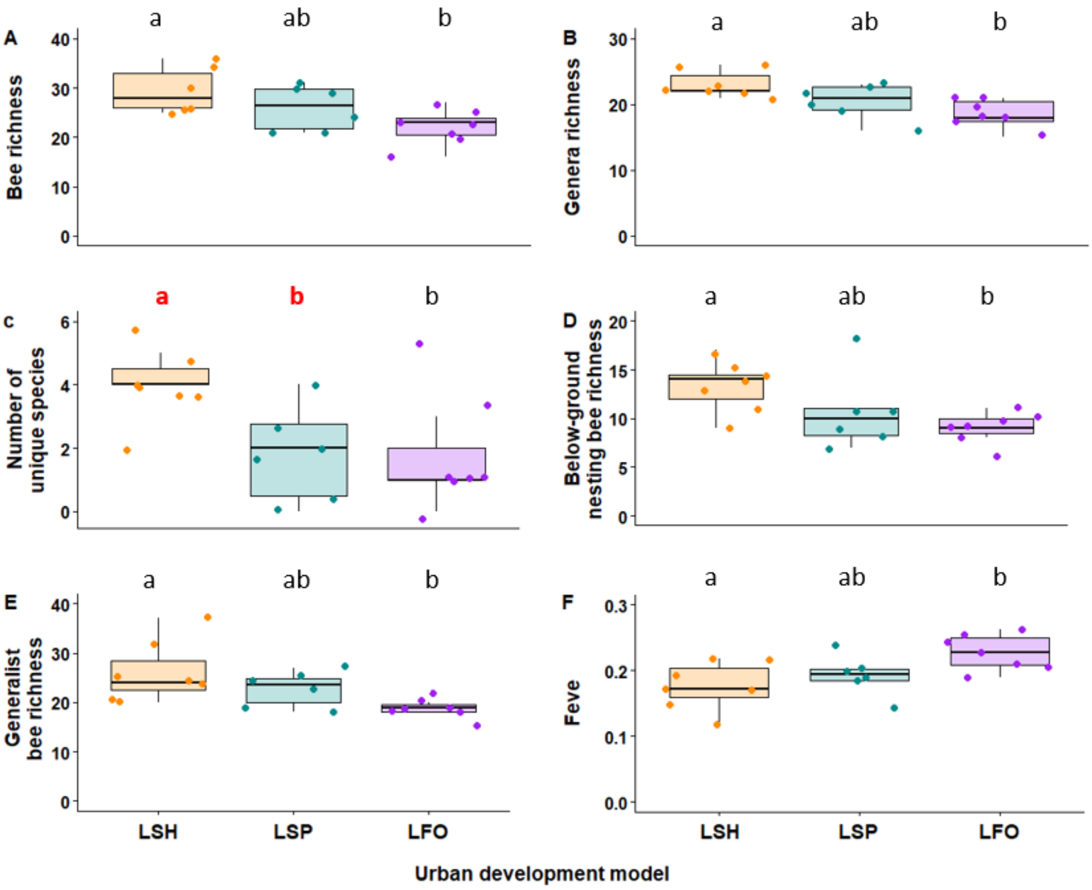

Fig.4 Comparison of bee richness, genera richness, number of unique species, below-ground nesting bee richness, generalist bee richness and Feve among land-sharing (LSH), land-sparing (LSP), and land fully occupied (LFO). The boxplots show the median (bar inside of rectangles), upper and lower quartiles and individual observations (points).

Table 1 Differences among the urban development models (means ± standard deviation). Values followed by the same letter do not differ significantly from one another (as determined by ANOVA/Tukey analysis). The p-values show significance levels of a one-way ANOVA test for differences among urban development models.

	Bee richness	**Genera richness**	**Number of unique species**	**Below-ground nesting bee richness**	**Generalist bee richness**	**Feve**
Land-sharing	31.14 ± 6.06 ^{a}	23.14 ± 2.03 ^{a}	4.14 ± 1.2 ^{a}	13.3 ± 2.6 ^{a}	26.1 ± 6.14 ^{a}	0.17 ± 0.036 ^{a}
Land-sparing	26 ± 4.56 ^{ab}	20.5 ± 2.7 ^{ab}	1.83 ± 1.6 ^{b}	10.7 ± 3.9 ^{ab}	22.7 ± 3.5 ^{ab}	0.19 ± 0.031 ^{ab}
Land fully occupied	22.14 ± 3.6 ^{b}	18.6 ± 2.2 ^{b}	1.71 ± 1.7 ^{b}	9 ± 1.6 ^{b}	18.7 ± 2.1^{b}	0.23 ± 0.027 ^{b}
p-value	0.01	0.006	0.01	0.03	0.01	0.02
Effect size	0.42	0.44	0.40	0.33	0.39	0.36
CI (Effect size)	0.08 – 1.00	0.11 – 1.00	0.07 – 1.00	0.02 – 1.00	0.11 – 0.71	0.04 – 1.00

In the whole sampling area, the BDtotal value based on abundance was 0.24, indicating low dissimilarity between areas. Concerning LCBD, only two sites had a significant contribution to the local beta diversity ($p < 0.05$; LCBD ≥ 0.07). They were situated in land-sharing areas. However, the LCBD values were not different among the urban development models (p=0.17). LCBD values for each site are available in the supplementary material.

The composition of species did not differ among the urban development models, neither for presence and absence nor for abundance data (PERMANOVA F=0.99, p=0.49; F=0.98, p=0.49, respectively). We also did not find significant clusters for species that were collected in at least four cities (PERMANOVA F=1.03, p=0.41; F=1.05, p=0.38), and for eusocial species (PERMANOVA F=1.12, p=0.3; F=1.14, p=0.33).

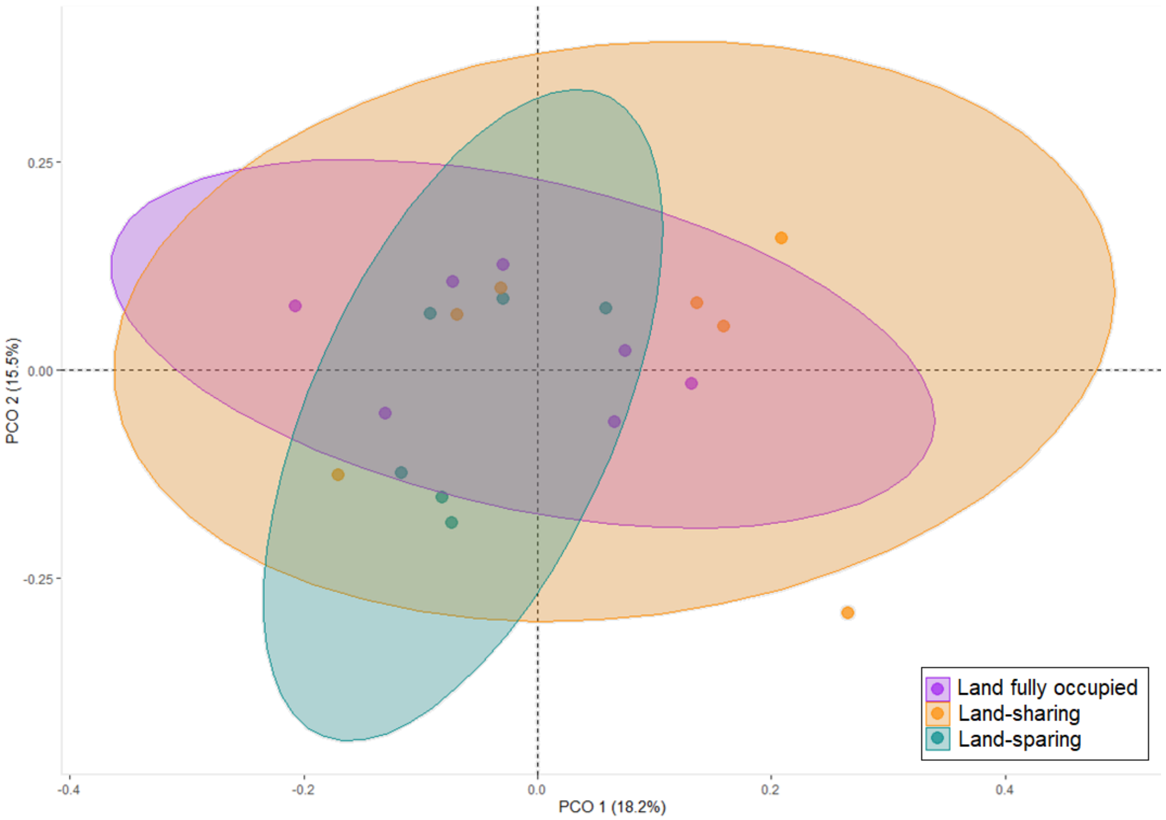

Fig. 5 PCOA of abundance data for the total species set. Points represent sites and each color represents an urban development model. The ellipses represent the grouping of classes.

4 Discussion

As predicted in our first hypothesis, the results indicated that the land-sharing urban development model presented a richness of species (total, below-ground nesting bees, and generalist species), and richness of genera higher than in land fully occupied model. The number of unique species was higher in land-sharing areas than land-sparing areas and in sites of land fully occupied. Other studies have also demonstrated greater taxonomic diversity in land-sharing areas, such as bird richness (Ibáñez-Álamo, 2020), butterflies (Soga et al., 2014), and trees (Collas et al., 2017), suggesting that other animals and plants may follow similar patterns.

Some hypotheses could explain the relation of greater taxonomic diversity of bees with urban land-sharing areas. First, based on the intermediate disturbance hypothesis, it has been suggested that species richness peaks at intermediate levels of disturbance in an urban gradient due to the number of available habitats (Callaghan et al., 2019; Jokimäki & Suhonen 1993; Luck & Smallbone 2010; Tratalos et al., 2007; Battisti et al., 2016). In contrast to land-sparing and land fully occupied, land-sharing areas can offer a greater diversity of habitats within the bee's range foraging. Human practices such as the maintenance of gardens, parks, squares, and urban gardens benefit many species of bees (Fortel et al., 2016; Rahimi et al., 2022). Second, the distance between an urban area and a green area is one of the decisive factors in the richness of bee species in a city, as it facilitates their movement between areas (Banaszak-Cibicka et al., 2016). This is particularly true for small bee species with small flight radii, which the higher accessibility to different land cover types allows them to find and use more diversified feeding and nesting resources (Greenleaf et al., 2007; Boscolo et al., 2017). In the land-sharing model, green areas are immersed in the urban matrix, and preserved areas, parks and gardens can potentially be springboards that allow the colonization of the city center by bees. In the land-sparing model, where green areas are further away from the urban area, the movement of bees can be difficult.

The lower functional uniformity (Feve) found in the land-sharing compared to land fully occupied model indicates that the distributions of functional traits were less uniformly distributed in these areas, probably due to the presence of species with unique traits (Mason et al., 2005; Villéger et al., 2008; Sitters et al., 2016). Sites without green areas may contain redundant species that are more spread out along gradients of functional characteristics (Mason et al., 2005; Villéger et al., 2008; Pakeman, 2011). Thus, these areas can act as filters and restrict the combinations of traits, increasing the similarity of bee species (Lamanna et al., 2014). We found no differences for richness and functional divergence between the urban development models. Functional richness (FRic) can remain constant when functional redundancy is high (Mason et al., 2005). However, as we used only three functional characteristics of the species, we may not have captured the variation in functional richness between conservation models. Regarding functional divergence, the permanence of the same species as the most abundant in the localities makes significant changes in their values impossible. This is particularly expected for the bee community, where eusocial species are ecologically dominant and most abundant in urban areas (Michener 2007; Chapman & Bourke 2001).

The local community beta diversity values were not different between the urban development models, indicating that we did not find an ecological singularity in the land-sparing areas, contrary to our hypothesis. Few studies have assessed LCBD values in urban environments, and two showed a decrease in their values for fish and bats with increasing urban coverage (Ortega et al., 2021; Bogoni et al., 2021). We have not found any previous studies evaluating this measure among development models in cities. The two areas that demonstrated significant LCBD values correspond to two university campi located within the urban areas. This indicates that different urban sectors can provide different responses to biodiversity. Universities are not fully inhabited areas and are usually composed of a high number of gardens, which can therefore house a larger set of bee species.

Although highly species-specific, urbanization tends to eliminate highly specialized species, homogenizing the fauna and making communities more similar (McKinney, 2006; Groffman et al., 2014; Russo & Ancillotto 2015; Allen et al., 2019). In our study we found a high taxonomic similarity among sites, which is characteristic of biotic homogenization (Zhang et al., 2022). However, 37 bee species were found exclusively in the land-sharing areas, in contrast to 16 and 14 species in the land-sparing and land fully occupied, respectively. In addition, the number of unique species was also higher at these sites, indicating that land-sharing areas can support more species of bees.

Contrary to our expectations, we found no differences in bee species composition. However, as our study covered six cities, factors on a regional scale (e.g., climate) may be more important in determining species composition than urbanization, which would have more influence on richness (Field et al., 2009; Geppert et al., 2022). Our results showed no differences in the diversity measures between land-sparing and land fully occupied. However, bee species with high habitat requirements that need large-diameter trees for nesting, and species with smaller body sizes and flight ranges, may be retained in the green areas and not have been collected in the urban areas. Besides, land-sparing areas showed more favorable for birds, beetles, and mammals, thus, it is possible that certain area-sensitive species may benefit from large green patches in urban areas (Sushinsky et al., 2013; Soga et al., 2014; Villaseñor et al., 2017; Jokimäki et al., 2019).

In this work, we present one of the few attempts thus far to assess the effects of urban development models on fauna. To our knowledge, our work is the first quantification of bee diversity under land-sharing and land-sparing scenarios in urban areas. We demonstrated that the land-sharing model can harbor a greater diversity of bees compared to other models, but we need research in cities with higher levels of urbanization for more comprehensive conclusions. Importantly, we carried out the research in small and medium-sized cities, with urbanization intensities lower than in metropolis. Unlike large urban centers, these cities are composed of grasslands, vacant lots, gardens, and green areas with a semi-natural characteristic. They are also permeated by agricultural crops and grasslands composing a diverse landscape, which can contribute to reducing the effects of urbanization on biodiversity. In addition, we need collections carried out within urban forest fragments to assess community composition in these sites.

Our study has demonstrated that the application of the land-sparing and land-sharing concept to urban planning is a significant advance over studies applied across simple urban gradients and should therefore be better evaluated in future research. For the protection of native biodiversity in the face of urban sprawl, the results of the present study have several implications. They show a remarkable conservation benefit of land-sharing for bee community. Land-sharing can exhibit some benefits beyond biodiversity conservation, such as residents being connected to nature due to the proximity of housing and green spaces. Conversely, land sparing is a vital strategy for urban development, to accommodate increasing urban populations while restoring areas of green space within cities.

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Supplementary material

Table SI Bee species found in each type of urban development model. Values 0 and 1 represent absence and presence, respectively.

Bee species	**Land fully occupied**	**Land-sharing**	**Land-sparing**
Acamptopoeum prinii Holmberg, 1884	0	0	1
Anthidiini sp1	0	1	0
Anthodioctes megachiloides Holmberg, 1903	1	0	0
Apis mellifera Linnaeus, 1758	1	1	1
Augochlora (Augochlora) sp1	0	1	0
Augochlora (Augochlora) sp2	0	1	1
Augochlora (Augochlora) sp3	0	1	0
Augochlora (Augochlora) sp4	0	0	1
Augochlora (Oxystoglossella) sp1	1	1	1
Augochlora (Oxystoglossella) sp2	1	0	1
Augochlora (Oxystoglossella) sp3	0	1	0
Augochlora esox Vachal, 1911	1	1	1
Augochlora morrae Strand, 1910	1	1	1
Augochlorella ephyra Schrottky, 1910	1	1	1

Augochloropsis (Augochloropsis) sp1	0	1	0
Augochloropsis (Paraugochloropsis) sp1	1	1	1
Augochloropsis (Paraugochloropsis) sp2	0	1	0
Augochloropsis (Paraugochloropsis) sp3	0	1	0
Augochloropsis (Paraugochloropsis) sp4	1	1	0
Bombus brasiliensis Lepeletier, 1836	0	0	1
Bombus morio Swederus, 1787	1	1	1
Bombus pauloensis Friese, 1913	1	1	1
Centris aenea Lepeletier, 1841	0	1	1
Centris analis Fabricius, 1804	1	1	0
Centris collaris Lepeletier, 1841	1	1	1
Centris discolor Smith, 1874	1	1	1
Centris fuscata Lepeletier, 1841	0	1	1
Centris mocsaryi Smith, 1874	0	1	0
Centris sp1	0	1	1
Centris tarsata Smith, 1874	1	1	0
Centris trigonoides Lepeletier, 1841	1	1	1
Cephalotrigona capitata Smith, 1854	0	1	1

Cephalurgus anomalus Moure & Lucas de Oliveira, 1962	0	1	1
Ceratina (Ceratinula) sp1	0	0	1
Ceratina (Ceratinula) sp2	1	0	0
Ceratina (Ceratinula) sp3	0	1	0
Ceratina (Ceratinula) sp4	0	0	1
Ceratina (Crewella) sp1	0	1	0
Ceratina (Crewella) sp2	0	1	0
Ceratina (Crewella) sp3	0	1	1
Ceratina canaliculata Roig-Alsina, 2016	0	1	0
Ceratina oxalidis Schrottky, 1907	0	1	1
Ceratina richardsoniae Schrottky, 1909	0	1	0
Ceratina sclerops Schrottky, 1907	0	1	0
Coelioxys sp1	0	1	0
Dialictus sp1	0	1	1
Dialictus sp2	0	1	0
Dialictus sp3	1	0	1
Dialictus sp4	1	0	0
Dialictus sp5	1	0	0

