Urbanization Effects on Wild Bee Communities and Their Plant Interactions

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Abstract

Urbanization has contributed greatly to the diminishment of habitat that supports diverse bee communities. Despite generally having negative effects on bees broadly, bees exhibit differential responses to local and landscape features associated with urbanization. As a result, cities possess the potential to harbor unique bee communities; however, determining which bees are vulnerable in such landscapes is essential to developing appropriate conservation initiatives that promote biodiversity in urban spaces. This study reviews the current known effects of urbanization on bees while recognizing knowledge gaps that require further research attention. Additionally, this study samples twenty-nine sites along an urban gradient to investigate the effects of urbanization on bee community structure and plant interactions. Bee communities were dominated by key functional traits and were found to be influenced by percent impervious surface and tree cover. Bee-plant interactions revealed the genus *Solidago* and other plant genera to be particularly attractive to various bee species.

Dedicated to Dr. Nancy Cowden whose introduction of native bees ignited a lifelong passion.

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General Introduction

With over 20,000 species represented globally (Michener 2007), bees are one of the most successful and recognizable pollinators on the planet, contributing to the pollination of 90% of the world's flowering plants (Ollerton et al. 2011). These pollinators have evolved predominantly obligate and mutualistic relationships with plant hosts of which they are dependent upon to meet their nutritional and reproductive requirements. Consequently, bees are both ecologically and economically important to humans. This is especially apparent within agricultural landscapes where bees are extensively relied upon for crop pollination (Klein et al. 2007; Tibesigwa et al. 2020) and their presence can significantly enhance fruit set yields (Garibaldi et al. 2013).

Several studies have indicated that bees are generally declining worldwide with some indicating a 25% reduction in species between 2006-2015 as compared to before 1990 (Potts et al. 2010; Zattara and Aizen 2021). Reported declines have been largely attributed to numerous anthropogenically driven factors such as climate change, land use change, pesticide use, disease and pathogen presence, as well as introductions from non-native species (Cariveau and Winfree 2015; Dicks et al. 2021; LeBuhn and Luna 2021) all of which often exert various compounding effects on bees (Goulson et al. 2015). Globally, roughly 51% of the terrestrial surface has been moderately to intensely modified by human activity (Kennedy et al. 2018) with land use drivers such as agricultural and urban expansion and intensification contributing most significantly to bee declines (Carivaeu and Winfree 2015). This trend is not exclusive to bees either as biodiversity declines broadly have been associated with human-mediated habitat loss (Fischer and Lindenmayer 2007; Newbold et al. 2015; Chase et al. 2020).

Declines as a response to land use change result from the destruction, fragmentation, and erosion of quality habitat that provide essential foraging and nesting resources for bees (Beismeijer et al. 2006; Goulson et al 2008; Potts et al. 2010; Cariveau and Winfree 2015). In industrial agriculture, many floral resources that exist are typically present as monocultures only available during a specific growing season (Kennedy et al. 2013; Di Pasquale 2016). Additionally, these environments today rely extensively on pesticides which can produce sublethal effects in bees (Goulson et al. 2015). Urbanization on the other hand, consists of frequently fragmented habitats resulting from buildings and other impervious surfaces. Not only does impervious surface make cities warmer in what is known as the heat island effect (Oke 1973), but it may also affect bees with limited mobility as suitable patches are spaced farther distances from one another throughout the landscape (Harrison and Winfree 2015; Greenleaf et al. 2007). What's more, urban environments possess an abundance of non-native plant species which may affect not only native plant communities but bee compositions as well (Hostetler and McIntyre 2001; Morales and Traveset 2009; Lowenstein et al. 2019). More research on the effects on non-native plants on bees in urban ecosystems is required though.

Despite bees being quite speciose, the bulk of the research conducted on these Hymenoptera has primarily focused on the European honey bee, *Apis mellifera*, unsurprisingly due to its extensive use and overreliance in agricultural settings. Unfortunately, the honey bee is not necessarily a reliable species from which to draw generalizable conclusions from as wild bee species may respond differently to the same environmental stressors (Cariveau and Winfree 2015). Therefore, continued research specifically evaluating wild bee response to anthropogenic activity is critical to developing a wholistic understanding of bee decline. Not only is this research necessary from a conservation perspective but also from an ecological one as wild bees provide essential pollination services even in the face of honey bee losses (Winfree et al. 2007) given that appropriate natural resources are also available (Garibaldi et al. 2011).

Research focused on wild bees in urban landscapes has been especially sparse throughout the literature when compared to work conducted in agricultural contexts even though urban agriculture can contribute to food security (Orsini et al. 2013) and promote bee diversity (Matteson and Langellotto 2008; Kaluza et al. 2016; Lanner et al. 2019). Studies that have been conducted in city spaces however indicate that the urban landscape generally reduces bee richness and abundance overall (Cardoso and Gonclaves 2018; Piano et al. 2019). This is not always the case however as seemingly contradictory studies have noted that in several cases cities can possess unique bee communities in which bee richness and abundance can exceed that found in agricultural landscapes and even semi-natural landscapes (Baldock et al. 2015; Sirohi et al. 2015; Kaluza et al. 2016; Banaszak-Cibicka et al. 2018; Theodorou et al. 2020; Prendergast et al. 2022). Furthermore, bees display differential responses to urbanization in which some bees appear to thrive in such spaces while others may become extirpated (Banaszak-Cibicka and Żmihorski 2012; Knop 2016). This lack of consensus has necessitated the demand for continued research within such environments especially as urban sprawl and densification continue.

Urban pollinator ecology holds additional value in that it not only attempts to promote biodiversity within the city, but it may also contribute to human physical and mental health and serve as an excellent opportunity for community outreach and engagement (Keeler et al. 2019; Pawelek et al. 2009). Urban agriculture and city parks are particularly important in this regard as green areas such as community gardens are reliant on pollinators, often involve varying degrees of community interaction, and have been attributed to increased well-being in humans (Wolch et al. 2014; Kondo et al. 2018; Keeler et al. 2019). Additionally, multiple studies, especially those dependent upon private and public property, enable researchers to communicate their findings with community members both directly and indirectly involved in the project (Southon et al. 2017). In many instances, the public is generally receptive of such outreach attempts and their participation in studies can substantiate feelings of satisfaction as they are able to learn about and contribute to conservation in a way that is meaningful to them (Pawelek et al. 2009). By advocating for the preservation of naturalized areas and other green spaces throughout cities, community members may experience health, educational, nutritional, and economic benefits especially when considering urban agriculture (Azurne et al. 2019; Keeler et al. 2019).

Overall, urban ecological studies are essential to the understanding of how organisms such as bees respond to extensively altered landscapes and future conservation initiatives are reliant on such work to establish well-informed decisions to promote and preserve species and communities sensitive to urban change. This study investigates the effects of urbanization on bee communities and their plant interactions to provide further insight into the complex and non-generalizable effects of urbanization on city bees. In

Chapter I, current understandings of bee response to urbanization are synthesized into a review that assesses the varying local and landscape factors that synergistically influence bee community compositions. Additionally, knowledge gaps in research are indicated such that future research can be directed towards areas where information is lacking. In Chapter II, the effects of urbanization on bee community structure and plant interactions were investigated along a gradient of urbanization and bee-plant interactions were employed to observe potential shifts in community interactions occurring within the urban matrix. The thesis concludes with a general discussion that summarizes the research and associated findings of this study and the implications such work has for the city of Toronto and urban environments generally.

Chapter I: Supporting Bees in Cities: How Bees Are Influenced by Local and Landscape Features

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Simple Summary

Cities are complex ecosystems that, while generally contributing to an overall reduction in biodiversity, can support surprisingly unique communities of organisms including bees. Bees are both ecologically and economically essential, therefore preserving and conserving these insects represents a significant challenge as cities continue to expand and diminish surrounding landscapes. Some attempts to support bees in cities have included establishing and improving urban green spaces. Exactly how bees and, to a lesser extent, other pollinators respond to these green spaces in addition to other urban landscape and local features, however, remains incompletely understood. Therefore, this review summarizes the current literature and generalizable trends in pollinator response to urban landscape and local features. While some functional traits or characteristics of bees such as dietary breadth and nesting strategy are more conclusively understood and supported, other characteristics such as sociality remain less generalizable. Lack of knowledge on bee responses to city features is in part due to the individual variation exhibited across different groups and species. To promote greater biodiversity in urban spaces, research should focus on specific responses to urban local and landscape features and how green spaces can be optimized for sustainable bee conservation.