Dialictus sp6	0	0	1
Dialictus sp7	0	0	1
Dicranthidium gregarium Schrottky, 1905	0	1	0
Epanthidium sp1	1	0	0
Epanthidium tigrinum Schrottky, 1905	1	1	1
Epicharis albofasciata Smith, 1874	0	1	0
Epicharis analis Lepeletier, 1841	1	1	1
Epicharis flava Friese, 1900	1	1	1
Euglossa cordata Linnaeus, 1758	1	1	0
Euglossa securigera Dressler, 1982	0	1	0
Euglossa townsendi Cockerell, 1904	1	1	0
Euglossa truncata Rebêlo & Moure, 1996	0	1	1
Eulaema nigrita Moure, 1950	1	1	1
Exaerete smaragdina Guérin, 1844	1	1	0
Exomalopsis analis Spinola, 1853	1	1	1
Exomalopsis auropilosa Spinola, 1853	1	1	1
Exomalopsis collaris Friese, 1899	0	1	0
Exomalopsis fernandoi Moure, 1990	0	1	0

Exomalopsis fulvofasciata Smith, 1879	1	1	1
Exomalopsis sp1	1	1	1
Exomalopsis sp2	0	1	0
Exomalopsis sp3	0	1	0
Friesella schrottkyi Friese, 1900	1	1	1
Geotrigona subterranea Friese, 1901	1	1	1
Habralictus sp	0	0	1
Hylaeus sp1	0	0	1
Hylaeus sp2	0	0	1
Leiopodus lacertinus Smith, 1854	0	0	1
Lophopedia minor Aguiar, 2009	1	0	0
Lophopedia nigrispinis Vachal, 1909	1	0	0
Megachile (Austromegachile) sp1	1	0	0
Megachile (Dactylomegachile) sp1	0	1	0
Megachile (Ptilosarus) sp1	0	1	0
Megachile apicipennis Schrottky, 1902	0	1	1
Megachile orba Schrottky, 1913	0	1	0
Megachile pseudanthidioides Moure, 1943	0	1	0
Megachile susurrans Haliday, 1836	0	0	1

Melipona marginata Moure, 1971	0	0	1
Melipona quadrifasciata Lepeletier, 1836	0	1	0
Melipona quinquefasciata Lepeletier, 1836	1	1	0
Melipona rufiventris Lepeletier, 1836	0	1	0
Melissodes nigroaenea Smith, 1854	0	1	1
Melissoptila cnecomala Moure, 1944	1	0	0
Melissoptila similis Urban, 1988	0	1	0
Melitoma segmentaria Fabricius, 1804	1	1	1
Monoeca sp1	0	0	1
Nannotrigona testaceicornis Lepeletier, 1836	1	1	1
Neocorynura codion Vachal, 1904	1	1	1
Oxaea flavescens Klug, 1807	1	1	0
Oxytrigona tataira Smith, 1863	0	1	0
Paratetrapedia conexa Vachal, 1909	1	0	0
Paratetrapedia flaveola Aguiar & Melo, 2011	1	1	0
Paratrigona lineata Lepeletier, 1836	1	1	1
Paratrigona subnuda Moure, 1947	1	1	1
Paroxystoglossa crossotos Vachal, 1904	1	0	0

Paroxystoglossa seabrai Moure, 1960	0	1	0
Partamona cupira Smith, 1863	1	0	0
Partamona helleri Friese, 1900	1	1	1
Partamona rustica Pedro & Camargo, 2003	0	1	1
Peponapis fervens Smith, 1879	0	1	1
Plebeia droryana Friese, 1900	1	1	1
Plebeia remota Holmberg, 1903	0	0	1
Pseudagapostemon arenarius Schrottky, 1902	0	1	0
Pseudaugochlora graminea Fabricius, 1804	1	1	1
Scaptotrigona bipunctata Lepeletier, 1836	1	1	1
Scaptotrigona postica Latreille, 1807	1	1	0
Schwarziana quadripunctata Lepeletier, 1836	0	1	1
Temnosoma sp1	0	1	0
Tetragona clavipes Fabricius, 1804	1	1	1
Tetragonisca angustula Latreille, 1811	1	1	1
Tetrapedia diversipes Klug, 1810	1	0	0
Thygater analis Lepeletier, 1841	1	1	1
Thygater palliventris Friese, 1908	1	0	0

Trigona fuscipennis Friese, 1900	1	1	1
Trigona spinipes Fabricius, 1793	1	1	1
Xylocopa frontalis Olivier, 1789	1	1	0
Xylocopa grisescens Lepeletier, 1841	0	1	0
Xylocopa hirsutissima Maidl, 1912	1	1	1
Xylocopa macrops Lepeletier, 1841	0	1	0
Xylocopa ordinaria Smith, 1874	0	0	1
Xylocopa subcyanea Pérez, 1901	0	1	0
Xylocopa suspecta Moure & Camargo, 1988	1	1	1
Total	64	100	70

Table SII LCBD values for each site and their respective urban development models. The sites with the greatest contribution to beta diversity (p-value < 0.05) shown in bold.

Site	**Code**	**Long**	**Lat**	**Urban development**	**LCBD**	**p-value**
1	ADO	-45.4343	-21.5812	Land fully occupied	0.03	0.88
2	ALT	-45.2633	-21.6876	Land-sparing	0.03	0.9
3	BAT	-46.5192	-21.7985	Land-sparing	0.07	0.07
4	CEL	-45.4379	-21.5438	Land fully occupied	0.04	0.73
5	COL	-45.9511	-22.2286	Land-sparing	0.04	0.76
6	ELD	-44.9864	-21.2459	Land fully occupied	0.03	0.96
7	ESA	-45.2571	-21.7025	Land fully occupied	0.06	0.14
8	ESP	-45.9319	-22.2159	Land fully occupied	0.04	0.71
9	FAT	-45.9159	-22.2243	Land-sparing	0.05	0.52
10	IME	-45.9635	-21.4317	Land-sharing	0.06	0.2
11	JDA	-45.9359	-21.4306	Land fully occupied	0.04	0.58
12	JDE	-46.585	-21.799	Land-sharing	0.05	0.47
13	MOR	-45.0218	-21.2366	Land-sharing	0.04	0.85
14	PAR	-46.5458	-21.7833	Land-sparing	0.04	0.71
15	PMA	-46.5487	-21.8013	Land fully occupied	0.04	0.74
16	POR	-45.8987	-22.2286	Land-sharing	0.03	0.96
17	SAO	-45.2758	-21.6683	Land-sharing	0.05	0.23
18	THE	-46.57	-21.7847	Land-sparing	0.05	0.48
19	UFL	-44.9766	-21.2261	Land-sharing	0.07	0.035
20	UNI	-45.9463	-21.4506	Land-sharing	0.09	0.004

ARTIGO III

Plant-pollinator interactions in the neotropics are affected by urbanization and the invasive bee *Apis mellifera*

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Abstract

Urbanization is one of the most intense forms of landscape change, and it is likely to increase in the coming years. Although there is a consensus that urbanization has drastic effects on biodiversity, recent discussions on the conservation of urban plant-pollinator interactions have not properly included biodiverse tropical regions. Here, we investigate how the structure of plant-pollinator networks changes along the urbanization gradient. We examined changes in structure of 21 plant-pollinator networks along six urbanization gradients. We also accessed the centrality of *Apis mellifera* (an exotic bee) and *Trigona spinipes* (a native bee), both generalist species, highly abundant and tolerant to urban environments. Finally, we identified important species of plants in urban pollination networks. We found that connectance and interaction evenness increases with urbanization, probably due to the loss of bee species. Complementary specialization (H2') and modularity were not affected by the urban landscape. Closeness centrality of *A. mellifera* increased with increasing impermeable cover reinforcing the hypothesis that invasive and super-generalist species are generally more central in more urbanized areas. In contrast, eigenvector centrality of *T. spinipes* decreased with the increase in urbanization, suggesting a decrease in the importance of this species for the network as urban areas get denser. Our results support to understand the effects of urbanization on mutualistic networks in tropical environments and can contribute to the protection of native biodiversity against urban expansion.

Keywords

mutualistic networks, urban biodiversity, urban bees, urban ecology.

Implications for insect conservation

Our results show that plant-bee interactions networks become simplified as urbanization increases. We also show that the invasive non-native bee Apis mellifera dominate urban plant-bee interactions in neotropical cities. To improve insect conservation in cities, it is recommended to plant native plant species and manage invasive non-native species.

Introduction

Urbanization is one of the most intensive and rapidly expanding forms of landscape change (UN 2010; Seto et al. 2013; McDonald et al. 2013). The process of urbanization is characterized by a severe transformation of the landscape's structure, resulting in the loss and fragmentation of natural areas (Alberti 2008; Liu et al. 2016). These changes in landscapes induce severe consequences for biodiversity and, thus, for ecosystem health and functioning (Mcdonald et al. 2008; Wenzel et al. 2020). Its impact on the group of pollinators has been a subject of great discussion, and significant declines have been reported for this group in recent years (Potts et al., 2010; Geslin et al. 2013; Wenzel et al. 2020). Plant-pollinator interactions are essential for the functioning of terrestrial ecosystems since most plants depend on biotic vectors for pollination and a great diversity of animals depends on floral resources (Ollerton et al. 2011). Consequently, a loss of key biotic interactions may have pervasive effects accelerating species local extinction and declining the ecosystem functions that provide services to humans (Tylianakis et al. 2010; Valiente-Banuet et al. 2014). Studies showed that urbanization has changed the dynamics of interactions between plants and pollinators (Silva et al. 2021, Fisogni et al. 2022). The number and diversity of interactions, the frequency of visits by specialist pollinators and solitary bees, as well the reproductive success of plant species was negatively affected by urbanization (Tonietto et al. 2011; Verboven et al. 2012; Geslin et al. 2013).

The number of studies investigating the impact of urban areas on pollinators has increased in the past few years, most of them focusing on the description of abundance and species diversity (Ahrné et al. 2009; Banaszak-Cibicka and Żmihorski 2012; Fortel et al. 2014; Graf et al. 2022). However, the negative effects of urbanization on pollinator communities are also likely to impact plant-pollinator interaction networks (Hennig and Ghazoul 2011).

Recently, there has been growing interest in plant-pollinator interactions in urban environments, and studies performed along diverse urban gradients have shown contrasting responses (Cheptou and Avendaño 2006; Van Rossum and Triest 2010; Geslin et al. 2013; Zotarelli et al. 2014; Baldock et al. 2015; Theodorou et al. 2017; Fisogni et al. 2022). However, most of the research has been conducted in cities located in the northern hemisphere, and the knowledge of these interactions in tropical cities is substantially underrepresented (Maruyama et al. 2019; Wenzel et al. 2020). Thus, it is possible that the effects of urbanization on plant-pollinator interactions may differ between regions and climates and depend on local species composition (Silva et al. 2021). Furthermore, most of the studies investigating the impact of urban areas on pollinators focused on the description of abundance and species diversity (Ahrné et al. 2009; Banaszak-Cibicka and Żmihorski 2012; Fortel et al. 2014; Graf et al. 2022), and the negative effects of urbanization on plant-pollinator interaction networks have been less studied (Hennig and Ghazoul 2011).

Considering the interactions between plants and pollinators allows a better understanding of the structure and dynamics of these systems and can contribute to conservation efforts (Bascompte and Jordano 2007; Maruyama et al. 2019). Thus, we evaluated how the structure of plant-pollinator interaction networks changed along an urbanization gradient in six Brazilian cities. We expected urban landscapes to influence network properties in many ways. Firstly, owing to an observed decrease in bee richness with increasing urbanization (Tavares-Brancher et al. 2023), we hypothesized an increase in connectance and in interaction evenness. Secondly, we hypothesized a network dominated by abundant and generalist species, thus decreasing complementary specialization (H2') and modularity. Thirdly, we assessed changes in the centrality of two important species of bees in Brazilian urban areas, *Apis mellifera* Linnaeus, 1758 (a non-native bee) and *Trigona spinipes* (Fabricius, 1793) (a native bee). With the increase in urbanization, we hypothesized an increase in the centrality of *A. mellifera*, as it is a generalist species, highly tolerant to urban environments (Giannini et al. 2015). Finally, we investigated the topological importance of plant species to identify key species in urban pollination networks. Although intense urbanization generally has a negative effect on pollinators, urban areas may harbor greater floral diversity than rural areas that are dominated by intense agriculture (Wenzel et al. 2020). Thus, the selection of plant species in urban environments can improve the conservation of urban pollinators (Garbuzov and Ratnieks 2014; Lowenstein et al. 2019, Staab et al. 2020; Nascimento et al. 2020). Understanding interactions in the urban context and finding which of these plants support the mutualistic network may have important consequences for the conservation of species and ecosystem services in urban ecosystems.

Material and methods

Study area

Our study was performed in six cities in southern Minas Gerais, Brazil: Alfenas, Poços de Caldas, Pouso Alegre, Varginha, Três Corações, and Lavras. The location map and information about the sites are available in the supplementary material. The region is characterized as a non-metropolitan region, consisting of small and medium-sized cities. The official classification carried out in the 2010 Demographic Census indicates that these cities had between 80,973 and 169,838 inhabitants with at least 84% of the population residing in urban spaces (IBGE 2010). Outside the urban areas, there is a predominance of intensive agricultural landscapes (mainly coffee and pasture crops), and remnants of the Atlantic Forest (IBGE 2017). The region has a predominantly mountainous relief with elevations ranging from 800 to 1,400 m (Alvares 2013). In the six sampled cities, we selected a total of 21 locations following an increasing gradient of impervious coverage (from 20 to 70%) within a radius of 1 km from the central collection point (centroid).

Sampling

We sampled plant-bee interactions in each site one day per month, four hours per day, for six months in 2020 and 2021. A detailed description of the sampling procedure is available in Tavares-Brancher et al. (2023). In short, we sampled floral visitors in all plant species showing fully opened flowers within each site, using the focal method (10 min of observation per plant). Flower-visiting bees were collected with entomological nets by one collector within a radius of 200 m around the centroid of the site. We defined an interaction whenever a bee was observed visiting flowers at a given plant. Bees were kept in bottles with ethyl acetate, processed, fixed, and identified. The determination of genera was performed using Silveira et al. (2002) and of species through taxonomic reviews performed by experts. Whenever there were doubts about identification, we requested the assistance of specialists.

Landscape metrics

We used Sentinel-2 images of the study areas (obtained in September 2019) with a resolution of 10 m to characterize the landscape around each study site. The Semiautomatic Classification (SCP) plugin (Congedo 2016) was used to classify the images in QGIS software version 3.10.0 (QGIS Development Team 2019). We considered four land cover classes within a 1 km radius: water bodies, impervious surfaces, tree cover, and grassland cover. We calculated four landscape metrics to investigate the relationship between landscape structure and the properties of the plant-pollinator networks: impervious cover, tree cover, grass cover and tree cover isolation (i.e., mean distance to the nearest neighbor patch) using the LeCos plugin (Jung 2016). These metrics reflect the landscape composition and configuration of urban areas and are expected to affect the presence of plants and bees and the interactions between species (Fahrig 2003; Schneiberg et al. 2020).

Data analysis

Network properties

We constructed different weighted interaction matrices with the sampling data listing plants in the rows, bees in the columns, and each matrix cell representing the number of recorded visits (Bascompte and Jordano 2013). We used quantitative (interaction frequency) matrices rather than binary since they are more robust against bias (Blüthgen et al. 2006; Dormann et al. 2009; Devoto et al. 2012). Firstly, we analyzed the complete network covering all sampling sites to describe in a general way the relationship between bees and plants in the urban environment. Then, we calculated independent network metrics for each site: connectance, interaction evenness (IE), complementary specialization (H2'), and modularity. We examined these metrics because they describe the basic structure of the mutualistic networks and are relevant because of their ecological importance and their sensitivity to environmental variations (Geslin et al. 2013; Fisogni et al. 2022).

Connectance is defined as the proportion of links observed in relation to the total number of links possible (Dormann et al. 2009). Higher ratios indicate that most pollinators are interacting with most of the available plants, whereas lower connectance values indicate that the interactions between pollinators and plants are limited (Olsson et al. 2021).

Interaction evenness is Shannon's evenness index, which reflects homogeneity in the distribution of interactions across species in the network (Blüthgen et al. 2006; Dormann et al. 2009). Interaction evenness values range from 0 (with heterogeneous distribution of interactions) to 1, representing complete evenness (Sakai et al. 2016). Complementary specialization (H2') measures interaction selectivity, that is, how species partition their interactions (Blüthgen et al. 2006). This metric is useful in network comparisons because it is not affected by network size or sampling effort. H2′ varies from 0 to 1 which indicates extreme generalization or specialization, respectively. Modularity is a measure of how compartmentalized the network structure is in relation to a random pattern, and is related to the presence of modules, i.e., subsets of species interacting more among themselves than with other species from the same network (Rodewald et al. 2014; Beal-Neves et al. 2020).

We also evaluated the centrality metrics for *A. mellifera* separately because it is a non-native invasive species that may also contribute to the decrease of native pollinators, and because it remains unclear how urbanization may mediate the impact of this species on plant-pollinator networks (Prendergast and Ollerton 2021). For that, we used the eigenvector degree centrality score and closeness centrality to assess their position with respect to the whole network. Eigenvector centrality is a true node-centrality when normalized using the Euclidean norm, and depends on the number and quality of links, roughly giving to each species a score proportional to the sum of the scores of its neighbors (Bonacich 2007; Pires et al. 2022). Standardized eigenvector degree scores vary between 0 (low centrality) and 1 (high centrality). Closeness centrality measures the proximity of a node to all other nodes in the network, in which species with high values can quickly affect other nodes or be affected (Pires et al. 2022). For comparison, we performed the same procedure for *T. spinipes,* a well-known native stingless bee and supergeneralist playing a crucial role in interaction networks (Biesmeijer et al 2005; Giannini et al. 2015; Zotarelli et al. 2014). Centrality metrics quantifies how connected species are with each other. Central species are highly connected to species that are themselves interconnected and are therefore important for network structure and stability (Fisogni et al. 2022).

Finally, in a descriptive analysis, we constructed a unified matrix of all sampling areas to identify plant species with the highest number of species of bees interacting. For this, we used the degree centrality value for each plant species, which represents the primary network structural properties for the number of interactions of each species (Pires et al. 2022).

Statistical analysis

We estimated the significance of each network metric based on comparisons with null models. Based on each of the networks, we created 1000 random networks using the ‘vaznull’ algorithm (Vázquez et al. 2007). This null model reshuffles interactions while maintaining the observed matrix dimensions and connectance by causing it to be the same as in the original network. Then we calculated each one of the metrics for the set of random networks, generating 95% confidence intervals. Observed values that departed from the confidence interval were considered significantly different from null. For network analyses, we used packages ‘igraph’ (Csardi and Csardi 2007) to calculate eigenvector degree and ‘bipartite’ (Dormann et al. 2008) for connectance, interaction evenness, complementary specialization, modularity, closeness centrality and degree.

We checked for correlations between predictor variables using the Pearson correlation and none of them showed strong collinearity ($R > 0.7$). Because the range of absolute values of all landscape metrics varied, each metric was centered to zero using the *standardize* function in the ‘vegan’ package (Oksanen et al. 2018). In addition, we assessed spatial autocorrelation in species richness and network metrics as a function of an inverse spatial distance weight matrix by the spatial autocorrelation coefficient Moran's I, using the R package ‘ape’ (Paradis et al. 2004). The analysis did not indicate spatial autocorrelation for any of the metrics.

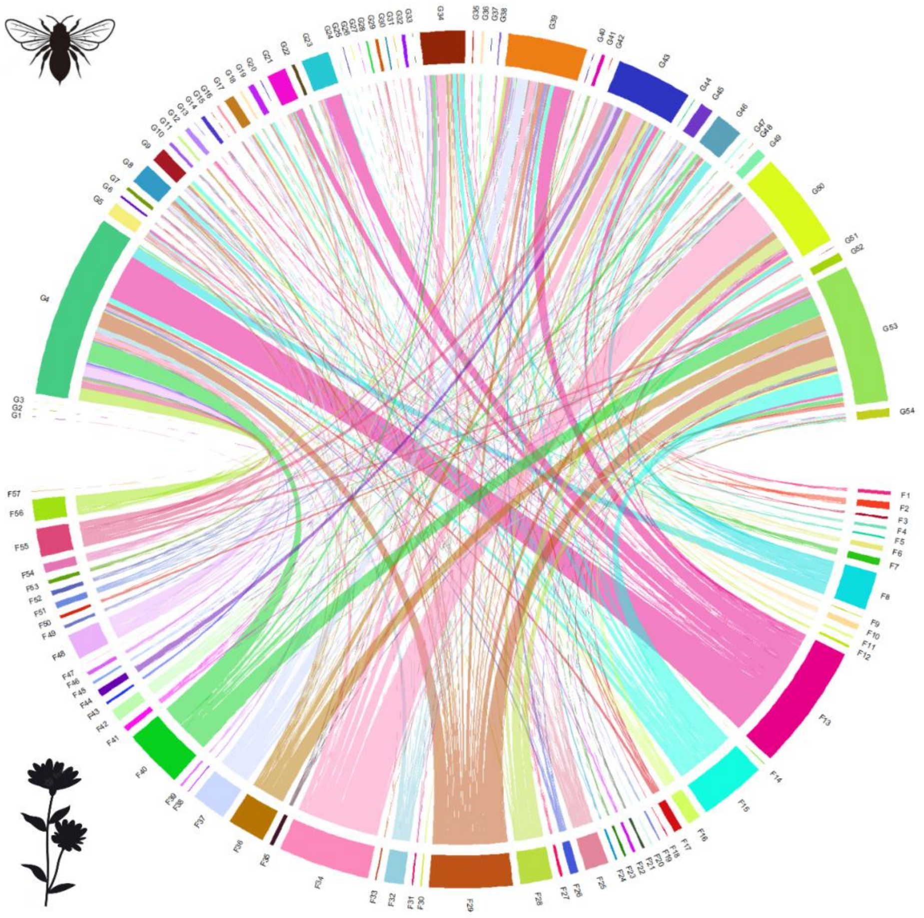
Next, to evaluate the effects of the landscape variables on the network properties, we constructed mixed and fixed-effects generalized linear models. Global and final models had their residuals checked for normality and homoscedasticity to ensure the models met these assumptions. Assuming a global model, i.e., a model that considers all explanatory variables (impervious surface, tree cover, grass cover, and isolation), we evaluated 3 different structures: (i) a model that included landscape variables; (ii) a model that incorporated "city" as fixed factor, (iii) a model that incorporated "city" as a random factor and (Zuur et al. 2009; Oliveira et al. 2019). The first and second models assumed a linear relationship between the explanatory variables and response variable and were estimated using generalized linear models (GLM) with Gaussian error distributions. The third model assumed a mixed effect with "city" as a random factor with the *lmer* function in the package ‘lme4’ in R (Bates et al. 2014). The best model was selected through the Akaike information criterion corrected for small samples (AICc), in which the lowest value represents the best model. After the best structure for the global model was found, we performed model selection to identify the best ones for the relationship between the urban landscape metrics and the response of the different measured network properties. We used the *dredge* function in the R package ‘MuMIn’ (Barton 2018), again assuming the lowest AICc values. Models with ΔAICc <2 were considered equally plausible, and no alternative model was considered when the null model was ΔAICc <2. All analyses were performed in R (R Development Core Team 2018).

Results

At the end of the sampling season in the 21 study sites, we sampled a total of 191 plant species and 132 pollinator species (available in Tavares-Brancher et al. 2023), accounting for 4,279 plant-pollinator visits overall (e.g., Fig. 1). Four bee species encompassed 57% of all interactions and were recorded in all 21 networks: *A. mellifera* (928 interactions), *T. spinipes* (651 interactions), *Tetragonisca angustula* (Latreille, 1811) (489 interactions) and *Plebeia droryana* (Friese, 1900) (378 interactions). These species are generalists and exhibit social behavior. Seven plant species stood out regarding the number of interactions, *Lagerstroemia indica* L. (392 interactions), *Callistemon rigidus* R.Br. (250 interactions), *Bidens pilosa* L. (182 interactions), *Pleroma granulosum* (Desr.) D. Don (154 interactions) *Cosmos sulphureus* Cav. (148 interactions), *Turnera subulata* Sm. (135 interactions) and *Tecoma stans* (L.) Juss. ex Kunth (130 interactions).

Fig. 1 Some of the interactions recorded in the survey. (A) *Eulaema nigrita* Lepeletier, 1841 in *Ipomoea cairica*; (B) *Epicharis flava* Friese, 1900 in *Tecoma stans*; (C) *Bombus brasiliensis* Lepeletier, 1836 in *Agapanthus africanus*; (D) *T. angustula* in *Lagerstroemia indica*; (E) *Oxaea flavescens* Klug, 1807 in *Macroptilium lathyroides* (F) *Pseudaugochlora graminea* (Fabricius, 1804) in *Pleroma mutabile.*

Nine plant species showed the highest degrees of interaction (highest number of interacting partners, i.e., bee species): *Bidens pilosa* L. (interacted with 26 species of bees), *Pleroma granulosum* (Desr.) D. Don (25 bee species), *Cosmos sulphureus* Cav. (22 bee species), *Cordia superba* Cham. (21 bee species), *Ipomoea cairica* (L.) Sweet (21 bee species), *Antigonon leptopus* Hook. & Arn. (20 bee species), *Podranea ricasoliana* (Tanfani) Sprague (20 bee species), *Tecoma stans* (L.) Juss. ex Kunth (20 bee species) and *Jacaranda mimosifolia* D. Don (19 bee species). Among these, *P. granulosum, C. superba* and *I. cairica* are native to the Atlantic Forest ecosystem; whereas *B. pilosa* and *T. stans* are considered invasive alien non-native species. Among botanical families, Asteraceae, Fabaceae, Bignoniaceae, Convolvulaceae, Malvaceae, Melastomataceae and Lythraceae showed the highest degrees of interaction with bee species and genera (Fig. 2). These families are commonly used as urban gardening plants in Brazil and are known to attract a wide range of pollinators in the Neotropical region (Agostini and Sazima 2003; Aleixo et al. 2014). The complete list with the other values is available in the supplementary material.



Botanical family	Code	Botanical family	Code	Bee genera	Code	Bee genera	Code
Asphodelaceae	F1	Hydrangeaceae	F30	*Acamptopoeum*	G1	*Melissodes*	G30
Acanthaceae	F2	Iridaceae	F31	Anthidiini*	G2	*Melissoptila*	G31
Acanthaceae	F3	Lamiaceae	F32	*Anthodioctes*	G3	*Melitoma*	G32
Adoxaceae	F4	Loranthaceae	F33	*Apis*	G4	*Monoeca*	G33
Aizoaceae	F5	Lythraceae	F34	*Augochlora*	G5	*Nannotrigona*	G34
Amaranthaceae	F6	Malpighiaceae	F35	*Augochlorella*	G6	*Neocorynura*	G35
Amaryllidaceae	F7	Malvaceae	F36	*Augochloropsis*	G7	*Oxaea*	G36
Anacardiaceae	F8	Melastomataceae	F37	*Bombus*	G8	*Oxytrigona*	G37
Apiaceae	F9	Meliaceae	F38	*Centris*	G9	*Paratetrapedia*	G38
Apocynaceae	F10	Muntingiaceae	F39	*Cephalotrigona*	G10	*Paratrigona*	G39
Arecaceae	F11	Myrtaceae	F40	*Cephalurgus*	G11	*Paroxystoglossa*	G40
Asparagaceae	F12	Nyctaginaceae	F41	*Ceratina*	G12	*Partamona*	G41
Asteraceae	F13	Oleaceae	F42	*Coelioxys*	G13	*Peponapis*	G42
Berberidaceae	F14	Pittosporaceae	F43	*Dialictus*	G14	*Plebeia*	G43
Bignoniaceae	F15	Plantaginaceae	F44	*Dicranthidium*	G15	*Pseudagapostemon*	G44
Boraginaceae	F16	Plumbaginaceae	F45	*Epanthidium*	G16	*Pseudaugochlora*	G45
Brassicaceae	F17	Poaceae	F46	*Epicharis*	G17	*Scaptotrigona*	G46
Cactaceae	F18	Polygalaceae	F47	*Euglossa*	G18	*Schwarziana*	G47
Caprifoliaceae	F19	Polygonaceae	F48	*Eulaema*	G19	*Temnosoma*	G48
Caricaceae	F20	Portulacaceae	F49	*Exaerete*	G20	*Tetragona*	G49
Caryocaraceae	F21	Proteaceae	F50	*Exomalopsis*	G21	*Tetragonisca*	G50
Clusiaceae	F22	Rosaceae	F51	*Friesella*	G22	*Tetrapedia*	G51
Combretaceae	F23	Rubiaceae	F52	*Geotrigona*	G23	*Thygater*	G52
Commelinaceae	F24	Rutaceae	F53	*Habralictus*	G24	*Trigona*	G53
Convolvulaceae	F25	Solanaceae	F54	*Hylaeus*	G25	*Xylocopa*	G54
Cucurbitaceae	F26	Turneraceae	F55	*Leiopodus*	G26		
Ericaceae	F27	Verbenaceae	F56	*Lophopedia*	G27		
Euphorbiaceae	F28	Vitaceae	F57	*Megachile*	G28		
Fabaceae	F29			*Melipona*	G29		

Fig. 2 Chord diagram representing the plant-pollinator network of all urban areas sampled. The upper part of the diagram represents the bee genera, and the lower part represents the botanical family. Each circle color represents a *taxa*, and the links represent the interactions. The table shows the botanical families, bee genera and their respective codes. * Anthidiini is a tribe, as it was not possible to identify at the gender level.

The plant-pollinator network of all sampled urban areas (Fig. 3) is modular when compared to the null model (p=0.001).

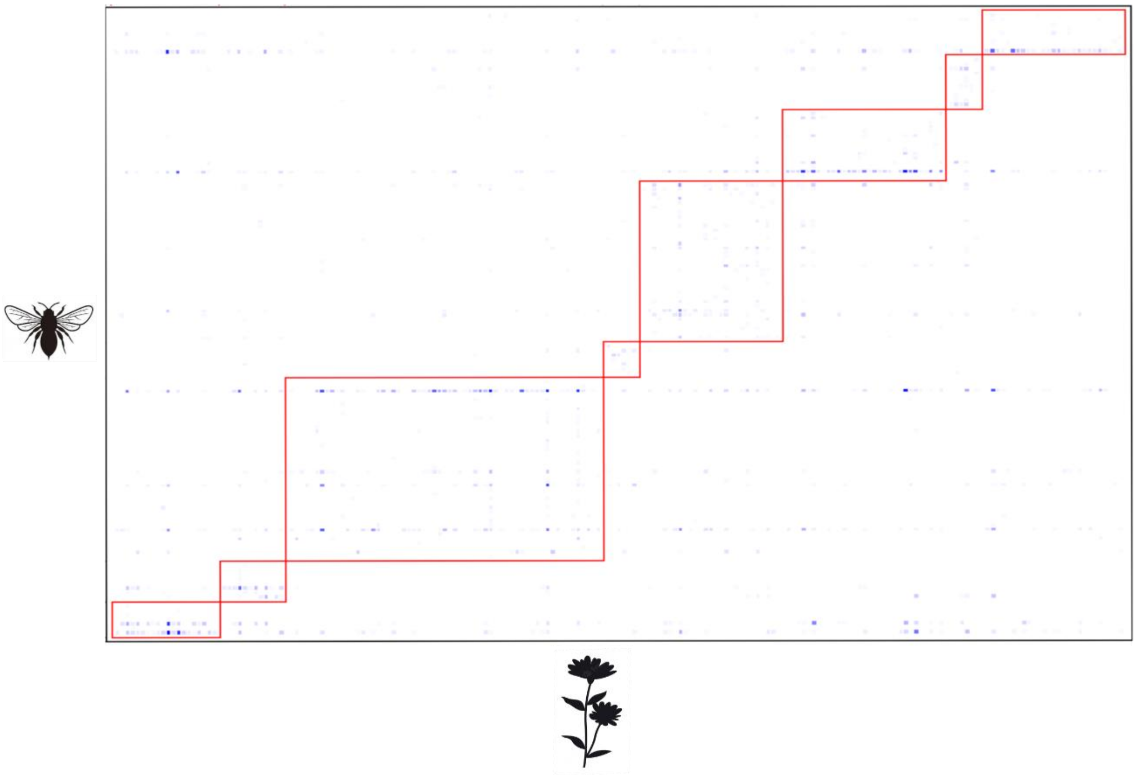


Fig. 3 Matrix evidencing a modular structure. Bee species are represented in the rows, and plant species in the columns. Red boxes represent the modules found and blue cells represent interactions (intense colors represent a higher frequency of interaction).

The models that best described the variation in connectance included impervious cover, tree cover, and grass cover. Connectance was positively related to impervious cover and tree cover (Table 1). Interaction evenness was positively related to impervious cover and tree cover (Table 1), which indicated that interaction patterns are more homogeneous in more densely urbanized landscapes. Complementary specialization (H2') and modularity were not affected by the urban landscape (ΔAICc < 2 for null model).

The centrality analysis for *A. mellifera* and *T. spinipes* showed contrasting results for the two metrics evaluated. The closeness centrality of *A. mellifera* was positively influenced by increased impervious cover and negatively correlated with increased tree cover (Table 1). Contrarily, the eigenvector centrality of *T. spinipes* was negatively correlated with increased impervious cover and positively associated with increased tree cover and isolation (Table 1).

Table 1 Models selected to determine plant-pollinator network responses to urban landscape indicators. The AICc, ΔAICc, weight, intercept, p value and adjusted R^2 values are represented for each selected model. IC = impervious cover, TC = tree cover, GC = grass cover. Statistical significance at $P = 0.05$ shown with *.