Abstract

Urbanization is a major anthropogenic driver of decline for ecologically and economically important taxa including bees. Despite their generally negative impact on pollinators, cities can display a surprising degree of biodiversity compared to other landscapes. The pollinating communities found within these environments, however, tend to be filtered by interacting local and landscape features that comprise the urban matrix. Landscape and local features exert variable influence on pollinators within and across taxa, which ultimately affects community composition in such a way that contributes to functional trait homogenization and reduced phylogenetic diversity. Although previous results are not easily generalizable, bees and pollinators displaying functional trait characteristics such as polylectic diet, cavity-nesting behavior, and later emergence appear most abundant across different examined cities. To preserve particularly vulnerable species, most notably specialists that have become underrepresented within city communities, green spaces like parks and urban gardens have been examined as potential refuges. Such spaces are scattered across the urban matrix and vary in pollinator resource availability. Therefore, ensuring such spaces are optimized for pollinators is imperative. This review examines how urban features affect pollinators in addition to ways these green spaces can be manipulated to promote greater pollinator abundance and diversity.

Keywords: urban bees; functional traits; urban heat island effect; pollinator health; phylogenetic diversity; habitat fragmentation; microclimate; dietary breadth; green spaces; body size

Introduction

Urbanization is a pernicious, anthropogenic alteration of the environment characterized by an increased proportion of impervious and built surfaces (roads, sidewalks, parking lots, buildings etc.), in addition to high human population density and total population size (Wu 2014). The development of urbanized areas, in conjunction with intensified agriculture, have been considered primary drivers of biodiversity loss, with declines noted for multiple insect taxa including coleopterans, lepidopterans, dipterans, and hymenopterans (Cardoso and Gonclaves 2018; Fenoglio et al. 2020; Kurylo et al. 2020; Piano et al. 2020; Sattler et al. 2010). Reduction in biodiversity is often due to varying interactive elements composing the urban environment. These factors range from habitat loss and fragmentation, the presence of exotic plant and animal species, urban warming or the urban heat island (UHI) effect, and the reduction in habitat quality (Figure1) (Harrison and Winfree 2015). These constituents of urbanized ecosystems can influence insect communities at either the landscape or local scale (Beninde et al. 2015; Geslin et al. 2016; Quistberg et al. 2016; Egerer et al. 2017; Ballare et al. 2019). As a result, cities have been described as "filters" that influence the composition of these urban-dwelling communities by favoring particular functional traits, or organism characteristics that influence fitness, and life history strategies (Williams et al. 2009; Dale and Frank 2018; Wenzel et al. 2020). Consequently, urban filtering may homogenize communities according to functional traits characteristics, some of which are described in Figure 2 (Deguines et al. 2016; Knop 2016).

Despite the generally negative impact the urban matrix exerts on city species, urban areas can represent biodiverse ecosystems that serve as refuge for many ecologically important groups such as pollinators (Banaszak-Cibicka and Zmihorski 2010; Egerer et al. 2017; Hamblin et al. 2017; Nagy et al. 2018). In fact, in some instances, cities may harbor greater diversity and abundance than surrounding agricultural and even semi-natural landscapes (Baldock et al. 2015; Sirohi et al. 2015; Kaluza et al. 2016; Banaszak-Cibicka et al. 2018).

The diversity and abundance observed within cities are in part due to the heterogeneity of the urban landscape in which various habitat or green space types exist (Tommasi et al. 2004; Sattler et al. 2010). Urban green spaces like parks, gardens, and residential yards are notable habitat types that can provide essential foraging and nesting resources for bees and other taxa (Baldock et al. 2019; Dylewski et al. 2020). Urban green spaces have also been used to enhance habitat connectivity by establishing green space corridors or "stepping-stone" habitats (Braaker et al. 2017). The use of green spaces to promote biodiversity and mitigate urbanization impacts has been an area of increasing interest in recent years. Understanding how these and other urban spaces can be optimized to better promote and maintain species richness and abundance is essential, especially when acknowledging the future growth of urbanized areas needed to accommodate an increasing global population. According to the United Nations, approximately 55% of the 2018 world population lived in urban areas—a percentage that is projected to increase to 68% by the year 2050 as the population continues to expand to a staggering 9.8 billion people (United Nations 2018). Canada and the US for instance exhibit high rates of urbanization, where >80% of the population can be found living in urban areas (Government of Canada 2019; University of Michigan 2020). Insects are an important study group due to their rapid response to environmental change (Jones and Leather 2012). Specifically, ascertaining insect pollinator response to the individual components of urbanization is particularly crucial not only because declines have already been reported for these animals (Potts et al. 2010), but also because they provide essential ecosystem services: the most notable of which being pollination. Over 90% of flowering plants depend on animal-mediated pollination to some extent to successfully reproduce, a significant portion of which is facilitated by bees (Kearns et al. 1998; Ollerton et al. 2011). These services not only impact plant fecundity, but they also affect the organisms that rely on the fruits, seeds, and other resources resulting from such services. Humans are no exception to this, especially considering the scale of agriculture and food production today. As regions become more urbanized, agricultural practices have even begun to be incorporated into urban contexts, which also greatly depends on pollinators (Lovell 2010; Siegner et al. 2018). Visitations by wild pollinators, for instance, has been shown to increase the fruit and seed set in agricultural and urban contexts even more so than managed honey bees (Garibaldi et al. 2013; Lowenstein et al. 2015). Therefore, wild pollinators can play an integral role in the economics of urban agriculture, in addition to potentially stabilizing food security in urban contexts.

The general appreciation of charismatic insects such as butterflies and bees amongst the public can also potentially be used as a means of facilitating community participation in and the promotion of insect conservation. For instance, a study by Southon et al. (2017) examined community response to urban meadows and found that not only did participants show a preference for meadows over managed, mown areas, but tolerance for urban meadows increased when participants were informed of the benefits such habitats can provide for pollinators. A study by Pawelek et al. (2009) also demonstrated a community's willingness to participate in pollinator conservation as most gardeners displayed a desire to learn more about the pollinators visiting their community garden in addition to allowing the planting of flowers that can attract pollinators into their plots.

The purpose of this review is threefold: (1) To summarize the effectiveness of green spaces and other management and policy strategies that have been implemented in ameliorating pollinator losses. (2) To detail the facets of urbanization that affect pollinating insect traits such as species richness and abundance, body size, generality, sociality, nesting habitat, and behavior with a primary emphasis applied to bees since the bulk of the current literature has largely focused on bees. (3) To discuss gaps in knowledge that exist to inform future research so that a holistic understanding of urbanization impacts on pollinators can be established with the intent to generate more effective policy and management measures.

Landscape and Local Features on Pollinators

Different urban features variably influence pollinating insects, the effects of which are dependent upon the local and landscape features that constitute those specific environments. Landscape features pertain to the environmental characteristics that surround habitat spaces, whereas local features refer to the features of such spaces (Kennedy et al. 2013; Pardee and Philpott 2014; Quistberg et al. 2016). Some of the features in this review are not exclusive to either feature. For instance, impervious surface can be classified as either landscape or local features depending on the goals of a particular study (McKinney 2008; Ballare et al. 2019). Factors such as impervious surface may perhaps be more impactful from a landscape perspective and therefore will be treated as such throughout the course of this review. Of the two, local features are presumed to influence insect diversity the most (Matteson and Langellotto 2010). Regardless, the improvement of surrounding landscapes in conjunction with local features can better enhance pollinator diversity (Williams and Kremen 2007; Viana 2012). The constituents relating to both landscape and local features will be discussed in further detail below in which knowledge gaps within each area will be addressed.

Landscape Features

Habitat Loss, Fragmentation and Heterogeneity

Fragmentation and habitat loss have been proposed as two of the most significant drivers contributing to bee species richness and abundance decline (Winfree et al. 2009). The development of buildings, roads, and other impervious surfaces across cityscapes produces a fragmented urban matrix containing habitats of reduced size and quality (Stenhouse 2004). Both habitat loss and fragmentation also influence landscape composition and configuration in such a way that alters plant and pollinator densities in addition to pollinator movement and behavior (Hadley and Betts 2011). The fragmentation of landscapes can complicate patch accessibility, especially for smaller bees with reduced mobility (Greenleaf et al. 2007; Hennig and Ghazoul 2012; Harrison and Winfree 2015). However, due to the probable different management practices implemented within each fragmented area, cities can become quite heterogeneous. Thus, the heterogeneity of the city landscape can produce idiosyncratic habitats featuring different resources.

Urban Heat Island Effect

Due to the pervasiveness of impervious surfaces throughout urban landscapes, cities typically exhibit warmer and drier local climates than surrounding locations (Oke 1973). This phenomenon, referred to as the urban heat island (UHI) effect, can elevate city temperatures 2–4 °C higher than rural areas, although one study has reported increases as high as 12 °C (Kłysik and Fortuniak 1999). This substantial influence on city climate can affect plant community densities and advance their phenology in addition to affecting insect characteristics such as physiology and abundance. The UHI effect has facilitated the movement of other insects including the exotic wasp species *Sceliphron curvatum* into warmer urban regions (Polidori et al. 2021). Such movements of alien species may also occur among bees; however, further studies should be conducted as some reports have suggested urban warming has no influence on exotic bees (Fitch et al. 2019). This may make sense as many exotic bees found within cities are cavity-nesting and therefore nesting availability may be exerting greater influence on their presence (Wilson and Jamieson 2019).