Dependent variable	**Model**	**AICc**	**ΔAICc**	**Weight (w_i)**	**Intercept (α)**	**p-value**	**R^2_{aj}**
Connectance	IC + TC + GC	-103.4	0	0.24	0.015 | 0.01 | -0.008	0.004* | 0.042* | 0.06	0.32
	IC	-102.8	0.62	0.18	0.008	0.05*	0.14
	IC + TC	-102.4	1.03	0.14	0.01 | 0.007	0.02* | 0.13	0.20
	IC + GC	-101.6	1.77	0.1	0.01 | -0.005	0.03* | 0.2	0.17
Interaction evenness	IC + TC	-97.0	0	0.57	0.016 | 0.018	0.007* | 0.003*	0.38
Closeness *A. mellifera*	TC	-124.2	0	0.24	-0.006	0.02*	0.21
	IC	-122.7	1.52	0.11	0.0055	0.04*	0.15
	IC + TC	-122.5	1.71	0.10	0.0031 | -0.004	0.3 | 0.12	0.22
	TC + isolation	-122.3	1.88	0.09	-0.05 | 0.003	0.09 | 0.31	0.21
Eigenvector *T. spinipes*	IC + TC + isolation	0.7	0	0.22	-0.11| 0.12 | 0.1	0.04* | 0.03* | 0.05*	0.40
	IC	1.5	0.85	0.14	-0.13	0.013*	0.24
	TC	1.8	1.11	0.13	0.13	0.015*	0.23
	IC + TC	1.9	1.25	0.12	-0.09 | 0.086	0.12 | 0.13	0.30
	TC + isolation	2.4	1.70	0.09	0.17 | 0.08	0.0057* | 0.15	0.28

Discussion

As hypothesized, connectance increased with increasing urbanization, indicating that most pollinators are interacting with most plants available in areas with high impervious cover. The loss of species can lead to an increase in connectance and, in urbanized areas, the presence of generalist species can contribute to this increase (Tylianakis et al. 2010). Another study with plant-pollinator interactions found that connectance was higher at medium urbanization, whereas no differences were found between low or medium urbanization and high urbanization level (Fisogni et al. 2022), reinforcing divergences about the effect of environmental disturbance on network connectance. However, connectance is known to be strongly biased by adding new species to the network, thus the sampling effort could explain these discrepancies (Vizentin-Bugoni et al. 2015). Connectance is assigned a stabilizing role, in which more connected networks can be more functionally robust (Dunne et al. 2002), potentially decreasing their fragility as urbanization advances. In contrast, other studies argued against such mechanisms, suggesting that highly connected networks had a higher probability of suffering extinction cascades (Vieira and Almeida-Neto. 2015; Heleno et al. 2012). Thus, there is not sufficient empirical evidence of a general relationship between urbanization and connectance.

Interaction evenness also increased with increasing urbanization. This may be explained by a higher diet generalization of bees feeding on all resources available, coupled with the decrease of species in these urban areas (as we showed in a previous study). In fact, the predominance of generalist species was related to higher interaction evenness in plant-pollination networks along a gradient of urbanization (Geslin et al. 2013; Baldock et al. 2015). In highly urbanized areas, the networks consist of bees tolerant to urban landscapes (i.e., broad environmental tolerance and low dietary specificity), which can move easily across the landscape exploring a wide range of resources (Theodorou et al. 2017). A similar effect was observed in Paris, France, where interaction evenness was higher in urban landscape networks than in suburban and agricultural landscape networks (Geslin et al. 2013). In contrast, a similar interaction evenness was found across the urban gradient in Lille, France, while a decreasing evenness was observed with increasing urbanization in Germany (Fisogni et al. 2022; Udy et al. 2020). These discrepancies among studies suggest the presence of regional variability of plant-pollinator networks in response to different gradients of urbanization (Fisogni et al. 2022). However, increasing urbanization has also led to an increase in the interaction evenness in plant-bird networks, showing that this effect can be observed for other groups in urban areas (Schneiberg et al. 2020). This homogenization of interactions can reduce the resilience of networks and affect the efficiency of ecosystem functions since the loss of specialized interactions may have cascading effects on the maintenance of some plant species (Schneiberg et al. 2020).

We did not find any significant variation in the level of network specialization along the urbanization gradient. Some studies showed the same result, indicating the prevalence of generalist species with redundant interactions in urban networks (Theodorou et al. 2017; Fisogni et al. 2022). However, studies that compared urban areas and semi-natural areas found higher specialization in urban areas, because bees interacted with a greater number of flower species in urban gardens (Baldock et al. 2015; Martins et al. 2017). Thus, even in areas with high impermeable coverage, a greater variety of flowers could influence specialization more than urbanization itself. Besides, it has been shown that mutualistic networks from temperate zones have higher specialization in comparison with tropical areas (Schleuning et al. 2012), which could partly explain our results.

The values for modularity were higher than those obtained by the null models. This supports the assumption that species do not show random patterns of interactions and that there are determining factors of interactions also in urban environments (Maruyama et al., 2019). However, modularity was not affected by urbanization. This result is supported by the biological content of modules, as a set of species with convergent traits related to their pollination biology or species closely related taxonomically (Olesen et al. 2007).

Closeness centrality of *A. mellifera* increased with increasing impermeable cover and decreased with increased tree cover, reinforcing the hypothesis that invasive and super-generalist species with long phenology are generally more central in more urbanized areas (Fisogni et al. 2022). It has been reported that, in urbanized areas, invasive species increase in importance, and can reduce the network size (Rodewald et al. 2014). We provide evidence that the relative importance of *A. mellifera* in mutualistic networks from urban ecosystems may be dependent on the level of urbanization. In contrast, eigenvector centrality of *T. spinipes* decreased with the increase in urbanization and increased with increase in tree cover, suggesting a decrease in the importance of this species for the network as urban areas get denser. Generalist bee species are usually central in mutualistic networks and are therefore important for maintaining their structure and cohesiveness, being at close distance to several species in the network and connecting different sub-groups of interacting species (Martín González et al. 2010; Fisogni et al. 2022). However, the non-native bee *A. mellifera* is often a dominant competitor that impacts native pollinators (Roubik and Villanueva-Gutierrez 2009; Nascimento et al. 2020; Garibaldi et al. 2021).

Studies demonstrated that floral resources can mitigate the negative effect of urbanization on pollinators (Lowenstein et al. 2014; Wilson & Jamieson 2019). From a conservation perspective in the cities, the plants with a higher number of links to bees deserve preference for the enhancement of the bees' diversity. For bumble bees, for instance, plant species diversity and abundance were more important than the urbanization for abundance and species richness in a German city (Hülsmann et al. 2015). In our study, we identified families and species of plants that are important for the sustenance of the bee species in urban areas. Botanical families more visited by bees have flowers relatively large and generally colorful and attractive. In Asteraceae, for example, nectar is easily accessed by several groups of insects, including bees. In other families, such as Bignoniaceae and Fabaceae, the nectar is in deep portions of the corolla, requiring attributes that enable the triggering of pollination mechanisms. Flowers of this type are predominantly pollinated by bees (Rech et al. 2014). We emphasize, however, many plant species collected in our research are considered non-native species, some of which are invasive (e.g., *B. pilosa* and *T. stans*) and pose a potential threat to native communities (Ziller et al. 2020; Zenni and Ziller 2011). Therefore, the use of invasive non-native plants in urban areas to attract pollinators should not be encouraged.

Although the number of studies on the effects of urban gradients on biodiversity is increasing, the patterns that govern plant-pollinator interactions are still under investigation and deserve attention, especially in tropical regions. Our study demonstrates the importance of evaluating environmental gradients in urban areas and their effects on mutualistic networks. Besides, the use of plants more attractive to pollinators can be an efficient solution to supporting a substantial part of the bee diversity in cities. In summary, our results can be useful for the management of urban green areas, aimed at preserving the diversity of interaction plant-pollinator networks in anthropized environments.

Statements and Declarations

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The authors have no relevant financial or non-financial interests to disclose.

Author contributions

All authors contributed to the development of the research. Study design: Karla Palmieri Tavares Brancher and Rafael Dudeque Zenni. Data collection, statistical analysis, and writing (original draft preparation): Karla Palmieri Tavares Brancher. Identification of collected material: Leticia Vanessa Graf and Walnir Gomes Ferreira Junior. Assistance in network analysis and writing: Lucas Del Bianco Faria. Supervision and writing: Rafael Dudeque Zenni. All authors read and approved the final manuscript.

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Supplementary material

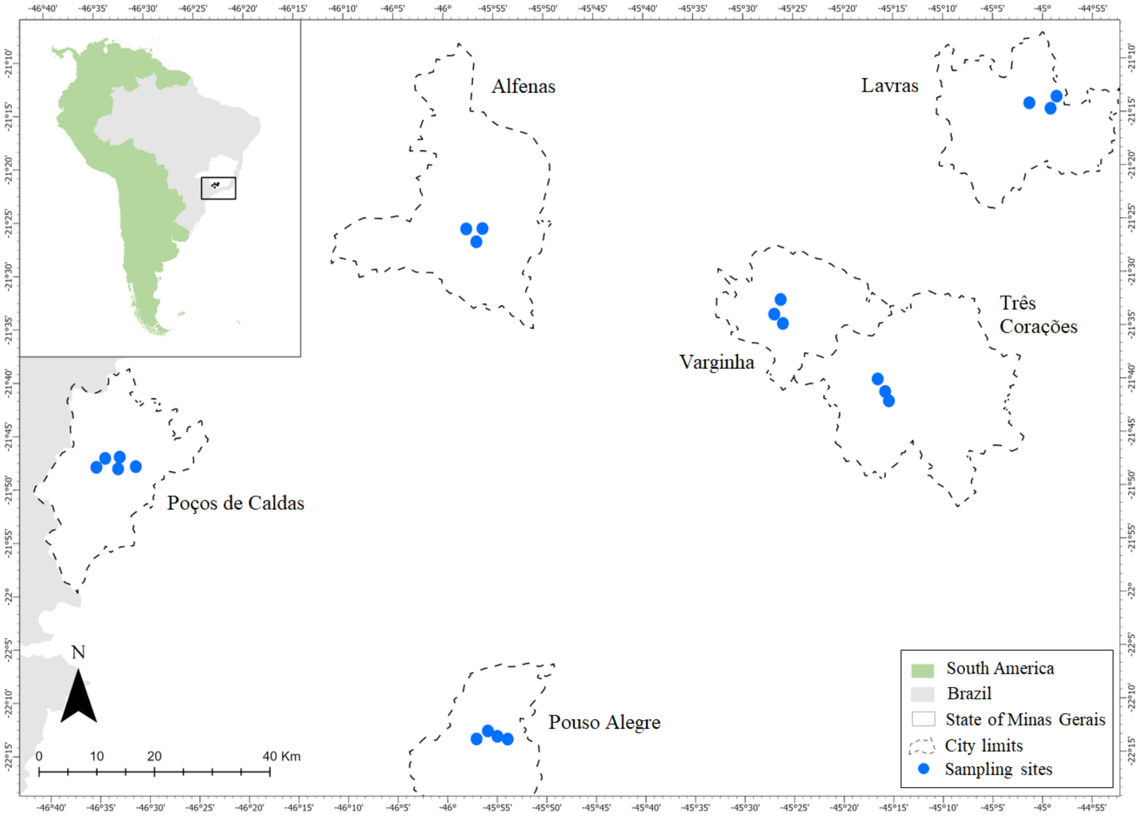


Fig S1. Study design and location of the 20 sites distributed across 6 Brazilian cities. The panel on the left represents South America (light green), Brazil (light gray), and the state of Minas Gerais (white) with the delimitation of the study region (black line square). The black dotted lines represent the city's limits and blue dots represent the sites. (Figure adapted from a previous study by the main author.)

Table S1. Sampling sites along a urbanization gradient of impervious surface in Brazil.

Site	Longitude	Latitude	Impervious surface
1	-45.4343	-21.5812	59.82%
2	-45.2633	-21.6876	59.31%
3	-46.5192	-21.7985	36.27%
4	-45.4379	-21.5438	57.88%
5	-45.4487	-21.5666	65.82%
6	-45.9511	-22.2286	41.11%
7	-44.9864	-21.2459	70.95%
8	-45.2571	-21.7025	67.48%
9	-45.9319	-22.2159	60.13%
10	-45.9159	-22.2243	47.88%
11	-45.9635	-21.4317	42.72%
12	-45.9359	-21.4306	54.55%
13	-46.585	-21.799	26.30%
14	-45.0218	-21.2366	31.06%
15	-46.5458	-21.7833	45.46%
16	-46.5487	-21.8013	64.51%
17	-45.8987	-22.2286	19.49%
18	-45.2758	-21.6683	39.46%
19	-46.57	-21.7847	62.63%
20	-44.9766	-21.2261	23.57%
21	-45.9463	-21.4506	20.71%

Table S1. Plant species, botanical families, origin (E = exotic and N = native), and their respective degrees. Degree values (number of bees found) refer to plant species.

Plant species	**Botanical family**	**Origin**	**Degree**
Bidens pilosa L.	Asteraceae	E	26
Pleroma granulosum (Desr.) D. Don	Melastomataceae	N	25
Cosmos sulphureus Cav.	Asteraceae	E	22
Cordia superba Cham.	Boraginaceae	N	21
Ipomoea cairica (L.) Sweet	Convolvulaceae	N	21
Antigonon leptopus Hook. & Arn.	Polygonaceae	E	20
Podranea ricasoliana (Tanfani) Sprague	Bignoniaceae	E	20
Tecoma stans (L.) Juss. ex Kunth	Bignoniaceae	E	20
Jacaranda mimosifolia D. Don	Bignoniaceae	E	19
Caesalpinia pulcherrima (L.) Sw.	Fabaceae	E	14
Cenostigma pluviosum (DC.) Gagnon & G.P.Lewis	Fabaceae	N	14
Lagerstroemia indica L.	Lythraceae	E	14
Schinus molle L.	Anacardiaceae	E	14
Turnera subulata Sm.	Turneraceae	N	14
Agapanthus africanus (L.) Hoffmanns.	Amaryllidaceae	E	12
Hibiscus rosa-sinensis L.	Malvaceae	E	12
Schinus terebinthifolia Raddi	Anacardiaceae	N	12
Bauhinia purpurea L.	Fabaceae	E	11
Bougainvillea spectabilis Willd.	Nyctaginaceae	N	11

Delonix regia (Bojer ex Hook.) Raf.	Fabaceae	E	11
Ligustrum lucidum W.T.Aiton	Oleaceae	E	11
Macroptilium lathyroides (L.) Urb.	Fabaceae	N	11
Tridax procumbens L.	Asteraceae	E	11
Callicarpa nudiflora Hook. & Arn.	Lamiaceae	E	10
Luffa cylindrica (L.) M.Roem.	Cucurbitaceae	E	10
Psidium guajava L.	Myrtaceae	E	10
Solanum lycocarpum A.St.-Hil.	Solanaceae	N	10
Callistemon rigidus R.Br.	Myrtaceae	E	8
Peltophorum dubium (Spreng.) Taub.	Fabaceae	N	8
Rosa chinensis Jacq.	Rosaceae	E	8
Calliandra brevipes Benth.	Fabaceae	N	7
Clerodendrum × *speciosum* Dombrain	Lamiaceae	E	7
Emilia sonchifolia (L.) DC.	Asteraceae	E	7
Euphorbia milii Des Moul.	Euphorbiaceae	E	7
Ipomoea carnea Jacq.	Convolvulaceae	N	7
Ipomoea purpurea (L.) Roth	Convolvulaceae	N	7
Lagerstroemia speciosa Pers.	Lythraceae	E	7
Rhododendron indicum var. simsii (Planch.) Maxim.	Ericaceae	E	7
Bulbine frutescens (L.) Willd.	Asphodelaceae	E	6
Callianthe striata (Dicks. ex Lindl.) Donnel	Malvaceae	N	6
Cuphea hyssopifolia Kunth	Lythraceae	E	6
Duranta erecta L.	Verbenaceae	E	6
Galinsoga parviflora Cav.	Asteraceae	E	6

Helianthus annuus L.	Asteraceae	E	6
Lippia alba (Mill.) N.E.Br. ex Britton & P.Wilson	Verbenaceae	N	6
Murraya paniculata (L.) Jack	Rutaceae	E	6
Parthenium hysterophorus L.	Asteraceae	E	6
Sonchus oleraceus L.	Asteraceae	N	6
Sphagneticola trilobata (L.) Pruski	Asteraceae	N	6
Thunbergia grandiflora Roxb.	Acanthaceae	E	6
Urochloa decumbens (Stapf) R.D.Webster	Poaceae	E	6
Abelia × *grandiflora* (Ravelli ex André) Rehder	Caprifoliaceae	E	5
Allamanda cathartica L.	Apocynaceae	N	5
Amaranthus spinosus L.	Amaranthaceae	E	5
Calliandra tweedii Benth.	Fabaceae	N	5
Chamaecrista neesiana (Mart. ex Benth.) H.S.Irwin & Barneby	Fabaceae	E	5
Combretum indicum (L.) Jongkind	Combretaceae	E	5
Hibiscus syriacus L.	Malvaceae	E	5
Lantana camara L.	Verbenaceae	E	5
Lavandula dentata L.	Lamiaceae	E	5
Leucanthemum vulgare Lam.	Asteraceae	E	5
Melaleuca linariifolia Sm.	Myrtaceae	E	5
Muntingia calabura L.	Muntingiaceae	E	5
Odontonema tubaeforme (Bertol.) Kuntze	Acanthaceae	E	5
Raphanus raphanistrum L.	Brassicaceae	E	5
Ricinus communis L.	Euphorbiaceae	E	5
Sambucus nigra L.	Adoxaceae	E	5

Waltheria indica L.	Malvaceae	N	5
Youngia japonica (L.) DC.	Asteraceae	E	5
Alternanthera brasiliana (L.) Kuntze	Amaranthaceae	N	4
Celosia argentea L.	Amaranthaceae	E	4
Clusia rosea Jacq.	Clusiaceae	E	4
Conyza bonariensis (L.) Cronquist	Asteraceae	N	4
Crotalaria micans Link	Fabaceae	N	4
Cuphea racemosa (L.f.) Spreng.	Lythraceae	N	4
Fridericia platyphylla (Cham.) L.G.Lohmann	Bignoniaceae	N	4
Handroanthus chrysotrichus (Mart. ex DC.) Mattos	Bignoniaceae	N	4
Lophanthera lactescens Ducke	Malpighiaceae	E	4
Malpighia coccigera L.	Malpighiaceae	E	4
Malvaviscus arboreus Cav.	Malvaceae	E	4
Mikania microdonta DC.	Asteraceae	N	4
Momordica charantia L.	Cucurbitaceae	E	4
Plectranthus scutellarioides (L.) R. Br.	Lamiaceae	E	4
Polygonum capitatum Buch.-Ham. ex D.Don	Polygonaceae	E	4
Richardia scabra L.	Rubiaceae	N	4
Russelia equisetiformis Schltdl. & Cham.	Plantaginaceae	E	4
Sinapis arvensis L.	Brassicaceae	E	4
Struthanthus flexicaulis	Loranthaceae	N	4
Aspilia camporum Chodat	Asteraceae	E	3
Bauhinia variegata L.	Fabaceae	E	3
Borreria verticillata (L.) G.Mey.	Rubiaceae	N	3

Brassica napus L.	Brassicaceae	E	3
Brassica nigra (L.) W.D.J.Koch	Brassicaceae	E	3
Brugmansia suaveolens (Willd.) Sweet	Solanaceae	E	3
Bryonia alba L.	Cucurbitaceae	E	3
Caryocar brasiliense Cambess.	Caryocaraceae	N	3
Cassia ferruginea (Schrad.) Schrad. ex DC.	Fabaceae	N	3
Cassia fistula L.	Fabaceae	E	3
Chlorophytum comosum (Thunb.) Jacques	Asparagaceae	E	3
Hypochaeris radicata L.	Asteraceae	E	3
Iochroma arborescens (L.) J.M.H. Shaw	Solanaceae	N	3
Ixora coccinea L.	Rubiaceae	E	3
Lafoensia pacari A.St.-Hil.	Lythraceae	N	3
Lepidaploa hagei (H.Rob.) H.Rob.	Asteraceae	E	3
Mesosphaerum suaveolens (L.) Kuntze	Lamiaceae	N	3
Pachystachys lutea Nees	Acanthaceae	E	3
Pandorea jasminoides (Lindl.) K.Schum.	Bignoniaceae	E	3
Pleroma mutabile (Vell.) Triana	Melastomataceae	N	3
Plumbago auriculata Lam.	Plumbaginaceae	E	3
Ruellia simplex C.Wright	Acanthaceae	E	3
Senna pendula (Humb.& Bonpl.ex Willd.) H.S.Irwin & Barneby	Fabaceae	N	3
Sida acuta Burm.f.	Malvaceae	N	3
Sida rhombifolia L.	Malvaceae	N	3
Tanacetum parthenium (L.) Sch.Bip.	Asteraceae	E	3
Tara spinosa (Molina) Britton & Rose	Fabaceae	E	3

Thevetia peruviana (Pers.) K.Schum.	Apocynaceae	E	3
Verbena officinalis L.	Verbenaceae	E	3
Washingtonia robusta H.Wendl.	Arecaceae	E	3
Aldama robusta (Gardner) E.E.Schill. & Panero	Asteraceae	E	2
Asemeia violacea (Aubl.) J.F.B.Pastore & J.R.Abbott	Polygalaceae	N	2
Aspilia reflexa (Sch.Bip. ex Baker) Baker	Asteraceae	E	2
Cassia grandis L.f.	Fabaceae	N	2
Chrysolaena obovata (Less.) Dematt.	Asteraceae	E	2
Cissus verticillata (L.) Nicolson & C.E.Jarvis	Vitaceae	N	2
Dietes bicolor (Steud.) Klatt ex Sweet	Iridaceae	E	2
Emilia fosbergii Nicolson	Asteraceae	E	2
Euphorbia pulcherrima Willd. ex Klotzsch	Euphorbiaceae	E	2
Gmelina arborea Roxb.	Lamiaceae	E	2
Grevillea banksii R.Br.	Proteaceae	E	2
Jatropha podagrica Hook.	Euphorbiaceae	E	2
Mangifera indica L.	Anacardiaceae	E	2
Mesembryanthemum cordifolium L.f.	Aizoaceae	E	2
Mussaenda philippica A.Rich.	Rubiaceae	E	2
Nerium oleander L.	Apocynaceae	E	2
Odontonema cuspidatum (Nees) Kuntze	Acanthaceae	E	2
Philadelphus coronarius L.	Hydrangeaceae	E	2
Pittosporum tobira (Thunb.) W.T.Aiton	Pittosporaceae	E	2
Portulaca grandiflora Hook.	Portulacaceae	N	2
Portulaca oleracea L.	Portulacaceae	E	2

Punica granatum L.	Lythraceae	E	2
Senna macranthera (DC. ex Collad.) H.S.Irwin & Barneby	Fabaceae	N	2
Solanum americanum Mill.	Solanaceae	N	2
Symphyopappus decemflorus H.Rob.	Asteraceae	E	2
Thunbergia erecta (Benth.) T. Anderson	Acanthaceae	E	2
Tipuana tipu (Benth.) Kuntze	Fabaceae	E	2
Tradescantia pallida (Rose) D.R.Hunt	Commelinaceae	E	2
Turnera ulmifolia L.	Turneraceae	E	2
Acmella ciliata (Kunth) Cass.	Asteraceae	N	1
Ageratum conyzoides L.	Asteraceae	N	1
Allamanda blanchetii A.DC.	Apocynaceae	E	1
Asparagus aethiopicus L.	Asparagaceae	E	1
Azadirachta indica A.Juss.	Meliaceae	E	1
Banisteriopsis argyrophylla (A.Juss.) B.Gates	Malpighiaceae	E	1
Banisteriopsis campestris (A.Juss.) Little	Malpighiaceae	E	1
Brunfelsia *uniflora* (Pohl) D.Don	Solanaceae	N	1
Cabralea canjerana (Vell.) Mart.	Meliaceae	N	1
Carica papaya L.	Caricaceae	E	1
Catharanthus roseus (L.) Don	Apocynaceae	E	1
Chaetogastra herbacea (DC.) P.J.F.Guim. & Michelang.	Melastomataceae	N	1
Chrysolaena platensis (Spreng.) H.Rob.	Asteraceae	N	1
Citrus × *limon* (L.) Osbeck	Rutaceae	E	1
Commelina erecta L.	Commelinaceae	N	1
Cucurbita máxima Duchesne ex Lam.	Cucurbitaceae	E	1

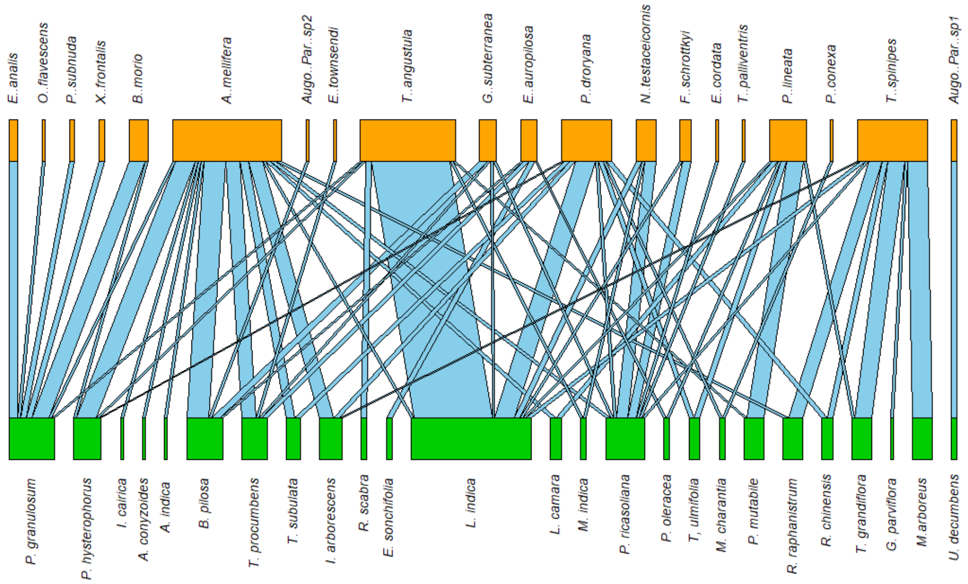
Cybistax antisyphilitica (Mart.) Mart.	Bignoniaceae	N	1
Eugenia involucrata DC.	Myrtaceae	N	1
Eugenia uniflora L.	Myrtaceae	N	1
Euphorbia hirta L.	Euphorbiaceae	N	1
Euphorbia hypericifolia L.	Euphorbiaceae	N	1
Grevillea robusta A.Cunn. ex R.Br.	Proteaceae	E	1
Gutenbergia boranensis (S.Moore) M.G.Gilbert	Asteraceae	E	1
Handroanthus serratifolius (Vahl) S.Grose	Bignoniaceae	N	1
Heteropterys tomentosa A.Juss.	Malpighiaceae	E	1
Justicia brandegeeana Wassh. & L.B.Sm.	Acanthaceae	E	1
Leucaena leucocephala (Lam.) de Wit	Fabaceae	E	1
Malvastrum coromandelianum (L.) Garcke	Malvaceae	N	1
Mirabilis jalapa L.	Nyctaginaceae	E	1
Nandina domestica Thunb.	Berberidaceae	E	1
Neomarica caerulea (Ker Gawl.) Sprague	Iridaceae	N	1
Nopalea cochenillifera (L.) Salm-Dyck	Cactaceae	E	1
Ocimum gratissimum L.	Lamiaceae	E	1
Penstemon grandiflorus Nutt.	Plantaginaceae	E	1
Petrea volubilis L.	Verbenaceae	N	1
Pimpinella anisum L.	Apiaceae	E	1
Senecio brasiliensis (Spreng.) Less.	Asteraceae	N	1
Solanum palinacanthum Dunal	Solanaceae	N	1
Stachytarpheta cayennensis (Rich.) Vahl	Verbenaceae	N	1
Tabebuia rosea (Bertol.) Bertero ex A.DC.	Bignoniaceae	E	1

Terminalia catappa L.	Combretaceae	E	1
Verbena bonariensis L.	Verbenaceae	N	1
Vernonanthura polyanthes (Sprengel) Vega & Dematteis	Asteraceae	N	1

SM 1

The mutualistic networks for each sampled site are represented below. Green color represents plants, yellow color represents bees and blue lines represent interactions.

Site 1



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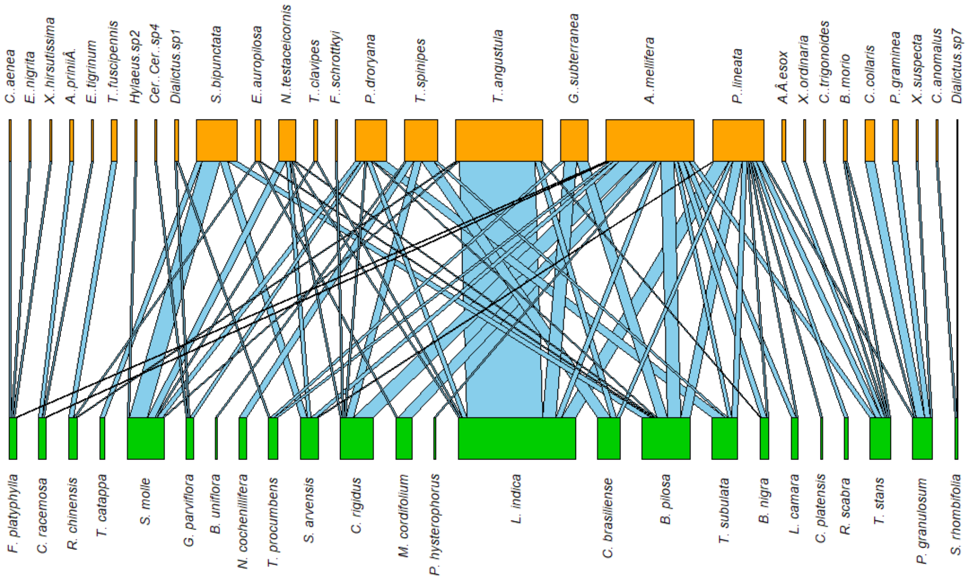

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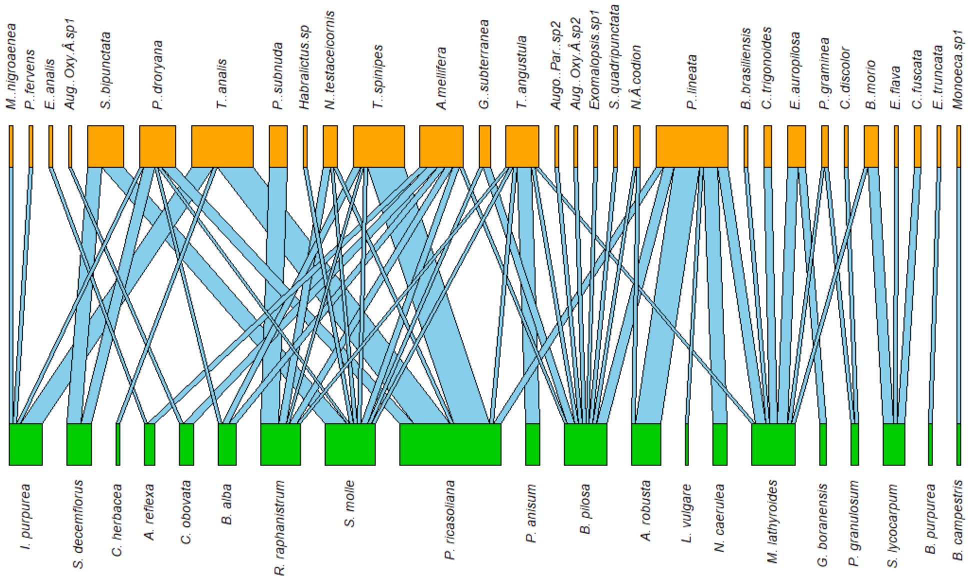
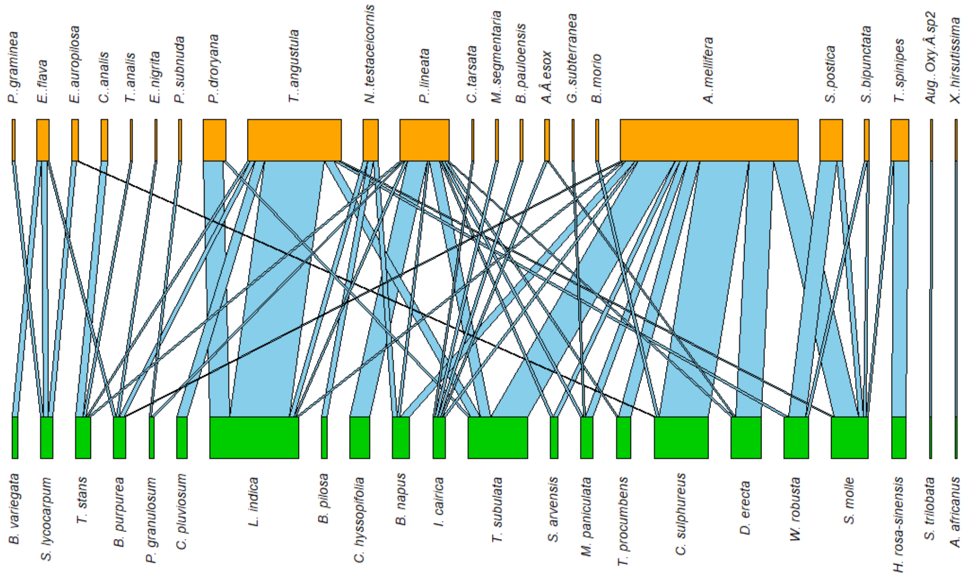
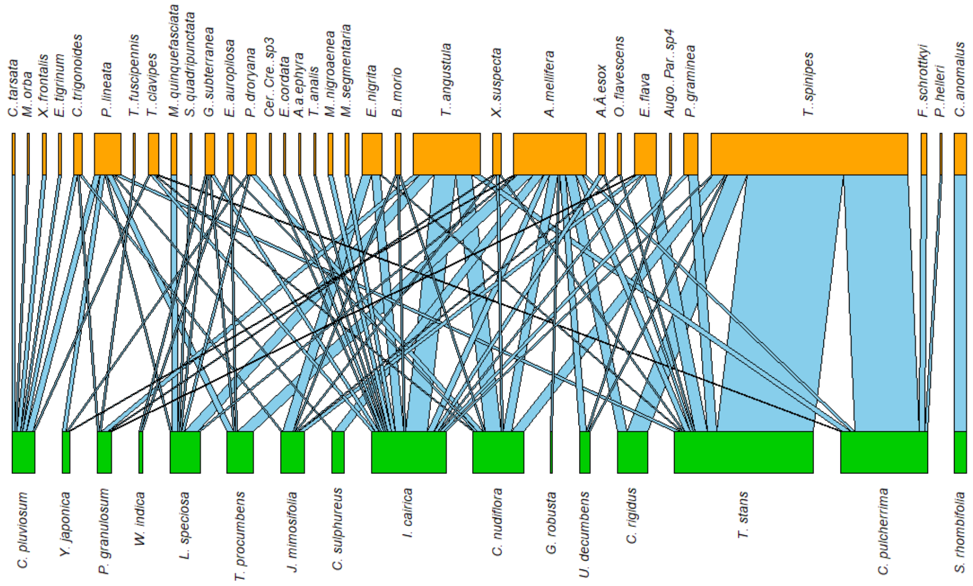

M..nigroaenea
P..fervens
E..analis
Aug..Oxy.Â.sp1
S..bipunctata
P..droryana
T..analis
P..subnuda
Habralictus.sp
N..testaceicornis
T..spinipes
A.mellifera
G..subterranea
T..angustula
Augo..Par..sp2
Aug..Oxy.Â.sp2
Exomalopsis.sp1
S..quadripunctata
N.Â.codion
P..lineata
B..brasiliensis
C..trigonoides
E..auropilosa
P..graminea
C..discolor
B..morio
E..flava
C..fuscata
E..truncata
Monoeca.sp1
I. purpurea
S. decemflorus
C. herbacea
A. reflexa
C. obovata
B. alba
R. raphanistrum
S. molle
P. ricasoliana
P. anisum
B. pilosa
A. robusta
L. vulgare
N. caerulea
M. lathyroides
G. boranensis
P. granulosum
S. lycocarpum
B. purpurea
B. campestris