The resultant changes associated with UHI effect affect different taxa variably (McIntyre et al. 2001). Differential effects can occur interspecifically within the same taxa as demonstrated in butterflies displaying varying desiccation and thermal tolerances (Kaiser et al. 2016). Recent research has used thermal maximum (CTmax) and critical water content (CWC) values as proxies for determining bee tolerance to urban warming (Hamblin et al. 2018; Burdine and McCluney 2019). The use of such metrics has revealed morpho-group specific responses to urban conditions including increased bumble bee thermal tolerance yet reduced desiccation tolerance compared to groups like sweat bees (Kaiser et al. 2016). Ultimately, cities may be selectively favorable to bees and other pollinators possessing higher thermal tolerances than thermally susceptible species (Kaiser et al. 2016; Hamblin et al. 2018; Burdine and McCluney 2019). Depending on city location, the UHI effect may facilitate insect growth and development in regions that are regionally cooler, as postulated by Burdine et al. (2019). However, in warmer locations or in the future as climate change raises global temperatures, cities may push species closer to their thermal tolerances and ultimately affect their abundance (Kaiser et al. 2016). For instance, studies in the US found that bee abundance decreased by 41% per 1 °C increase (Hamblin et al. 2018). In this sense, the establishment of green spaces may provide an additional role in cities creating urban cooling island (UCI) effects in pocketed regions of cities (Chang et al. 2007; Bowler et al. 2010). Buildings themselves can produce UCI effects during certain times of day i.e., mornings; however, green spaces can absorb additional heat during warmer times of the day and year depending on how impervious and vegetation dense such spaces are (Chang et al. 2007; Gonclaves et al. 2018).

Surrounding Landscape and Impervious Surface

The type of landscape surrounding an area can impact the presence of pollinators in a region, especially within agroecosystems where pollinator presence can influence fruit set (Ricketts and Regetz 2008; Klein et al. 2012; Kennedy et al. 2013; Ballare et al. 2019). In cities, it has also been predicted that higher species richness and abundance should occur at locations within closer proximity to natural areas and those furthest from urban cores (Jones and Leather 2012). Studies conducted in Poland and France have substantiated this hypothesis while examining urbanization impacts on wild bees along urbanization gradients (Banaszak-Cibicka and Zmihorski 2012; Geslin et al. 2016). Additionally, increasing the proportion of green spaces in the surrounding landscape can increase the richness and abundance of bees (Tonietto et al. 2011). Furthermore, the presence of nearby semi-natural areas and green spaces within urban areas can be especially useful for pollinator visitations as these resources enhance the total number of resources that can be utilized within or near landscapes (Phillips and Gardiner 2015). Semi-natural areas surrounding orchards, for instance, possess gastropod shells that can be repurposed by bees to serve as nests (Bogusch et al. 2020). It is possible that maintaining the semi-natural areas surrounding cities may also preserve resources necessary for some bees that are found near urban areas to persist.

Urban areas tend to be surrounded by and diffused with impervious surfaces. Several studies have investigated impervious influence on pollinator abundance, species richness, and community structure using urbanization gradients (Geslin et al. 2016; Egerer et al. 2017; Senapathi et al. 2017; Kurylo et al. 2020; Piano et al. 2020). Despite recent criticisms regarding the use of imperviousness as a defining metric for urbanization, its use has become relatively standardized within urban pollinator ecology (Wenzel et al. 2020). Inconsistencies in the classification methods may affect results in such a way that over or underestimates the actual urban impact on pollinators. Regardless, species richness and abundance generally appear to decrease in association with increased proportions of impervious surfaces (Sattler et al. 2010; Kuussaari et al. 2020). Intensification of impervious surfaces has also been associated with shifts in pollinator community structure where greater proportions of impervious surface generally possess a higher abundance of cavity-nesting bees compared to ground-nesting bees (Cane et al. 2006; Gestlin et al.

2011; Kuussaari et al. 2020). Such results appear intuitive, given that impervious surfaces diminish the amount of available nesting space that can be utilized by ground-nesting insects; however, such trends are not entirely generalizable as city compositions may vary uniquely to affect bees differently. Studies should be conducted to further substantiate the filtering out of pollinators that nest in the ground.

Local Features

Microclimate

Microclimates, or local climatic conditions within habitats, can vary across urban environments and even within individual habitat patches depending on the biotic and abiotic qualities of a space (Dale and Frank 2018; Pincebourde et al. 2016; Fisogni et al. 2020). Vegetation type and cover along with background environmental warming are two such characteristics that can influence local microclimate (Crum and Jenerette 2017). Vegetation can generally reduce surrounding temperature (Change et al. 2007) and at an even finer scale, flowers including daffodils possess independent microclimates which, in some cases, act as warming pads for bees (Herrera 1995). Shade produced by vegetation cover or other environmental factors can also influence the microclimates of nests used by cavity-nesting bees (Richards et al. 2020). Such microclimate effects within the nest can influence the metabolic rate and development of bee larvae (Radmacher and Strohm 2009; Richards et al. 2020). Abiotic factors i.e., nitrogen deposition, which is prevalent in urban areas, can interact synergistically with climate change in such a way that may influence local microclimates as well (WallisDeVries and Van Swaay 2006; Harrison and Winfree 2015). Both factors can hasten spring plant growth (a factor that reduces microclimate temperatures) which has been previously shown to ultimately affect the developmental success of thermophilic butterflies by reducing their abundance (WallisDeVries and Van Swaay 2006). Such a pattern may also be observed in bees and other pollinators. Despite the knowledge that landscapes can display heterogeneous microclimates, few studies have conducted microclimate studies at extremely fine scales within cities (Hamblin et al. 2018; Burdine and McCluney 2019). Understanding how species respond to specific habitat variables is essential as shifts in microclimate may impact pollinator populations either through extirpation or dispersal.

Urban Vegetation

Exotic and ornamental plant species can be found extensively throughout urban areas especially within residential yards and gardens (Threlfall et al. 2016). This increase in plant variety contributes to the increased species richness and/or abundance of plant communities which may enhance the species richness of pollinators and other insects (Hennig and Ghazoul 2012; Braaker et al. 2017; Leston and Koper 2017; Baldock et al. 2019; Wilson and Jamieson 2019). This correlation obviously largely depends on increasing the species of plants attractive to bees and lepidopterans rather than just generally increasing plant richness (Martins et al. 2017). Floral abundance and frequency, however, may be more impactful than promoting richness itself (Stewart et al. 2018; Lanner et al. 2019). Other factors including increased floral area (area occupied by blooming plants) have also been shown to influence butterfly and bee abundance (Werrell et al. 2009; Mattesson and Langellotto 2010).

Due to the high prevalence of exotic plants within urban areas, determining non-native influence on the local environment and native pollinators is important. Previous reviews have suggested that exotic plants can negatively affect pollinator communities by influencing visitations and the reproductive success of native plant species (Morales and Traveset 2009). A more recent review, however, indicated that non-native plants are not preferred over native plants among pollinators (Harrison and Winfree 2015). This lack of preference was, in part, attributed to potential design flaws in the approach of several previous studies (Harrison and Winfree 2015). Although preferences may not vary drastically among generalists, oligolectic species associated with few or a single native species are particularly vulnerable to alterations in plant communities (Hostetler and McIntyre 2001). Therefore, preserving native plant species is one essential aspect of sustaining specialist, native bees. Additional research suggests, however, that exotic species may negligibly affect pollinator presence (Mach and Potter 2018; Rollings and

Goulson 2019; Giovanetti et al. 2020). In fact, exotic plants may benefit areas by extending floral resource availability throughout the season and contributing to the overall abundance of floral resources (Salisbury et al. 2015). Due to these seemingly conflicting results, further attention should be directed towards understanding the influence exotic plants possess over pollinators more conclusively. This is especially apparent given that some evidence suggests that native and perennial plants exhibit greater bee abundance compared to exotic and annual species (Pardee and Philpott 2014; Lowenstein and Matteson 2019).

Green Space Size

Habitat size is an important factor potentially capable of influencing pollinator presence by limiting the quantity of resources able to occupy green spaces. In order to sufficiently accommodate adequate amounts of floral and nesting resources necessary for pollinators, green spaces must be of adequate size. However, the total area needed to support pollinators remains poorly understood and is perhaps dependent upon bee mobility (Greenleaf et al. 2007; Aronson et al. 2017; Lepczyk et al. 2017). Current research conducted on habitat area primarily investigates components of green space area like the proportion of floral cover and, to an extremely lesser extent, nesting resource availability (Bogusch et al. 2020). Beninde et al. (2015) examined space requirements for bees and indicated that areas larger than 50 ha should be established to prevent losses in species richness. Too much green area may not provide any particular benefit for certain taxa though as bee diversity has in some instances plateaued outside of a 100-m buffer radius (Hennig and Ghazoul 2012). Regardless, establishing larger habitat areas has been shown to positively affect butterfly and bee species richness, abundance, and diversity (Konvicka and Kadlec 2011; Jauker et al. 2012; Stewart et al. 2018; Tzortzakaki et al. 2019). Such variations in size may be more influential on the richness and abundance of smaller bees than large bees, such as *Bombus* spp., which exhibit greater flight distances and increased mobility associated with size (Gunnarsson and Federsel 2014). Nevertheless, creating spaces of both sustainable size and resource availability are important considerations when attempting to mitigate habitat fragmentation and increase connectivity, especially for less mobile, smaller species (Zurbuchen et al. 2010).