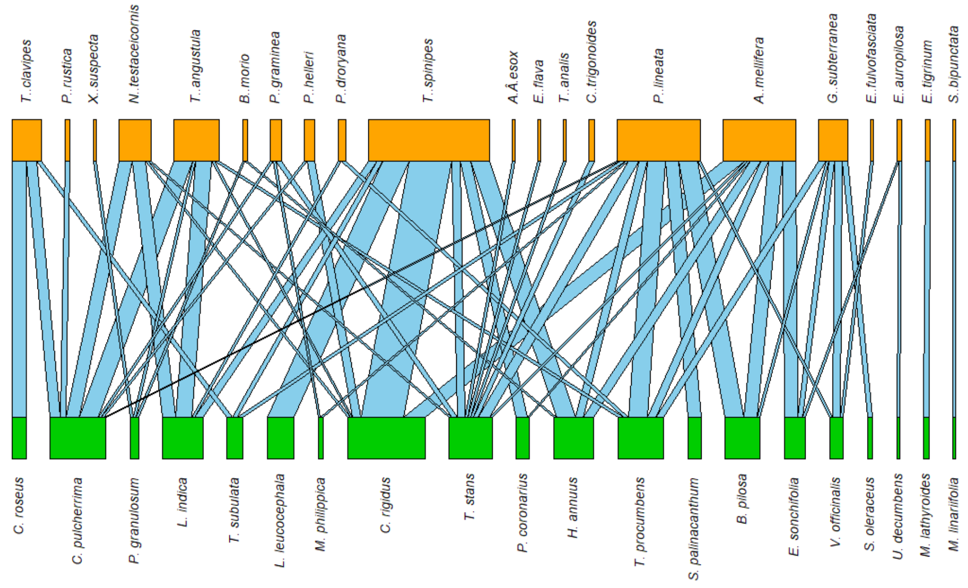
Site 4


P..graminea
E..flava
E..auropilosa
C..analis
T..analis
E..nigrita
P..subnuda
P..droryana
T..angustula
N..testaceicornis
P..lineata
C..tarsata
M..segmentaria
B..pauloensis
A.Â.esox
G..subterranea
B..morio
A..mellifera
S..postica
S..bipunctata
T..spinipes
Aug..Oxy.Â.sp2
X..hirsutissima
B. variegata
S. lycocarpum
T. stans
B. purpurea
P. granulosum
C. pluviosum
L. indica
B. pilosa
C. hyssopifolia
B. napus
I. cairica
T. subulata
S. arvensis
M. paniculata
T. procumbens
C. sulphureus
D. erecta
W. robusta
S. molle
H. rosa-sinensis
S. trilobata
A. africanus

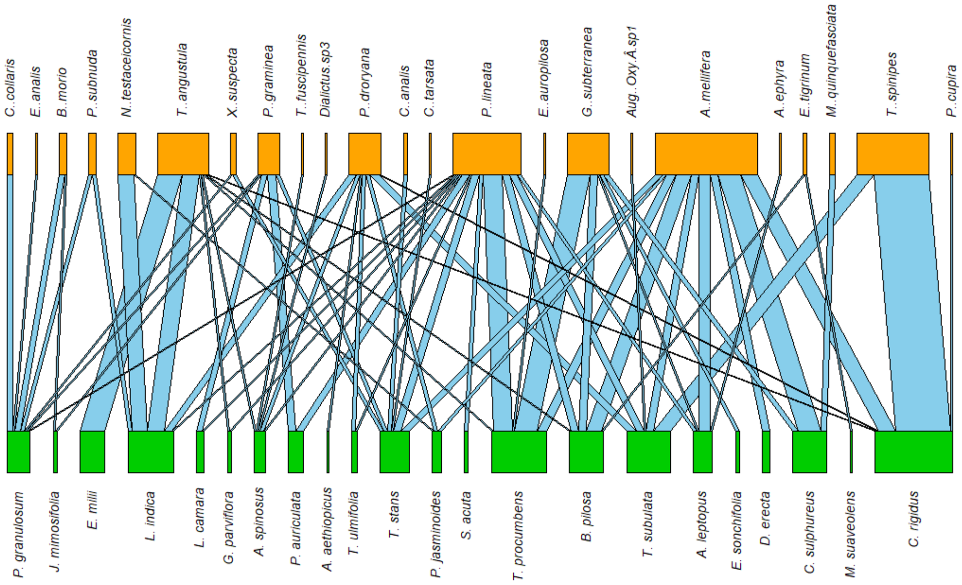
Site 5


C..tarsata
M..orba
X..frontalis
E..tigrinum
C..trigonoides
P..lineata
T..fuscipennis
T..clavipes
M..quinquefasciata
S..quadripunctata
G..subterranea
E..auropilosa
P..droryana
Cer..Cre..sp3
E..cordata
A.a.ephyra
T..analis
M..nigroaenea
M..segmentaria
E..nigrita
B..morio
T..angustula
X..suspecta
A..mellifera
A.Â.esox
O..flavescens
E..flava
Augo..Par..sp4
P..graminea
T..spinipes
F..schrottkyi
P..helleri
C..anomalus
C. pluviosum
Y. japonica
P. granulosum
W. indica
L. speciosa
T. procumbens
J. mimosifolia
C. sulphureus
I. cairica
C. nudiflora
G. robusta
U. decumbens
C. rigidus
T. stans
C. pulcherrima
S. rhombifolia

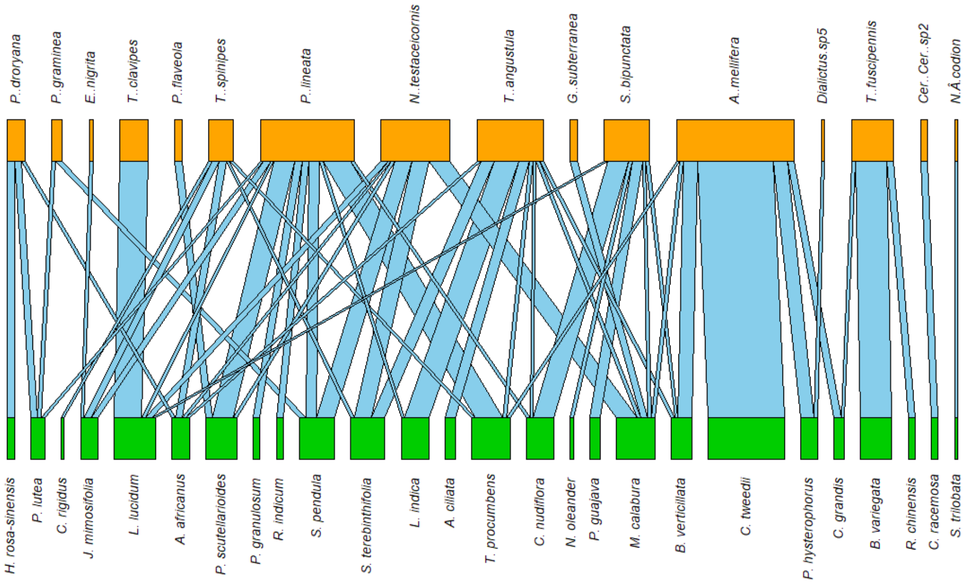
Site 6


T..clavipes
P..rustica
X..suspecta
N..testaceicornis
T..angustula
B..morio
P..graminea
P..helleri
P..droryana
T..spinipes
A.Â.esox
E..flava
T..analis
C..trigonoides
P..lineata
A..mellifera
G..subterranea
E..fulvofasciata
E..auropilosa
E..tigrinum
S..bipunctata
C. roseus
C. pulcherrima
P. granulosum
L. indica
T. subulata
L. leucocephala
M. philippica
C. rigidus
T. stans
P. coronarius
H. annuus
T. procumbens
S. palinacanthum
B. pilosa
E. sonchifolia
V. officinalis
S. oleraceus
U. decumbens
M. lathyroides
M. linariifolia

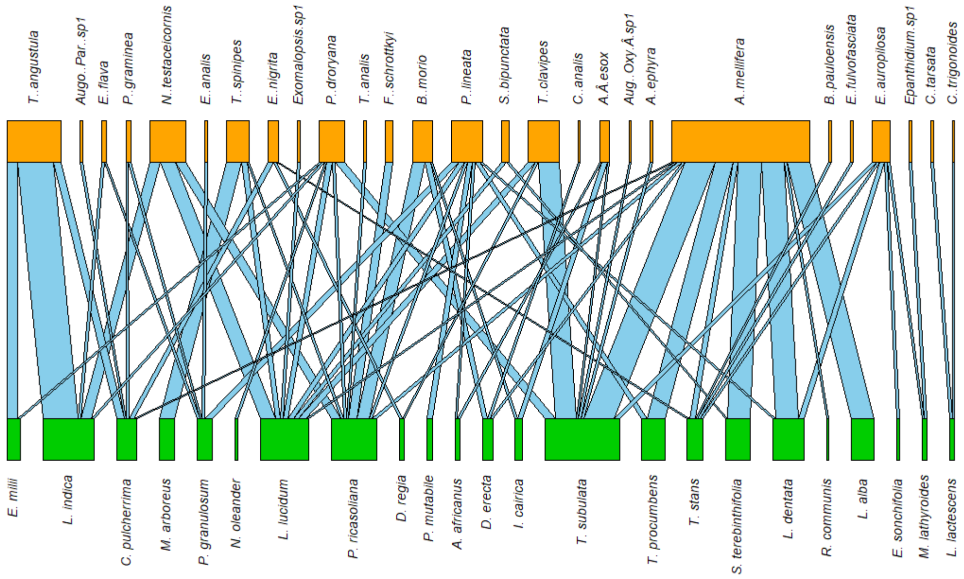
Site 7


C..collaris
E..analis
B..morio
P..subnuda
N..testaceicornis
T..angustula
X..suspecta
P..graminea
T..fuscipennis
Dialictus.sp3
P..droryana
C..analis
C..tarsata
P..lineata
E..auropilosa
G..subterranea
Aug..Oxy.Â.sp1
A..mellifera
A..ephyra
E..tigrinum
M..quinquefasciata
T..spinipes
P..cupira
P. granulosum
J. mimosifolia
E. milii
L. indica
L. camara
G. parviflora
A. spinosus
P. auriculata
A. aethiopicus
T. ulmifolia
T. stans
P. jasminoides
S. acuta
T. procumbens
B. pilosa
T. subulata
A. leptopus
E. sonchifolia
D. erecta
C. sulphureus
M. suaveolens
C. rigidus

Site 8


P..droryana
P..graminea
E..nigrita
T..clavipes
P..flaveola
T..spinipes
P..lineata
N..testaceicornis
T..angustula
G..subterranea
S..bipunctata
A..mellifera
Dialictus.sp5
T..fuscipennis
Cer..Cer..sp2
N.Â.codion
H. rosa-sinensis
P. lutea
C. rigidus
J. mimosifolia
L. lucidum
A. africanus
P. scutellarioides
P. granulosum
R. indicum
S. pendula
S. terebinthifolia
L. indica
A. ciliata
T. procumbens
C. nudiflora
N. oleander
P. guajava
M. calabura
B. verticillata
C. tweedii
P. hysterophorus
C. grandis
B. variegata
R. chinensis
C. racemosa
S. trilobata

Site 9



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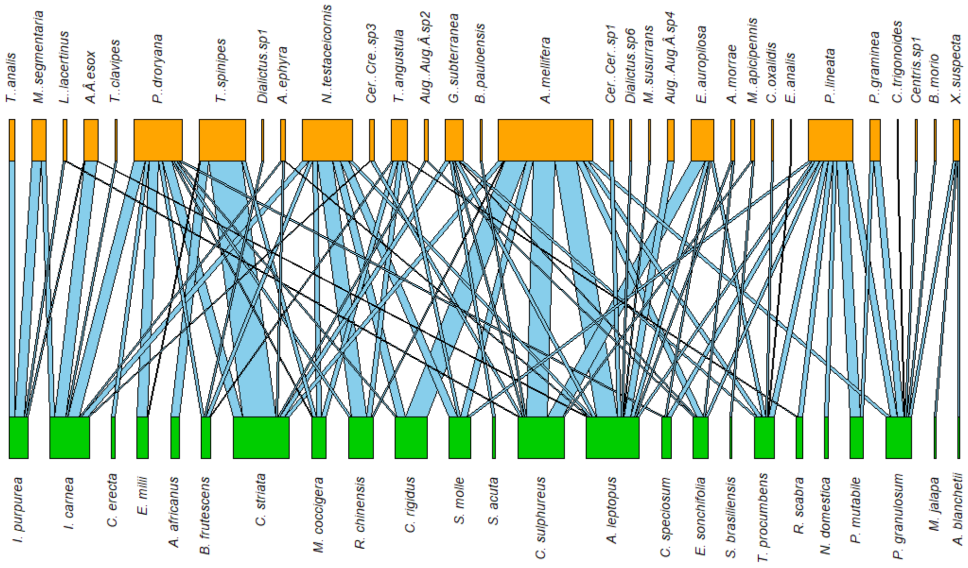

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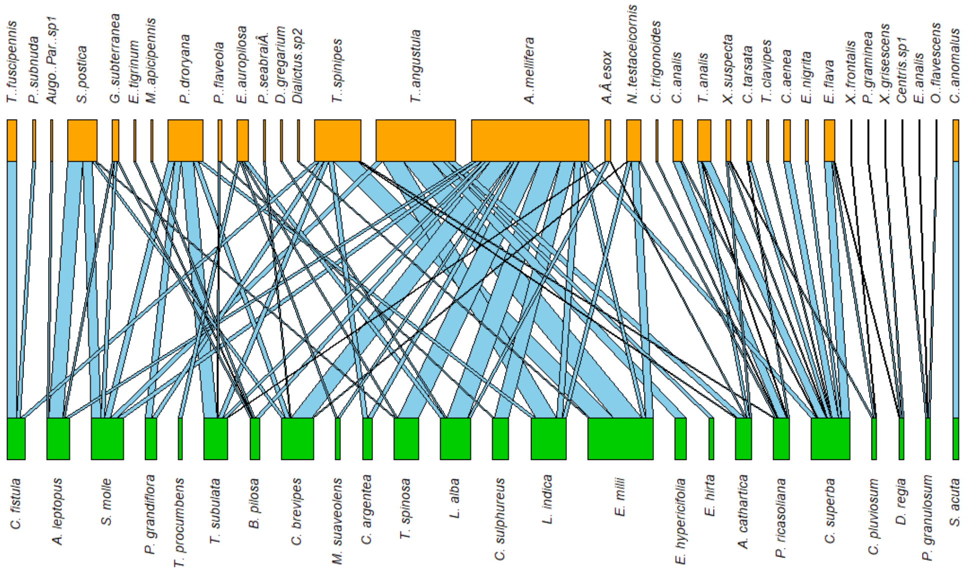

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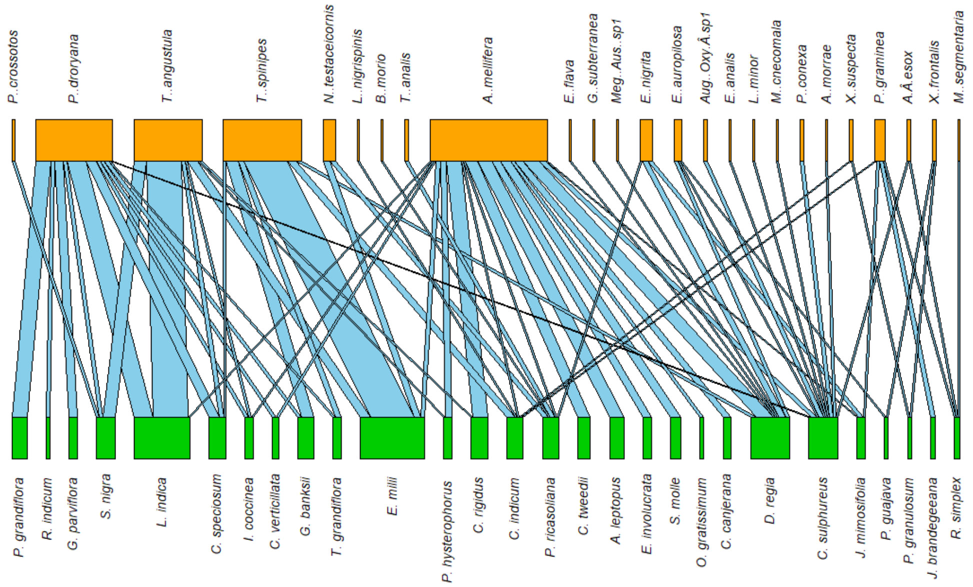

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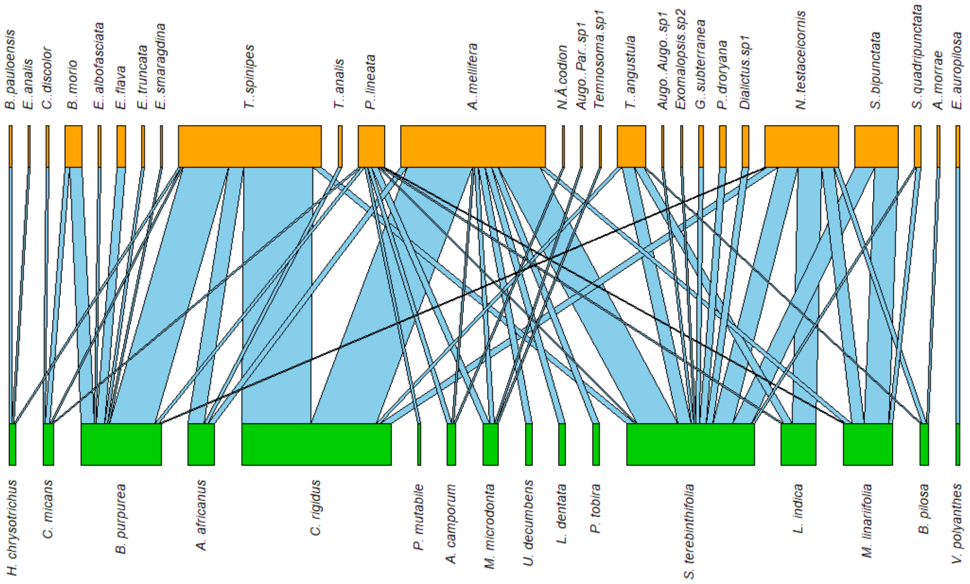

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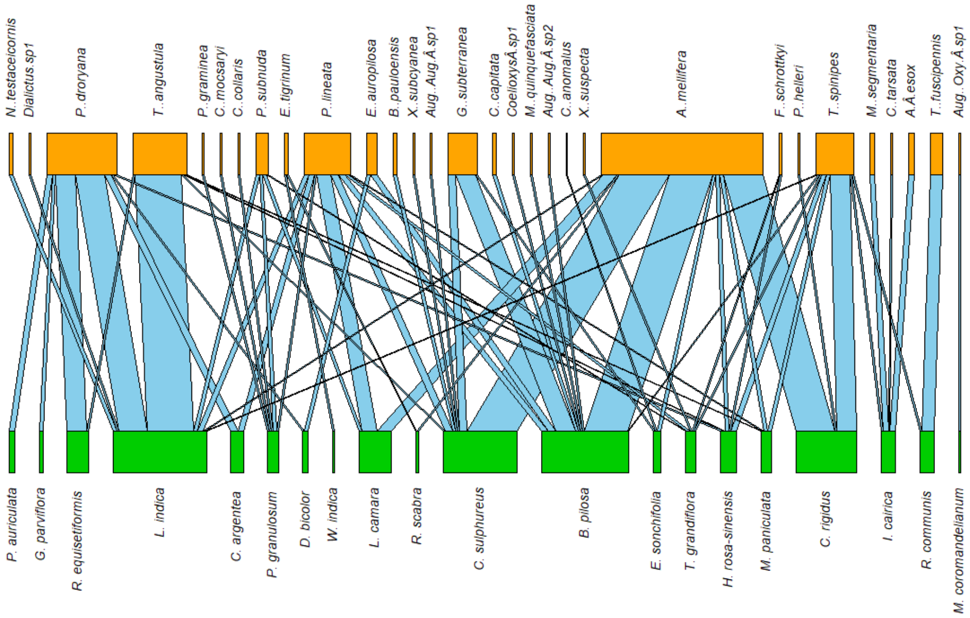

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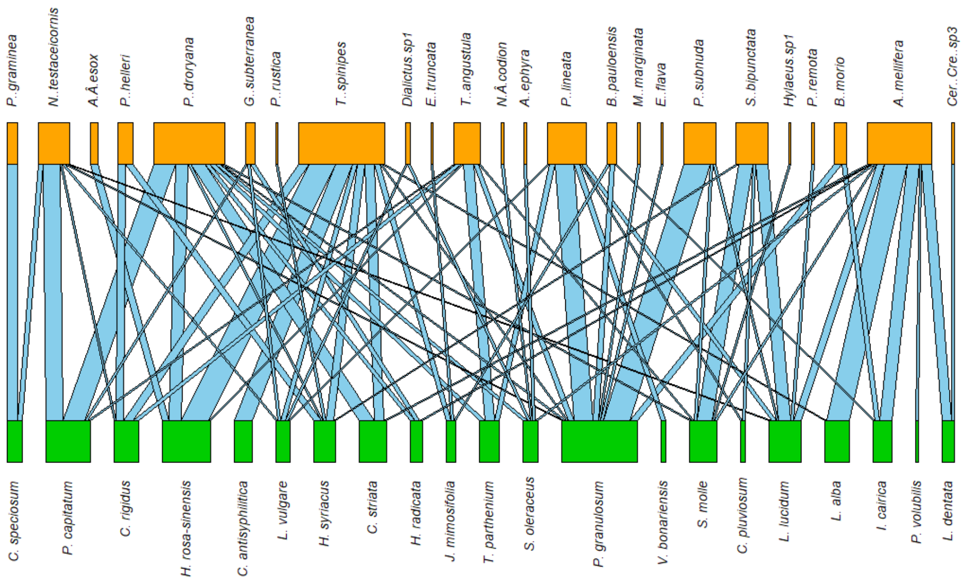

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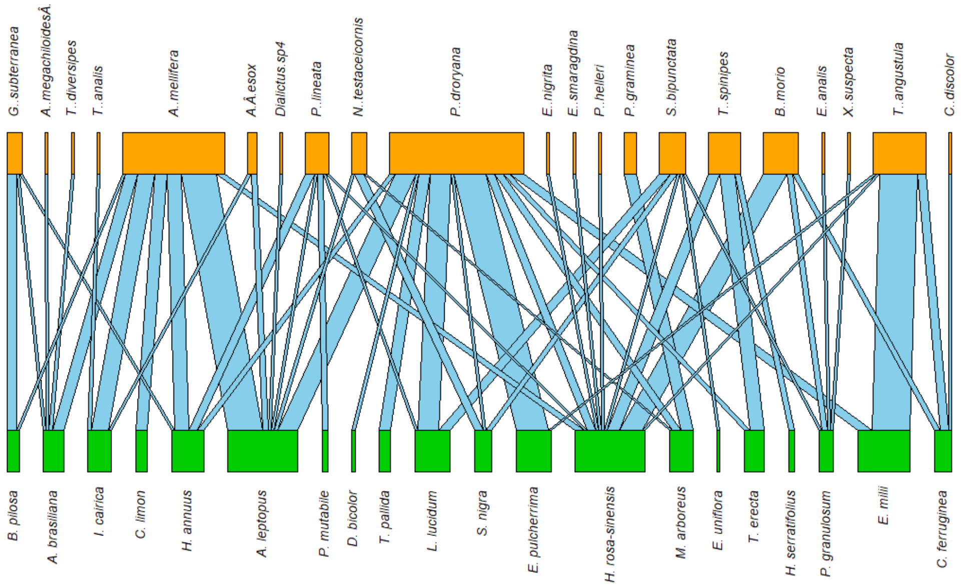

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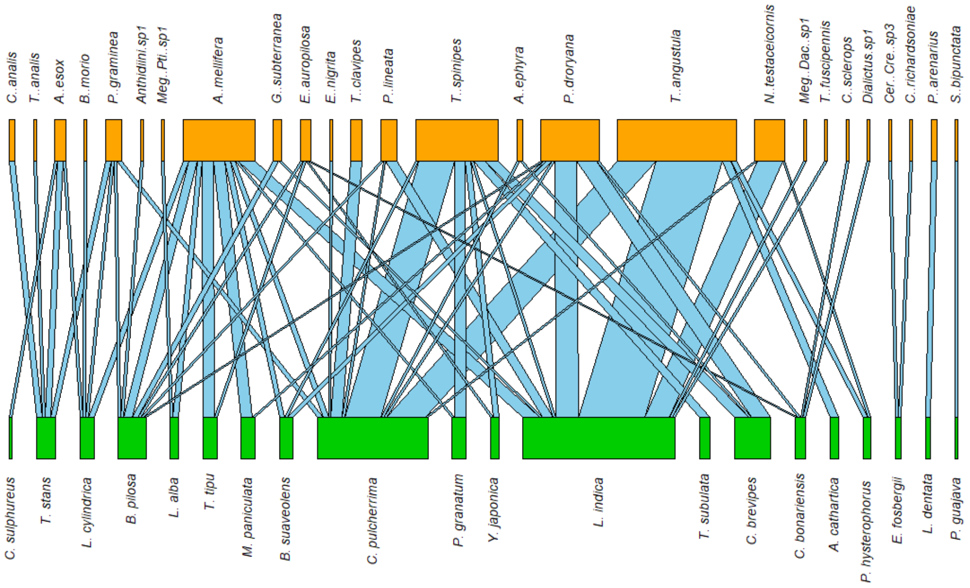

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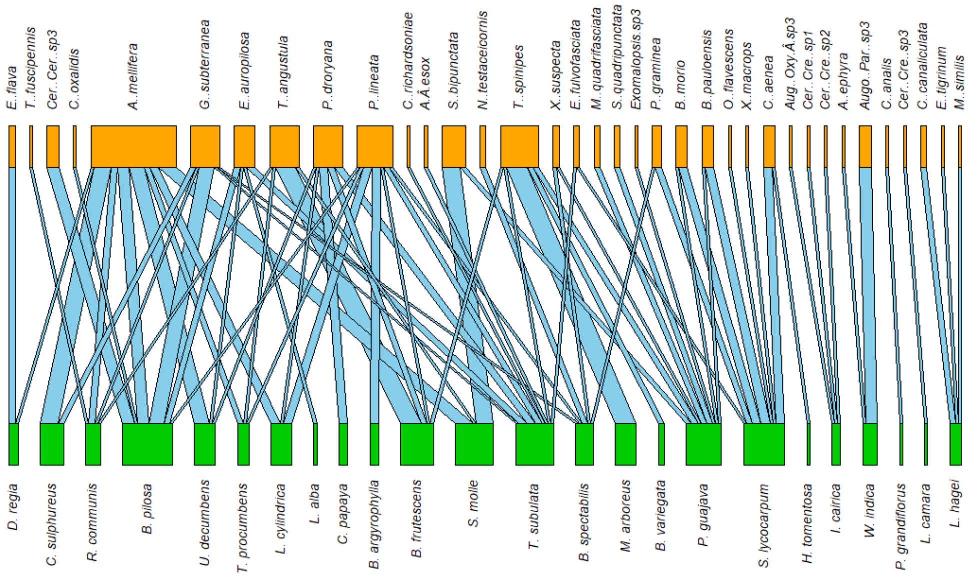

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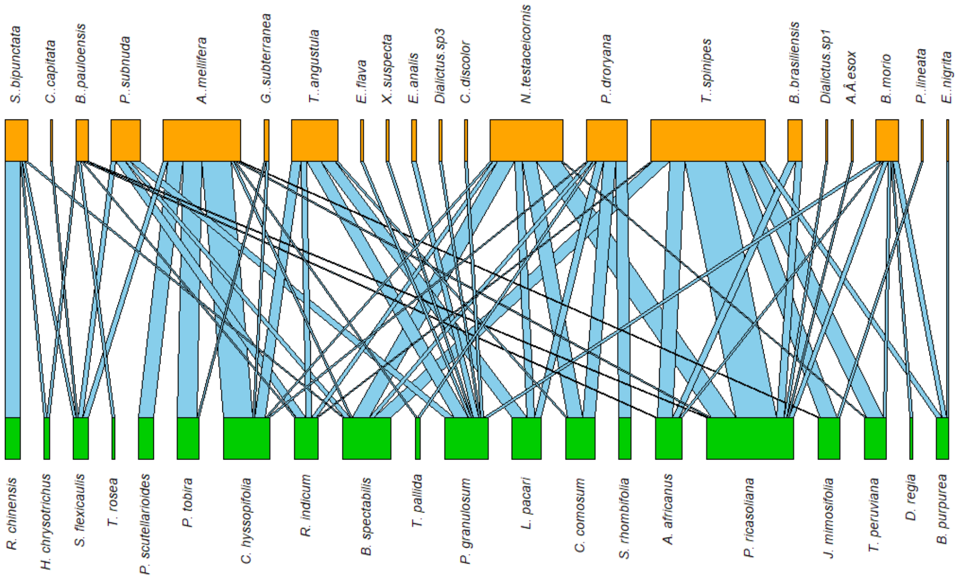

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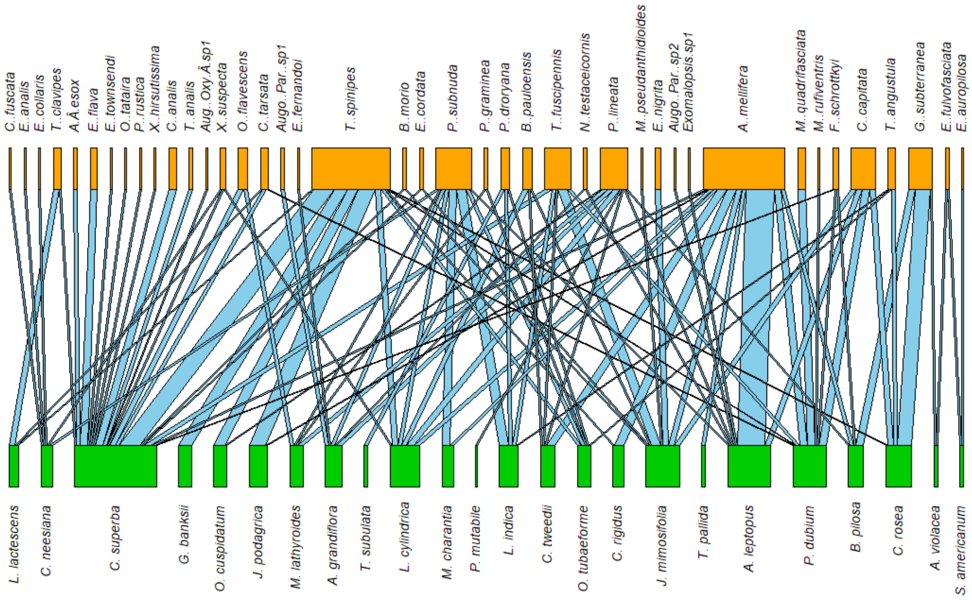

Site 21

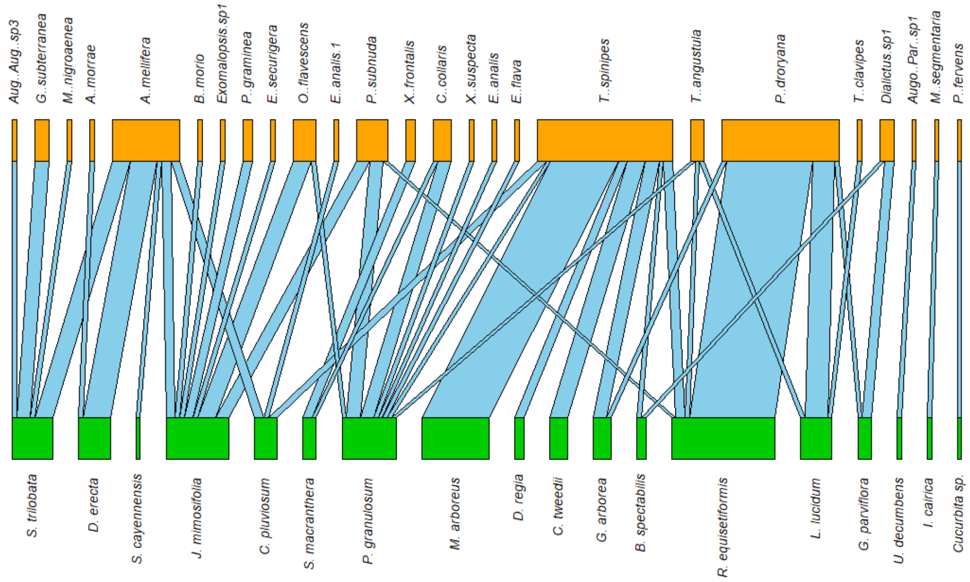

Table S3. Acronyms used in network images.