Green Space/Habitat Type

Habitat types can differ in their ability to support pollinating insects due to variation in site-specific management practices and resource availability. For instance, green spaces like remnant vegetation, urban parks, residential neighborhoods, and golf courses exhibit variability in plant species composition and vegetation cover which can influence their resourcefulness to pollinators (Tonietto et al. 2011; Sirohi et al. 2015; Threlfall et al. 2016; Dylewski et al. 2020). The availability of resources at specific green spaces depends on what the functions of those sites are. Residential yards tend to be maintained for aesthetic value and, therefore, implement vigorous management regimes such as frequent mowing that negatively influence bee abundance and diversity through the removal of weeds and other useful flower resources (Lerman et al. 2018). Green spaces like urban grasslands, which may experience less frequent management, have been found to contain higher butterfly, hoverfly, and bee abundance compared to urban parks and housing estates which is perhaps unsurprising as reduced management preserves pollinator floral and nesting (Dylewski et al. 2019). Other random wildflower patches can also be particularly important as they can host ground nesting bees such as *Andrenidae* spp. despite occasional mowing (Sirohi et al. 2014). Urban gardens can also be hotspots for bee abundance and functional trait diversity perhaps due to the presence of a variety of plant species, many of which are reliant upon pollinators (Tommasi et al. 2004; Matteson and Langellotto 2010; Normandin et al. 2017; Baldock et al. 2019; Lanner et al. 2019). Normandin et al. (2017) found that, in some instances, community gardens are only slightly less efficient in attracting bees compared to urban parks despite being typically smaller spaces.

Different park types can also vary in their ability to support pollinators. Recreational parks for example could improve floral quality (Daniels et al. 2020) and planting gardens within these areas may be one means of accomplishing such a task (Middle et al. 2014). Informal green spaces including those found interspersed throughout residential areas may be useful to pollinators if they exhibit variation in management intensity (Fischer et al. 2016). Other urban areas including brownfields, which represent previously developed urban industrial locations, may also be repurposed in ways that promote bee biodiversity (Hunter 2014) especially if sites are not entirely isolated and possess available foraging resources (Twerd and Banaszak-Cibicka 2019; Turo et al. 2021). Due to lack of use, derelict and other post-industrial sites may also be of interest as they can be unmanaged and experience reduced pesticide and/or chemical exposure, unless located at former chemical plants (Twerd and Banaszak-Cibicka 2019; Baldock 2020). Currently, few studies have concurrently examined the quality of multiple green spaces, often focusing on one or a few specific types (Normandin et al. 2017; Buchholz and Egerer 2020). Examining the value of multiple green spaces within an urban environment is important to understand which spaces are especially beneficial for their conservation value and which should be investigated further to improve their overall habitat quality.

Functional Traits Affected by Urbanization

Urbanization has been previously described as a filter that selectively favors pollinators possessing functional traits which render such taxa less vulnerable to heavily disturbed environments (Williams et al. 2009; Dale and Frank 2018; Wenzel et al. 2020). Despite a city's ability to support a breadth of biodiversity, the filtering associated with cities may produce homogenized communities based upon functional traits or phylogenetic relatedness (the summary of which can be found in Table 1) (Baldock et al. 2015; Harrison and Winfree 2015; Knop 2016; Martins et al. 2017). Various studies have noted several similar trends regarding urban bee taxa and functional traits, however particular observations may not be easily generalizable due to species specific variation in response (Cariveau and Winfree 2015; Buchholz and Egerer 2020). Amongst pollinators, general functional traits of taxa observed in urban areas pertain to differences in dietary breadth, nesting strategy, body size, behavior via phenology or sociality, and phylogenetic diversity.

Dietary Breadth

Most studies that have examined species composition across urban areas have reported consistent, relatively general trends regarding pollinator lecty or dietary breadth. There is ample evidence to suggest that cities support greater abundances of polylectic (i.e., generalist) pollinators displaying broader foraging preferences compared to oligolectic (i.e., specialist) species displaying limited dietary preferences restricted to one or few plant hosts (Banaszak-Cibicka and Zmihorski 2012; Geslin et al. 2016; Normandin et al. 2017; Senapathi et al. 2017; Lanner et al. 2019). Although specialists are under-represented and even rare in cities (Hernandez et al. 2009), their presence is not entirely lacking, particularly if species-specific requirements are available within the landscape (Da Rocha-Filho 2018; Lanner et al. 2019).

Urban environments may inadvertently advantage generalist species as floral landscapes, although diverse, are largely dominated by exotic, ornamental and other species which are not hosts to specialists (Frankie et al. 2005; Threlfall et al. 2016; Garbuzov et al. 2017). Flowers possessing deeper corollas may limit resource availability for bees and other pollinators possessing short tongues by being inaccessible to such species (Geslin et al. 2013). The lack of host plant species in an area may thus effectively turn urban spaces into resource deserts for specialists. Understanding the specific associations between pollinators and the plants they utilize is important if appropriate and effective conservation measures are to effectively preserve target species such as specialists. Currently, some studies examining pollinator trends still fail to record species-specific interactions at the expense of using morpho-group classifications in the field (Baldock et al. 2015; Geslin et al. 2016). While the use of morpho-groups provides relevant information about plant–pollinator relationships, interactions identified to the species will be most informative of the diversity and specificity of relationships existing between plants and pollinators.

Nesting Strategy

Nesting strategy primarily applies to bees as the nesting of other pollinators such as butterflies and syrphids is dependent on the surrounding vegetation. Bees are broadly categorized as either subterranean ground-nesters or above-ground cavity-nesters. The vast majority of the >20,400 bee species distributed world-wide are ground-nesting; however, cavity-nesting bees appear overrepresented across many urban studies likely as a result of the conversion of bare ground into impervious surface (Cane et al. 2006; Michener 2007; Geslin et al. 2016; Martins et al. 2017; Buchholz end Egerer 2020). Additionally, urban spaces tend to possess novel, above-ground nesting resources such as cracks and holes in structures and, to a lesser extent, bee hotels that can be exploited by above-ground nesters (Verboven et al. 2014). For example, *Xylocopa virginica* is a species found in proximity of anthropogenic disturbance having now adapted to using milled lumber as a nesting substrate (Hurd 1978). Community gardens and urban park sites may promote ground-nesting species, however, as these green spaces often contain bare soil and stem-nesting substrate (Lanner et al. 2019).

Body Size

The effects of urbanization on pollinator body size have received conflicting results within the literature despite some suggestion that cities may promote smaller body sizes (Banaszak-Cibicka and Zmihorski 2012). While some studies observe greater proportions of large-bodied pollinators including both bees and butterflies, others notice an opposite or undetectable trend across urban landscapes (Fortel et al. 2014; Wray et al. 2014). Since flight distance for pollinators such as bees has been correlated with body size, it has been assumed that large-bodied bees, for instance *Bombus*, are able to navigate between patches more efficaciously than smaller-bodied bees including *Lasioglossum*, which exhibit shorter flight ranges (Greenleaf et al. 2007; Gunnarsson et al. 2014). In semi-natural grasslands, it is suspected that this greater mobility associated with size explains the higher species richness of larger bees (Jauker et al. 2012). This trend may be paralleled in cities where a greater abundance of larger pollinators such as butterflies has also been reported (Kuussaari et al. 2020).

Despite the greater mobility of larger species, however, smaller species may require less resources to sustain themselves in urban areas (Cane et al. 2006; Fortel et al. 2014). Additionally, factors such as UHI effects and reduced nutrition availability could be driving reduced body size in traditionally larger pollinators such as *Bombus lapidaries* and *B. pascuorum* (Eggenberger et al. 2019); however, other sources have reported the opposite effect in *B. terrestris* better attributed to fragmentation. It could be the case that different factors not only idiosyncratically influence body size but do so in a way that varies intra and inter-specifically across varying taxa as well (Merckx et al. 2018a; 2018b). Additional studies are needed to better disentangle which urban features are more greatly impacting body size.

Behavior

Urbanization affects several pollinator behavioral traits ranging from foraging and nesting decisions, anti-predator response, to potentially filtering species based on their degree of sociality. Through factors such as the microclimate, potential nest sites in cities may alter the nest-site decisions of some bees as was observed in *Megachile rotundata.* In this study using artificial nest boxes, tubes possessing lower temperatures were occupied more frequently than those displaying higher temperatures (Wilson et al. 2020). Several studies evaluating foraging decisions in urban environments or across urbanization gradients typically do so using plant–pollinator interaction networks. The degree of urbanization can influence these interaction networks and visitation rates between wild bees and available urban plants. Sweep netting across urban locations has revealed preference for native floral resources and reduced visitation to exotic plants (Buchholz and Kowarik 2019).

Whether solitary or social species are most prevalent across urban landscapes remains inconclusive within the literature. While some studies report a greater abundance of solitary bee species (Martins et al. 2017), others indicate that social species appear most frequently in urban areas (Harrison et al. 2017; Banaszak-Cibicka et al. 2018; Wenzel et al. 2020). A systemic review analyzing urban bee functional traits, however, found no generalizable trend for sociality (Buchholz and Egerer 2020). Discretions in results could be a result of contrasting methodologies. For example, Wilson and Jamieson (2019) incorporated cleptoparasitic and sub-social bees into their solitary category whereas other studies may examine these group separately. Future studies should continue to examine urban effects on functional traits including sociality, but as found with most other traits, trends may be regionally specific and not generalizable due to the variation of response occurring across bee species and the variation of study regions themselves (Cariveau and Winfree 2015).

When dissecting the urbanization impact on pollinator phenology, some work suggests that cities may support later season bees more so than early emerging species (Banaszak-Cibicka and Zmihorski 2012; Wenzel et al. 2020). Such changes are likely a result of climatic changes which can produce mismatches between flowering plants and pollinators (Goulson et al. 2015). Bees that display greater adaptive response to phenological shifts, like some social bees with prolonged foraging seasons, may be able to take advantage of resources more effectively than species with shorter active seasons (Harrison and Winfree 2015).

Phylogenetic Diversity

Although many studies tend to focus on functional trait homogenization, recent work has investigated similarities from an evolutionary perspective (Harrison et al. 2018; Odanaka and Rehan 2019). Phylogenetic diversity may be correlated with functional traits; phylogenetic diversity changes may be more useful than functional trait changes in more accurately reflecting taxonomic changes within a community (Harrison et al. 2018; Xu et al. 2019). Phylogenetic studies in conjunction with functional trait studies may also be additionally useful in further determining vulnerable urban species within urban environments (Baiser and Lockwood 2010). Despite the potential benefit associated with phylogenetically based studies, few have occurred within urban contexts. Such approaches implemented in cities, however, were able to detect family level phylogenetic homogenization, or predominance of few families over others, even when species homogenization was not apparent (Harrison et al. 2018). The results of Harrison et al. (2018) indicate that urban areas within the New Jersey region possess phylogenetic homogenization represented by communities dominated by bees within the Halictidae family.

Ascertaining shifts in phylogenetic diversity resulting from urban land use is imperative, especially considering the reduction in such diversity equates to a loss of bee evolutionary history and a reduction in ecosystem services (Grab et al. 2019). Former phylogenetic studies have noted that genera such as *Lasioglossum (Dialictus)* and *Bombus* are more abundant/resilient than others, such as *Andrena* and *Nomada* who may be particularly sensitive to land-use change (Matteson et al. 2008; Normandin et al. 2017; Harrison et al. 2018; Grab et al. 2019; Odanaka and Rehan 2019). Such clades may be increasingly vulnerable to urbanization due to their specialized diets, earlier and/or shorter flight seasons, and other characteristics that are phylogenetically correlated (Harrison et al. 2018). Additionally, some vulnerable bee guilds, such as cleptoparasites, may be useful in serving as bio-indicators of community health (Sheffield et al. 2013).

Conservation Aims and Future Directions

Conservation initiatives within urban areas aimed at minimizing pollinator declines largely include the establishment and protection of green spaces throughout the urban matrix. Ensuring that these dedicated locations, which may differ in resources depending on the type of space, sufficiently provide quality resources directed towards multiple pollinating taxa is essential considering the different needs of pollinators. While some studies provide recommendations on how to modify spaces for pollinators, striking a balance between appeasing both the public and stakeholders while achieving conservation goals remains a complex issue (Aronson et al. 2017; Turo and Gardiner 2019). The economic and political component of conservation and restoration, however, may be especially challenging as policymakers may be reluctant to implement costly changes that do not administer immediate results (Howes et al. 2017).

The public often holds considerable influence in selecting plant species, which are decisions made based on aesthetic value (Byrne 2005; Burr et al. 2018). Additionally, green space approval and preferences amongst the public depends on socioeconomic conditions such as median house income, gender, and level of education for example (Southon et al. 2017; Baldock et al. 2019; Zhao et al. 2019). The inclusion and/or preservation of green areas may not solely benefit pollinators; however, as positive human health benefits have been associated with green space presence (Wolch et al. 2014; Hunter et al. 2019; Keeler et al. 2019). Green space exposure has previously been suggested to be negatively associated with health factors such as mortality and positively associated with factors including physical activity and some aspects of mental health (Kondo et al. 2018). Additionally, green spaces such as urban gardens can reconnect individuals with nature and encourage community engagement of conservation objectives (Duchemin et al. 2009; Pawelek et al. 2009; Lanner et al. 2019).

Economic costs typically hold precedence over ecological and recreational concerns (Tibesigwa et al. 2020). As a result, effective measures should be developed to ensure that environmental projects are not only of high-quality and meet expectations but are also cost-effective. Despite any hesitancy expressed by potential stakeholders, the inclusion of green spaces and/or modified management practices may reduce total costs over time. For instance, a reduction in intensive management practices such as excessive and frequent mowing not only benefits pollinators by preserving floral resources but also reduces costs associated with mowing (Leston and Koper 2017; Aguilera et al. 2018; Lerman et al. 2018) while maintaining site aesthetic value (Southon et al. 2017). Additionally, the inclusion of perennial plants may also reduce management costs by mitigating the frequency at which seeds need to be re-sown in comparison with more labor-intensive annuals (MacIvor et al. 2013).

Improving upon plant and seed mix selections placed within green spaces could also enhance habitat quality and prevent ineffective spending. Seed mixes applied in urban settings can undoubtedly attract pollinators such as bumble bees and hoverflies; however, the plant species incorporated into such mixes are important. The inclusion of sometimes specific plant species can greatly enhance pollinator visitation rates within habitats (Pawelek et al. 2009). Several plant species used in current seed mixes, sold in stores, and generally found in urban spaces may be of little value to pollinators, and those that are described as pollinator-attracting plant species lack empirical evidence (Harmon-Threatt and Hendrix 2015; Garbuzov et al. 2017; Rollings and Goulson 2019). Since pollinators exhibit a wide variety of dietary preferences, elucidating species-scale preferences is imperative to maintain greater aspects of pollinator communities (Turo and Gardiner 2019).

Establishing plant–pollinator interaction networks could be one method of empirically determining species resolution pollinator resource usage and floral visitation as done in bumble bees (Sikora et al. 2020). These networks are typically constructed using field-recorded observations or pollen extractions and direct bee sampling from flowers (Geslin et al. 2013; Tucker and Rehan 2016; Lowenstein et al. 2019). Additionally, such networks have previously illustrated that the inclusion and/or exclusion of plants incorporated in seed mixes used in prairie restoration can significantly affect bee richness and abundance (Harmon-Threatt and Hendrix 2015). Constructed networks can then depict how different pollinators depend on different floral resources and show how network characteristics such as generality can shift across urban landscapes. Not only can this be important for determining if certain pollinating groups, especially oligolectic specialists, have sufficient floral resources, but conversely, interaction networks can also indicate whether a plant species is receiving sufficient pollinating visitors.

The successful implementation of management and other pollinator protection strategies, however, in part greatly depends on the passage of appropriate legislature from national and regional governments. While pollinator-protecting legislature has only until recently begun to gain traction, many countries have made several steps to improve efforts. For instance, 110 laws associated with pollinators have been passed at the US state-level from 2000 to 2017 (Hall and Steiner 2019). Actions within cities have begun taking place, as the City of Toronto government, for example, has developed a pollinator protection strategy to promote pollinator awareness and conservation (City of Toronto 2018). Invertebrate conservation groups such as the Xerces Society have recognized cities within the United States and Canada that promote pollinator biodiversity as “Bee Cities” (Xerces Society 2020). Not only can the passage of such policies provide some direct degree of ensured protection for pollinators, but they can be used to garner public support and promote community engagement and learning (Baldock 2020).

In order to accurately assess the extent to which urbanization affects pollinators, researchers should modify their general approaches to urban research. To start, long term studies should be established over those lasting only a few years so that more stable results and trends can be ascertained. Additionally, studies should place greater emphasis on the South American, Asia, and Australian continents as the current literature is overrepresented by North American and European studies (Williams et al. 2009; Dale and Frank 2018; Buchholz and Egerer 2020; Kurylo et al. 2020). As a result, future studies should direct their attention to understudied regions of the world as results may not be easily extrapolated to such locations (Stewart et al. 2018).