Plant species	**Acronyms**	**Bee species**	**Acronyms**
Abelia × grandiflora	*A. grandiflora*	*Acamptopoeum prinii*	*A. prinii*
Acmella ciliata	*A. ciliata*	*Anthidiini sp1*	*Anthidiini sp1*
Agapanthus africanus	*A. africanus*	*Anthodioctes megachiloides*	*A. megachiloides*
Ageratum conyzoides	*A. conyzoides*	*Apis mellifera*	*A. mellifera*
Aldama robusta	*A. robusta*	*Augochlora (Augochlora) sp1*	*Aug (Aug) sp1*
Allamanda blanchetii	*A. blanchetii*	*Augochlora (Augochlora) sp2*	*Aug (Aug) sp2*
Allamanda cathartica	*A. cathartica*	*Augochlora (Augochlora) sp3*	*Aug (Aug) sp3*
Alternanthera brasiliana	*A. brasiliana*	*Augochlora (Augochlora) sp4*	*Aug (Aug) sp4*
Amaranthus spinosus	*A. spinosus*	*Augochlora (Oxystoglossella) sp1*	*Aug (Oxy) sp1*
Antigonon leptopus	*A. leptopus*	*Augochlora (Oxystoglossella) sp2*	*Aug (Oxy) sp2*
Asemeia violacea	*A. violacea*	*Augochlora (Oxystoglossella) sp3*	*Aug (Oxy) sp3*
Asparagus aethiopicus	*A. aethiopicus*	*Augochlora morrae*	*A. morrae*
Aspilia camporum	*A. camporum*	*Augochlora esox*	*A. esox*
Aspilia reflexa	*A. reflexa*	*Augochlorella ephyra*	*A. ephyra*
Azadirachta indica	*A. indica*	*Augochloropsis (Augochloropsis) sp1*	*Augo (Augo) sp1*
Banisteriopsis argyrophylla	*B. argyrophylla*	*Augochloropsis (Paraugochloropsis) sp2*	*Augo (Par) sp2*
Banisteriopsis campestris	*B. campestris*	*Augochloropsis (Paraugochloropsis) sp3*	*Augo (Par) sp3*
Bauhinia purpurea	*B. purpurea*	*Augochloropsis*	*Augo (Par) sp4*

		(Paraugochloropsis) sp4	
Bauhinia variegata	*B. variegata*	*Augochloropsis (Paraugochloropsis) sp1*	*Augo (Par) sp1*
Bidens pilosa	*B. pilosa*	*Bombus brasiliensis*	*B. brasiliensis*
Borreria verticillata	*B. verticillata*	*Bombus morio*	*B. morio*
Bougainvillea spectabilis	*B. spectabilis*	*Bombus pauloensis*	*B. pauloensis*
Brassica napus	*B. napus*	*Centris aenea*	*C. aenea*
Brassica nigra	*B. nigra*	*Centris analis*	*C. analis*
Brugmansia suaveolens	*B. suaveolens*	*Centris collaris*	*C. collaris*
Brunfelsia uniflora	*B. uniflora*	*Centris discolor*	*C. discolor*
Bryonia alba	*B. alba*	*Centris fuscata*	*C. fuscata*
Bulbine frutescens	*B. frutescens*	*Centris mocsaryi*	*C. mocsaryi*
Cabralea canjerana	*C. canjerana*	*Centris sp1*	*Centris sp1*
Caesalpinia pulcherrima	*C. pulcherrima*	*Centris tarsata*	*C. tarsata*
Calliandra brevipes	*C. brevipes*	*Centris trigonoides*	*C. trigonoides*
Calliandra tweedii	*C. tweedii*	*Cephalotrigona capitata*	*C. capitata*
Callianthe striata	*C. striata*	*Cephalurgus anomalus*	*C. anomalus*
Callicarpa nudiflora	*C. nudiflora*	*Ceratina (Ceratinula) sp1*	*Cer (Cer) sp1*
Callistemon rigidus	*C. rigidus*	*Ceratina (Ceratinula) sp2*	*Cer (Cer) sp2*
Carica papaya	*C. papaya*	*Ceratina (Ceratinula) sp3*	*Cer (Cer) sp3*
Caryocar brasiliense	*C. brasiliense*	*Ceratina (Ceratinula) sp4*	*Cer (Cer) sp4*
Cassia ferruginea	*C. ferruginea*	*Ceratina (Crewella) sp1*	*Cer (Cre) sp1*
Cassia fistula	*C. fistula*	*Ceratina (Crewella) sp2*	*Cer (Cre) sp2*
Cassia grandis	*C. grandis*	*Ceratina (Crewella) sp3*	*Cer (Cre) sp3*
Catharanthus roseus	*C. roseus*	*Ceratina canaliculata*	*C. canaliculata*
Celosia argentea	*C. argentea*	*Ceratina oxalidis*	*C. oxalidis*
Cenostigma pluviosum	*C. pluviosum*	*Ceratina richardsoniae*	*C. richardsoniae*
Chaetogastra herbacea	*C. herbacea*	*Ceratina sclerops*	*C. sclerops*
Chamaecrista neesiana	*C. neesiana*	*Coelioxys sp1*	*Coelioxys sp1*
Chlorophytum comosum	*C. comosum*	*Dialictus sp1*	*Dialictus sp1*
Chrysolaena obovata	*C. obovata*	*Dialictus sp2*	*Dialictus sp2*
Chrysolaena platensis	*C. platensis*	*Dialictus sp3*	*Dialictus sp3*
Cissus verticillata	*C. verticillata*	*Dialictus sp4*	*Dialictus sp4*
Citrus × limon	*C. limon*	*Dialictus sp5*	*Dialictus sp5*
Clerodendrum × speciosum	*C. speciosum*	*Dialictus sp6*	*Dialictus sp6*
Clusia rosea	*C. rosea*	*Dialictus sp7*	*Dialictus sp7*
Combretum indicum	*C. indicum*	*Dicranthidium gregarium*	*D. gregarium*
Commelina erecta	*C. erecta*	*Epanthidium sp1*	*Epanthidium sp1*
Conyza bonariensis	*C. bonariensis*	*Epanthidium tigrinum*	*E. tigrinum*
Cordia superba	*C. superba*	*Epicharis albofasciata*	*E. albofasciata*
Cosmos sulphureus	*C. sulphureus*	*Epicharis analis*	*E. analis*
Crotalaria micans	*C. micans*	*Epicharis flava*	*E. flava*
Cucurbita máxima	*C. maxima*	*Euglossa cordata*	*E. cordata*
Cuphea hyssopifolia	*C. hyssopifolia*	*Euglossa securigera*	*E. securigera*
Cuphea racemosa	*C. racemosa*	*Euglossa townsendi*	*E. townsendi*
Cybistax antisyphilitica	*C. antisyphilitica*	*Euglossa truncata*	*E. truncata*
Delonix regia	*D. regia*	*Eulaema nigrita*	*E. nigrita*

Dietes bicolor	*D. bicolor*	*Exaerete smaragdina*	*E. smaragdina*
Duranta erecta	*D. erecta*	*Exomalopsis analis*	*E. analis*
Emilia fosbergii	*E. fosbergii*	*Exomalopsis auropilosa*	*E. auropilosa*
Emilia sonchifolia	*E. sonchifolia*	*Exomalopsis collaris*	*E. collaris*
Eugenia involucrata	*E. involucrata*	*Exomalopsis fernandoi*	*E. fernandoi*
Eugenia uniflora	*E. uniflora*	*Exomalopsis fulvofasciata*	*E. fulvofasciata*
Euphorbia hirta	*E. hirta*	*Exomalopsis sp1*	*Exomalopsis sp1*
Euphorbia hypericifolia	*E. hypericifolia*	*Exomalopsis sp2*	*Exomalopsis sp2*
Euphorbia milii	*E. milii*	*Exomalopsis sp3*	*Exomalopsis sp3*
Euphorbia pulcherrima	*E. pulcherrima*	*Friesella schrottkyi*	*F. schrottkyi*
Fridericia platyphylla	*F. platyphylla*	*Geotrigona subterranea*	*G. subterranea*
Galinsoga parviflora	*G. parviflora*	*Habralictus sp*	*Habralictus sp*
Gmelina arborea	*G. arborea*	*Hylaeus sp1*	*Hylaeus sp1*
Grevillea banksii	*G. banksii*	*Hylaeus sp2*	*Hylaeus sp2*
Grevillea robusta	*G. robusta*	*Leiopodus lacertinus*	*L. lacertinus*
Gutenbergia boranensis	*G. boranensis*	*Lophopedia minor*	*L. minor*
Handroanthus chrysotrichus	*H. chrysotrichus*	*Lophopedia nigrispinis*	*L. nigrispinis*
Handroanthus serratifolius	*H. serratifolius*	*Megachile (Austromegachile) sp1*	*Meg (Aus) sp1*
Helianthus annuus	*H. annuus*	*Megachile (Dactylomegachile) sp1*	*Meg (Dac) sp1*
Heteropterys tomentosa	*H. tomentosa*	*Megachile (Ptilosarus) sp1*	*Meg (Pti) sp1*
Hibiscus rosa-sinensis	*H. rosa-sinensis*	*Megachile apicipennis*	*M. apicipennis*
Hibiscus syriacus	*H. syriacus*	*Megachile orba*	*M. orba*
Hypochaeris radicata	*H. radicata*	*Megachile pseudanthidioides*	*M. pseudanthidioides*
Iochroma arborescens	*I. arborescens*	*Megachile susurrans*	*M. susurrans*
Ipomoea cairica	*I. cairica*	*Melipona marginata*	*M. marginata*
Ipomoea carnea	*I. carnea*	*Melipona quadrifasciata*	*M. quadrifasciata*
Ipomoea purpurea	*I. purpurea*	*Melipona quinquefasciata*	*M. quinquefasciata*
Ixora coccinea	*I. coccinea*	*Melipona rufiventris*	*M. rufiventris*
Jacaranda mimosifolia	*J. mimosifolia*	*Melissodes nigroaenea*	*M. nigroaenea*
Jatropha podagrica	*J. podagrica*	*Melissoptila cnecomala*	*M. cnecomala*
Justicia brandegeeana	*J. brandegeeana*	*Melissoptila similis*	*M. similis*
Lafoensia pacari	*L. pacari*	*Melitoma segmentaria*	*M. segmentaria*
Lagerstroemia indica	*L. indica*	*Monoeca sp1*	*Monoeca sp1*
Lagerstroemia speciosa	*L. speciosa*	*Nannotrigona testaceicornis*	*N. testaceicornis*
Lantana camara	*L. camara*	*Neocorynura codion*	*N. codion*
Lavandula dentata	*L. dentata*	*Oxaea flavescens*	*O. flavescens*
Lepidaploa hagei	*L. hagei*	*Oxytrigona tataira*	*O. tataira*
Leucaena leucocephala	*L. leucocephala*	*Paratetrapedia conexa*	*P. conexa*
Leucanthemum vulgare	*L. vulgare*	*Paratetrapedia flaveola*	*P. flaveola*
Ligustrum lucidum	*L. lucidum*	*Paratrigona lineata*	*P. lineata*
Lippia alba	*L. alba*	*Paratrigona subnuda*	*P. subnuda*
Lophanthera lactescens	*L. lactescens*	*Paroxystoglossa crossotos*	*P. crossotos*
Luffa cylindrica	*L. cylindrica*	*Paroxystoglossa seabrai*	*P. seabrai*
Macroptilium lathyroides	*M. lathyroides*	*Partamona cupira*	*P. cupira*

Malpighia coccigera	*M. coccigera*	*Partamona helleri*	*P. helleri*
Malvastrum coromandelianum	*M. coromandelianum*	*Partamona rustica*	*P. rustica*
Malvaviscus arboreus	*M. arboreus*	*Peponapis fervens*	*P. fervens*
Mangifera indica	*M. indica*	*Plebeia droryana*	*P. droryana*
Melaleuca linariifolia	*M. linariifolia*	*Plebeia remota*	*P. remota*
Mesembryanthemum cordifolium	*M. cordifolium*	*Pseudagapostemon arenarius*	*P. arenarius*
Mesosphaerum suaveolens	*M. suaveolens*	*Pseudaugochlora graminea*	*P. graminea*
Mikania microdonta	*M. microdonta*	*Scaptotrigona bipunctata*	*S. bipunctata*
Mirabilis jalapa	*M. jalapa*	*Scaptotrigona postica*	*S. postica*
Momordica charantia	*M. charantia*	*Schwarziana quadripunctata*	*S. quadripunctata*
Muntingia calabura	*M. calabura*	*Temnosoma sp1*	*Temnosoma sp1*
Murraya paniculata	*M. paniculata*	*Tetragona clavipes*	*T. clavipes*
Mussaenda philippica	*M. philippica*	*Tetragonisca angustula*	*T. angustula*
Nandina domestica	*N. domestica*	*Tetrapedia diversipes*	*T. diversipes*
Neomarica caerulea	*N. caerulea*	*Thygater analis*	*T. analis*
Nerium oleander	*N. oleander*	*Thygater palliventris*	*T. palliventris*
Nopalea cochenillifera	*N. cochenillifera*	*Trigona fuscipennis*	*T. fuscipennis*
Ocimum gratissimum	*O. gratissimum*	*Trigona spinipes*	*T. spinipes*
Odontonema cuspidatum	*O. cuspidatum*	*Xylocopa frontalis*	*X. frontalis*
Odontonema tubaeforme	*O. tubaeforme*	*Xylocopa grisescens*	*X. grisescens*
Pachystachys lutea	*P. lutea*	*Xylocopa hirsutissima*	*X. hirsutissima*
Pandorea jasminoides	*P. jasminoides*	*Xylocopa macrops*	*X. macrops*
Parthenium hysterophorus	*P. hysterophorus*	*Xylocopa ordinaria*	*X. ordinaria*
Peltophorum dubium	*P. dubium*	*Xylocopa subcyanea*	*X. subcyanea*
Penstemon grandiflorus	*P. grandiflorus*	*Xylocopa suspecta*	*X. suspecta*
Petrea volubilis	*P. volubilis*		
Philadelphus coronarius	*P. coronarius*		
Pimpinella anisum	*P. anisum*		
Pittosporum tobira	*P. tobira*		
Plectranthus scutellarioides	*P. scutellarioides*		
Pleroma granulosum	*P. granulosum*		
Pleroma mutabile	*P. mutabile*		
Plumbago auriculata	*P. auriculata*		
Podranea ricasoliana	*P. ricasoliana*		
Polygonum capitatum	*P. capitatum*		
Portulaca grandiflora	*P. grandiflora*		
Portulaca oleracea	*P. oleracea*		
Psidium guajava	*P. guajava*		
Punica granatum	*P. granatum*		
Raphanus raphanistrum	*R. raphanistrum*		
Rhododendron indicum	*R. indicum*		
Richardia scabra	*R. scabra*		
Ricinus communis	*R. communis*		
Rosa chinensis	*R. chinensis*		
Ruellia simplex	*R. simplex*		
Russelia equisetiformis	*R. equisetiformis*		

Sambucus nigra	*S. nigra*
Schinus molle	*S. molle*
Schinus terebinthifolia	*S. terebinthifolia*
Senecio brasiliensis	*S. brasiliensis*
Senna macranthera	*S. macranthera*
Senna pendula	*S. pendula*
Sida acuta	*S. acuta*
Sida rhombifolia	*S. rhombifolia*
Sinapis arvensis	*S. arvensis*
Solanum americanum	*S. americanum*
Solanum lycocarpum	*S. lycocarpum*
Solanum palinacanthum	*S. palinacanthum*
Sonchus oleraceus	*S. oleraceus*
Sphagneticola trilobata	*S. trilobata*
Stachytarpheta cayennensis	*S. cayennensis*
Struthanthus flexicaulis	*S. flexicaulis*
Symphyopappus decemflorus	*S. decemflorus*
Tabebuia rosea	*T. rosea*
Tanacetum parthenium	*T. parthenium*
Tara spinosa	*T. spinosa*
Tecoma stans	*T. stans*
Terminalia catappa	*T. catappa*
Thevetia peruviana	*T. peruviana*
Thunbergia erecta	*T. erecta*
Thunbergia grandiflora	*T. grandiflora*
Tipuana tipu	*T. tipu*
Tradescantia pallida	*T. pallida*
Tridax procumbens	*T. procumbens*
Turnera subulata	*T. subulata*
Turnera ulmifolia	*T. ulmifolia*
Urochloa decumbens	*U. decumbens*
Verbena bonariensis	*V. bonariensis*
Verbena officinalis	*V. officinalis*
Vernonanthura polyanthes	*V. polyanthes*
Waltheria indica	*W. indica*
Washingtonia robusta	*W. robusta*
Youngia japonica	*Y. japonica*

CONCLUSÃO GERAL

A perda de biodiversidade devido à urbanização constitui um grande desafio para a governança e planejamento da cidade, e a preocupação com a conservação de abelhas em ambientes urbanos tem se tornado mais frequente. Nos três capítulos desenvolvidos nessa tese, conseguimos avaliar os impactos da urbanização sobre as abelhas em uma região no Brasil caracterizada pela presença de cidades pequenas e médias, as quais tem sido dada pouca atenção nos estudos até agora. Através dos resultados destes três capítulos vimos que assim como nas metrópoles, a comunidade de abelhas foi influenciada pela urbanização em escala local e de paisagem em cidades menores. Demonstramos a importância de se manter uma maior diversidade de hábitats e áreas permeáveis nas cidades, bem como utilização de plantas nativas no paisagismo urbano, a fim de abrigar uma maior diversidade de espécies, principalmente aquelas que utilizam o solo para nidificação e especialistas alimentares.

Os resultados deste estudo mostraram também várias implicações para a proteção das abelhas frente à expansão urbana. Eles mostram um notável benefício do modelo de desenvolvimento urbano “land-sharing”, ou compartilhamento de terras, sobre a comunidade de abelhas. Além dos benefícios para a conservação da biodiversidade, esse modelo tem outras vantagens, como a conexão dos moradores com a natureza devido à proximidade de moradias e espaços verdes e maior facilidade de ser implantado nas cidades comparado às grandes áreas preservadas (land-sparing). A aplicação do conceito de economia e compartilhamento de terras ao planejamento urbano é um avanço significativo em relação aos estudos aplicados em gradientes urbanos simples no que diz respeito à conservação da biodiversidade.

Nosso estudo demonstrou também a importância dos efeitos da urbanização nas redes mutualísticas, já que a perda das principais interações bióticas pode acelerar a extinção local de espécies e diminuir as funções do ecossistema que prestam serviços aos seres humanos. Dado que a maioria das plantas depende das abelhas para a polinização e as abelhas dependem dos recursos florais para sua sobrevivência, o uso de plantas mais atrativas esses polinizadores pode ser uma solução eficiente para sustentar uma parte substancial da sua diversidade nas cidades. Portanto, os esforços direcionados à conservação das abelhas nas cidades devem se concentrar tanto em relação aos fatores da paisagem, promovendo uma maior diversidade de hábitats e áreas permeáveis para as abelhas, quanto aos fatores locais, como a incorporação de plantas nativas na flora urbana.

Somados aos manuscritos da tese, desenvolvemos também um catálogo ilustrado das abelhas coletadas no nosso estudo, descrevendo seu comportamento, hábito de nidificação, especialização trófica, sua distribuição e as espécies de plantas onde foram encontradas. Nosso objetivo aqui foi fornecer informações para a população fora do ambiente acadêmico, já que o interesse pela conservação das abelhas tem crescido e há pouco conhecimento sobre as características das espécies regionais e sobre quais plantas podem ser mais atrativas. Esperamos, a partir destes trabalhos, fornecer mais informações acerca da conservação das abelhas em ambientes urbanos, tanto no meio acadêmico quanto para a população em geral.