Conclusions

Although urban landscapes may more broadly reduce pollinator abundance (Piano et al. 2019) and favor particular functional and taxonomic traits over others (Banaszak-Cibicka and Zmihorski 2012), cities can still hold value as pollinator habitats (Hamblin et al. 2017). Such shifts in pollinating communities, which support traits such as polylecty and cavity-nesting, are consequences of interacting local and landscape features which exert differential, non-generalizable effects on species within and across taxa (Cane et al. 2006; Banaszak-Cibicka and Zmihorski 2012; Cariveau and Winfree 2015; Fischer et al. 2016). Therefore, disentangling these urban effects on pollinators is important to understand how cities can best support pollinating communities.

Green spaces able to execute informed design principles and management schemes may effectively thwart pollinator biodiversity losses. However, implemented green spaces should be structured in such a way that meets pollinator and other vulnerable target group demands. Determining which aspects are most important to integrate requires further study. In the meantime, landowners should consider restorative measures including, but not limited to, reducing management intensity (Zurbuchen et al. 2010), promoting native floral abundance and richness (Braaker et al. 2017), and establishing bare patch areas for ground-nesting bees (Cane et al. 2006). Cities themselves should seek to green roofs and other green infrastructure to reduce fragmentation and promote connectedness, pollinator resource availability and pollinator movement (Beninde et al. 2015; Braaker et al. 2017).

Establishing a general scientific consensus on urban pollinator ecology is also imperative if implemented policy guidelines are to be successful in promoting pollinator biodiversity and appealing to both policy makers and the public. If a single party remains unmotivated to act, pollinator health may continue to decline. Science communication in this regard is especially important to ensure meaningful change can occur collaboratively. This approach should, of course, not solely apply to pollinators but to all threatened biodiversity. Pollinators, however, can serve as an important group to vocalize conservation initiatives amongst the public and foster the healthy co-existence of nature and urban society.

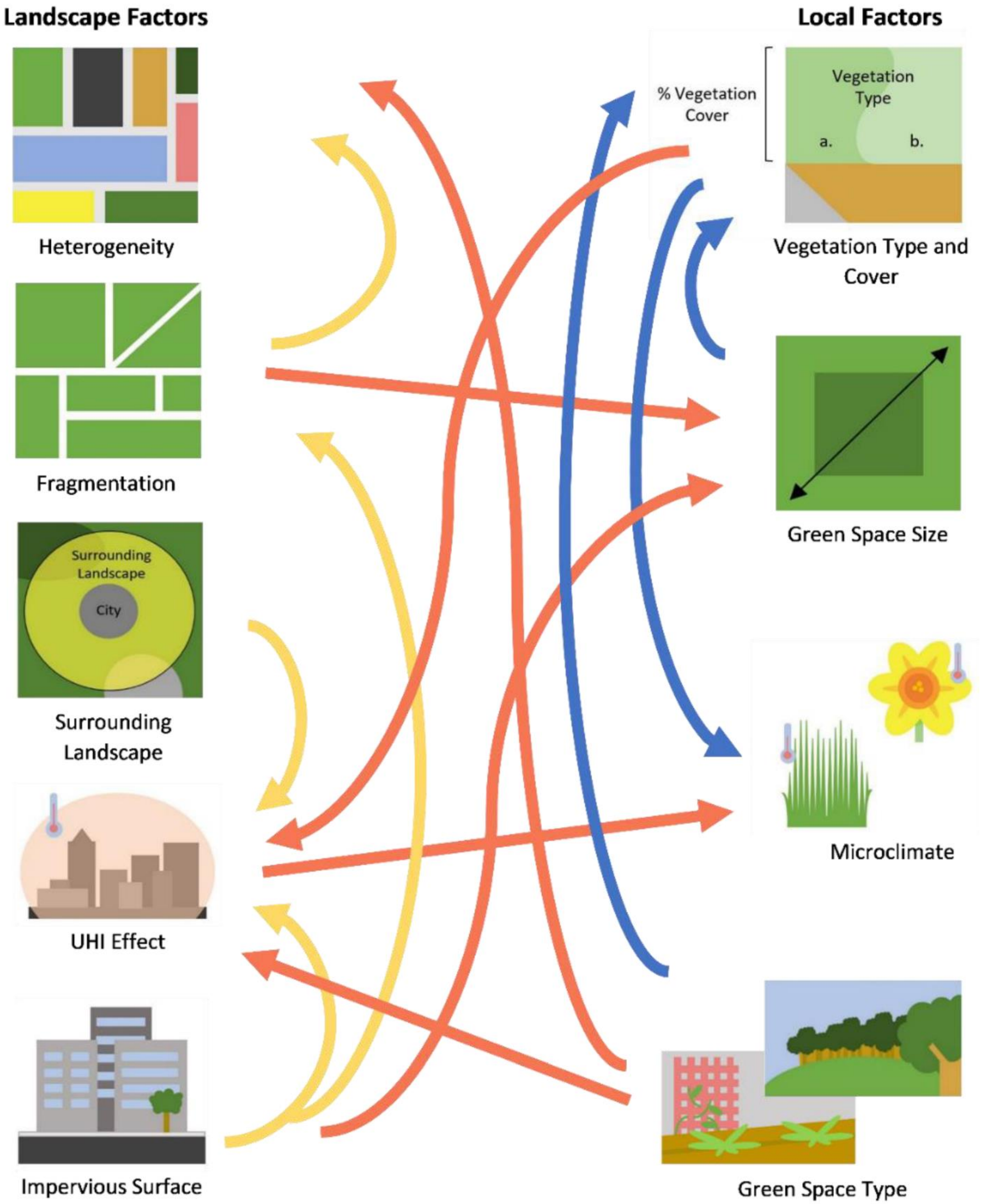

Figure 1. Diagram displaying some of the interactions between landscape and local features. Arrows represent features affected by other features from which the arrow originates. Local–local (blue), landscape–local (red), and landscape–landscape (yellow) interactions are shown.

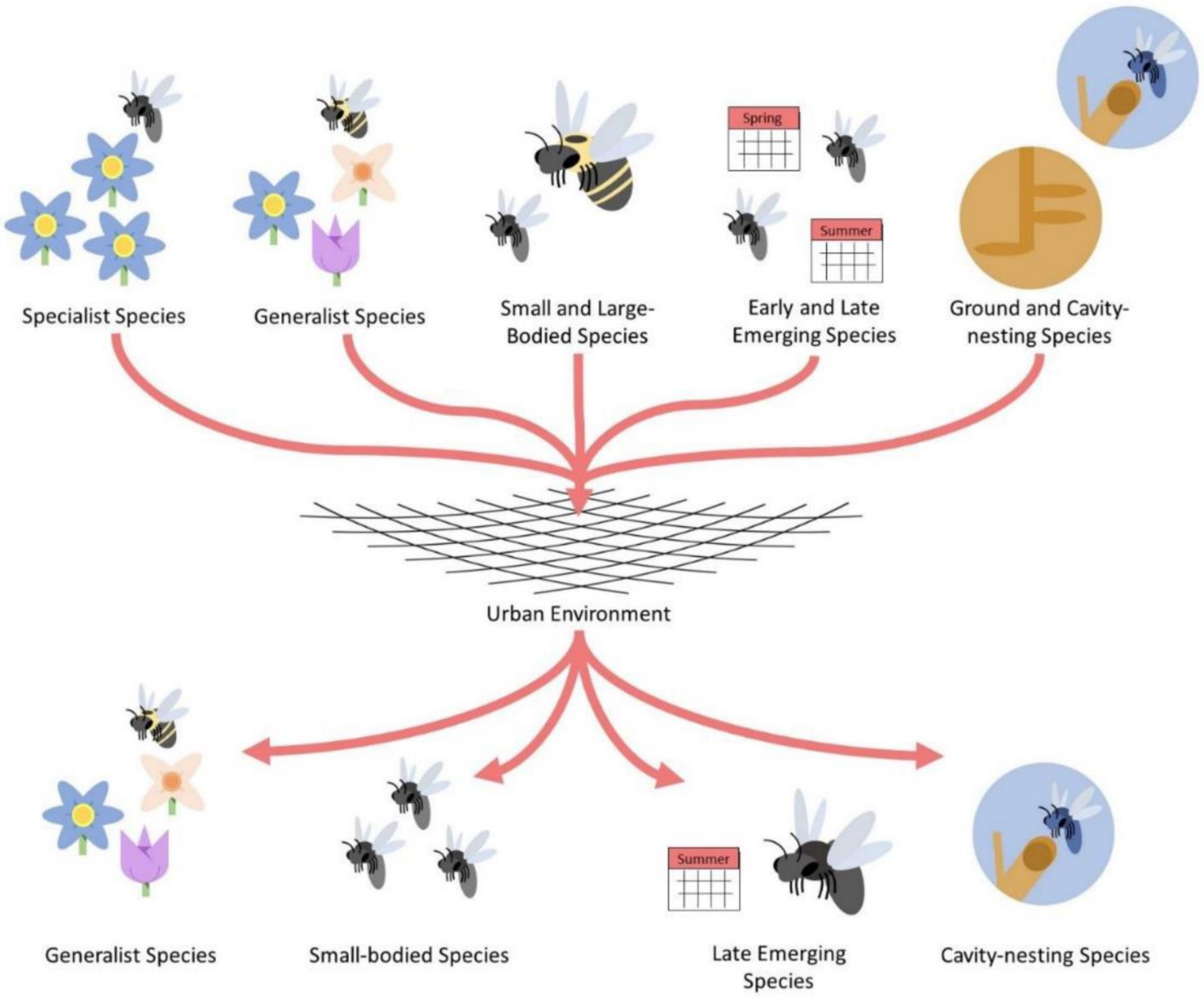

Figure 2. Simplistic diagram depicting the filtering of some functional traits comprising urban bee communities. The "net" in the center of the diagram represents a generic urban environment with all its associated local and landscape features that may influence bee community structure. General bee functional traits are presented at the top of the figure whereas traits selectively favored by cities are presented at the bottom.

Table 1. Summarization of some of the functional traits affected by some of the varying urban factors presented throughout the review.

Functional Trait	Favored Strategy	Urban Factors Affecting Traits	References
Body size	Inconclusive (Mixed results)	UHI effect, Habitat fragmentation, Vegetation cover and type	Forest et al. 2014; Senapathi et al. 2017; Eggenberger et al. 2019; Merckx et al. 2018
Diet strategy	Polylecty	Green space type, Vegetation type and cover	Banaszak-Cibicka and Zmihorsk 2012; Geslin et al. 2016; Normandin et al. 2017; Lanner et al. 2019; Bogusch et al. 2020
Nesting strategy	Cavity nesting	Impervious service, Green space type, Green space size	Herrera 1995; Senapathi et al. 2017; Baldock et al. 2019; Bogusch et al. 2020
Phenology	Late emerging	UHI effect, Vegetation type and cover	Banaszak-Cibicka and Zmihorsk 2012; Goulson et al. 2015; Wenzel et al. 2020
Sociality	Inconclusive (Mixed results)	Impervious surface, Vegetation cover and type	Banaszak-Cibicka and Zmihorsk 2012; ; Harrison et al. 2017; Banaszak-Cibicka et al. 2018; Buchholz et al. 2020; Wenzel et al. 2020
Phylogenetic diversity	Groups such as *Lasioglossum (Dialictus)*, in some instances *Bombus*	Impervious surface, Vegetation cover and type, UHI effect, Fragmentation, Green space size	Matteson et al. 2008; Harrison et al. 2015; Normandin et al. 2017; Grab et al. 2019; Odanaka and Rehan 2019

Chapter II: Bee-Plant Interaction and Community Response Along an Urbanization Gradient

Anthony C. Ayers

Abstract

Elucidating bee response to urbanization is essential to promoting pollinator diversity in cities especially considering such landscapes are projected to expand to support future global populations. To determine how bee community composition and plant-pollinator interactions respond to urbanization, twenty-nine sites representing three urban categories (high, medium, and low urbanization) were monitored biweekly from May through October in Toronto, Canada. Bees were collected passively using pan and blue vane traps as well as actively using aerial nets and vacuums so that later analyses comparing community structure and plant-pollinator networks between urban categories could be performed, respectively. Functional traits such as dietary breadth, behaviour, nesting substrate, and native or nonnative status were also recorded for species to examine whether such traits contribute to bee community assemblages. In total, 5477 bees, comprising 26 genera and 164 species, were represented in this study. The urban landscape was largely supportive of species within the family Apidae and Halictidae as well as ground-nesting, native, and generalist species. Overall, community composition was affected by urban landscape characteristics such as percent tree cover and impervious surface surrounding sites. Bee richness and abundance; however, was significantly influenced by plant richness rather than by landscape variables. A total of 3267 interactions were observed throughout the study region with characteristics of plant-pollinator networks remaining consistent along the urban gradient with a few floral host plants such as *Solidago* dominating interactions in certain urban contexts. These results aim to broaden current understandings of urban bee ecology and influence policy decisions targeting pollinator conservation and habitat restoration.

Introduction

Assessing organismal response to anthropogenic activities such as urbanization is imperative to ensuring appropriate conservation methods are employed to mitigate further community and species losses. This task is especially pertinent in a rapidly changing world where cities already possess 55% of the global population yet are projected to sustain 68% of people by the year 2050 (United Nations 2018). Accommodating a population of 9.8 billion people by mid-century will undoubtedly necessitate a demand for increasingly urbanized landscapes (United Nations 2017). As a result, there is real potential risk of further environmental damage being sustained should precautions and measures to preserve semi-natural and natural landscapes alike be disregarded and unimplemented. Currently, urbanization has in several instances been associated with species and abundance reductions for a variety of taxa including birds (Silva et. al 2015; Isaksson 2018, Sol et al. 2020), reptiles (Kolbe et al. 2016; French et. al 2018), and arthropods broadly (McKinney 2008; Cardoso and Gonclaves 2018; Fenoglio et. al 2020; Piano et. al 2020) broadly. Such inter-taxon responses are driven by urbanization associated alterations of the environment, such as urban sprawl and intensification, which result in habitat loss, fragmentation, and degradation in addition to species introductions, pesticide application, and pollution presence (Cariveau and Winfree 2015; Baldock 2020; Wenzel et al. 2020).

Despite declines and community fluctuations related to urbanization being reported widely throughout the literature, such trends are not readily generalizable (Buchholz and Egerer 2020). In fact, some species within inter-taxonomic groups appear resilient in urban spaces. Consequentially, however, the diminishment of particular species and the prevalence of others within such ecosystems can result in community homogenization in which species displaying similar functional traits or life history strategies permeate the landscape (Williams et al. 2009; Baldock et al. 2015). For groups such as bees, traits commonly reported in cities include polylectic or generalist foraging, cavity nesting, and sociality (Banaszak and Zmihorski 2012; Ayers and Rehan 2021).

Wild bees are one such group of animals that have, until recently, remained significantly understudied, especially within urban contexts. This is perhaps due to a strong reliance being placed on non-native bees, primarily *Apis mellifera*, and their pollination services regarding global food production and associated economic implications in agricultural ecosystems. Cities, which often include urban gardens and other forms of green space, however, can support native bee populations (Baldock et al. 2019) and, in turn, benefit from the ecosystem services they provide (Lowenstein et al. 2015, Theodorou et al. 2020). Moreover, when comparing bee richness between urban and agricultural landscapes, most studies comparing the two environments report higher bee richness in cities (reviewed in Prendergast et al. 2021). The bee communities thriving within urban landscapes, however, are dependent on the resources available throughout and around its green spaces (Ayers and Rehan 2021). Like nearly all other animals, these requirements include foraging and nesting resources which for bees pertain to sufficient ground cover (for ground nesting species) and suitable plant hosts from which to provision pollen and nectar from and/or create nests within in the case of cavity nesting species such as carpenter, masked, leaf-cutting and mason bees (Michener 2007). As a result, certain green spaces may be more effective at promoting pollinators than others as resource availability and quality vary among sites (Dylewski et al. 2019). Therefore, bee communities ultimately reflect the environments they inhabit.

Due to most bee species' obligately mutualistic relationship with plants, flower presence represents an essential local resource for bees throughout cities (Wilson and Jamieson 2019; Ayers and Rehan 2021; Gerner and Sargent 2021). Despite their importance, however, understanding which plants are most beneficial to bees remains an intensely researched subject. Non-native plants are pervasive throughout urban areas and are planted for a variety of purposes that are not necessarily ecologically motivated (Nilon 2014; Fineschi and Loreto 2020). The replacement of native plants with non-native species, however, may have significant implications for bee communities, especially for specialist bee species with narrow floral host breadth. For generalist species, the consensus is less clear. For example, when determining bee floral preferences there appears to either be an affinity for native plant species

(Pardee and Philpott 2014; Lowenstein et al. 2019), non-native ornamental or "weedy" species (Matteson and Langelloto 2009; O'Connell 2020; Turo et al. 2020), or no significant preference for any group over the other (Rahimi et al. 2022). Additionally, a significant number of plants within cities including plants sold in garden centers marketed as "pollinator friendly" may still be largely unattractive to pollinators (Garbuzov et al. 2017; Lowenstein et al. 2019). As a result, the promotion of these plants may prove counterproductive particularly among individuals and organizations attempting to genuinely enhance local habitats for bees and other pollinators. Regardless, in several instances plant richness has demonstrated to positively influence bee richness and abundance (Blackmore and Goulson 2014; Quitsburg et al. 2016; Baldock et al. 2019; Gerner and Sargent 2021) even though other landscape and local factors such as floral patch size and habitat connectivity can equally be important in sustaining bee communities (Braaker et al. 2017; Plascencia and Philpott 2017).

Plant-pollinator interaction networks offer one method of evaluating floral resource use and bee visitation within the environment. This could be especially beneficial in determining the efficacy of plantings or seed mixes targeted to promote specific bee groups or species (Blackmore and Goulson 2014; Harmon-Threatt and Hendrix 2015). For instance, an evaluation of seed mixes using plant-pollinator networks in North Dakota Great Plains revealed wild bees most frequently visited plant species entirely different from species visited most by non-native honey bees, *Apis mellifera* (Otto et al. 2017). In this sense, plant-pollinator networks may empirically assist in elucidating plants of value to multiple pollinators in specific urban spaces. Use of plant-pollinator networks in urban spaces for this purpose however has not been extensively applied. Such networks can also be useful in visualizing important interactions occurring within a landscape or even reveal weakened and lost interactions occurring along environmental gradients (Geslin et al. 2013; Udy et al. 2020) or over periods of time (Burkle et al. 2013). Shifts in networks, especially in the case of urban gradients, can then potentially be extrapolated to drivers expected to influence such interactions such as habitat loss, climate change, and plant invasions (Harrison and Winfree 2015; Para-Tabla and Gomez 2021).

Toronto is the most populous city in Canada with roughly three million inhabitants (City of Toronto 2022a) and provides a unique opportunity to understand what pollinator communities are currently inhabiting and interacting with urban areas. Additionally, as the Greater Toronto Area (GTA) has traditionally experienced an annual urban growth rate of approximately 1.6% (Wang et al. 2015), illuminating potential patterns in community response to urbanization will be imperative as sprawl and intensification continue into the foreseeable future. An equal understanding of plant-pollinator networks may also reveal interactions that are vulnerable to increasing urbanization while recognizing groups that may display some degree of urban tolerance. As a result, this study aims to: 1) assess whether the urban landscape gradient and other landscape characteristics are influencing bee community structure, and 2) determine which bees and plants are driving interactions within plant-pollinator networks along the urban gradient, highlighting potentially high-value plants.

Methods

Site Selection

Geographic Information Systems (ArcMap 10.7.1, Redlands, CA, USA) were used to select sites located within the south-western portion of the city of Toronto. The high-resolution land cover dataset used to aid selection was obtained from a 2018 urban tree study published by Toronto Parks, Forestry, & Recreation (https://open.toronto.ca/dataset/forest-and-land-cover/). Initially, the pre-existing landscape features present within the dataset were reclassified into simplified categories such that the features “buildings”, “roads”, and “other impervious” were grouped together into a single feature called “impervious surface.” All pervious features (“bare ground,” “trees,” “grass,” “shrub”, and “water”) were left unmodified.

To establish an urbanization gradient, potential sites were classified into one of three categories determined by calculating the percentage of impervious surface surrounding sites within a 125m buffer radius (Tscheulin et al. 2011). These categories include low urban (<49% impervious), moderate urban ($50\% \geq x \leq 74\%$ impervious), and high urban (>74% impervious) intensity (Birdshire et al. 2020). A total of 29 green spaces (with 10 low, 10 moderate and 9 highly urban category sites) spaced ~1km apart were selected (Figure 1).

Site monitoring and bee collection

Site monitoring began 3 May 2021 and continued bi-weekly through 1 October 2021. To ensure that bee communities in Toronto were accurately represented in the study and avoid collection biases resulting from relying on any one particular collection method, sampling consisted of a combination of passive and active sampling techniques (Prendergast et al. 2020). Passive sampling involved the deployment of ten, alternating blue, white, and yellow pan traps (New Horizons Support Services, Inc.; 3.5 oz.) and a single blue vane trap (BanfieldBio™) at each site. Pan traps were filled with water containing a few drops of dish detergent (blue Dawn™) to break the surface tension of the water and placed approximately 1 meter apart. These traps are deployed before 9:30 hrs and collected after 16:00 hrs, a slight modification from Tucker and Rehan 2016. Blue vane traps were hung un-baited from tree limbs using twine and deployed before 9:30 hrs during initial site visits. Every two-weeks the contents of the vane traps were emptied into vials of 70% ethanol and the traps were redeployed (Kimoto et al. 2012). All collected specimens from both pan and blue vane traps were stored in 70% ethanol until they were later processed and identified.

Active sampling consisted of aerial netting and vacuuming (*InsectaVac Aspirator*) specimens at focal plant species. At parks or focal plants that could withstand sweeping and/or appeared to be consistently visited by numerous bees, 30 s sweeps followed by 1-minute breaks (spanning 5 minutes) occurred (Tucker and Rehan 2016). Flowers present in residential yards were observed for 10 minutes in which any bees interacting with the flowers during that observational period were captured. All netted bees were labeled and placed into vials containing 70% ethanol or stored temporarily in a freezer until later pinning and processing (Geslin et al. 2013). Flowers from which bees were collected, were identified in-field using *Newcomb's Wildflower Guide* (Newcomb 2011) and iNaturalist. Sampling occurred in ambient conditions (low wind (<2.5 m/s), sunny, warm) from ~10:00-16:00 hrs (Ullmann et al. 2010; Odanaka and Rehan 2019).

Bee processing and identification

Collected specimens were removed from ethanol or the freezer for pinning and labeling. Identification of specimens was accomplished using a variety of keys and online resources (Mitchell 1960, 1962; Michener, McGinley, Danforth 1994; Gibbs 2010; Sheffield and Rehan 2011; Sheffield et al. 2011; Ascher and Pickering 2012; Williams et al. 2014). After specimen identifications were complete, the bee functional traits lecty, origin, nesting, and behaviour were recorded for each species using resources found in published literature (Harrison et al. 2018; McCravy et al. 2019; Odanaka and Rehan 2019; Cecala and Wilson 2021; Pei et al. 2022). Lecty refers to a bee's dietary breadth or foraging diversity. Bees were classified as either polylectic (generalist) or oligolectic (specialist). Origin refers to whether a species is native or introduced to North America. Bees were classified as either native or non-native. Nesting refers to whether species nest in the ground or within cavities and other above-ground structures. Lastly, behaviour refers to the social behaviour expressed in a particular species. Behaviour classifications fell into four categories: solitary, subsocial, eusocial, or cleptoparasitic. Solitary species were those in which females provisioned for their offspring alone. Subsocial species were those capable of nesting in a colony consisting of daughters and founding mothers (Odanaka and Rehan 2019). Eusocial species were those that lived in colonies and have an established division of labour. Cleptoparasitic species were those that did not provision for offspring resources and instead invaded and laid eggs in the nest of a host (solitary or social) nest.

Bee Community Analysis

All statistical analyses were performed in R version 3.6.3 (R Core Team, 2022). Rarefaction curves were generated to examine the robustness of sampling employed across all sites and for each urban category using the R package ‘iNEXT’ (Hsieh et al. 2016). Richness and abundance between urban categories were compared using ANOVAs. Richness and abundance of the functional trait categories behaviour and family were compared using Kruskal-Wallis one-way analysis of variance with the Dunn’s tests for multiple comparisons being performed post-hoc. Wilcoxon rank sums analyses were used to compare abundance and richness for the functional traits orgin, nesting, and lecty. Spearman’s rank coefficient correlation tests were conducted to detect any correlations between bee abundance, richness, and functional trait response to the environmental landscape variables percent impervious surface, tree cover, and bare ground. Linear regression analyses were also performed to determine bee and plant variable response to the urban gradient and associated urban landscape variables (% impervious surface, % tree cover, % bare ground). Bee abundance and plant richness was log transformed to meet assumptions associated with normality when performing linear regressions. Non-metric multidimensional scaling (NMDS) with Hellinger transformed bee species abundance data was performed using the R-package ‘*vegan’* (Oksanen et al. 2022) to investigate urban landscape influence on the study area’s bee communities (Wilson and Jamieson 2019). Permutational Multivariate Analysis of Variance (ADONIS) was used to further determine landscape variables significantly influencing community compositions among sites. PCA analysis was conducted to explore how the landscape was influencing the functional composition of bee communities within the study area. Like the NMDS analysis, PCA analysis also utilized Hellinger transformed abundance data for the bee species found at each site. PCA analysis; however, also incorporated the community weighted mean (CWM) of each trait using the *envfit* function in the ‘vegan’ package (Odanaka and Rehan 2019).

Plant-bee Interaction Networks

Plant-bee interaction networks were constructed from strictly netting and vacuuming data using the R package ‘bipartite’ (Dormann et al. 2008). Plant-bee interaction networks for each urban category and across all sites were visualized using the *plotweb* function. The *networklevel* and *specieslevel* functions were used to analyze metrics at the entire network/community level and at the species level, respectively (Table 1; Dormann et al. 2008; Tucker and Rehan 2016). For network level analysis, the indices connectance, interaction evenness (IE), weighted nestedness (WN), and robustness were evaluated (Geslin et al 2013; Tucker and Rehan 2016; Udy et al. 2020). For species level analysis, the indices degree (D), normalized degree (ND), and pollinator service index (PSI) were evaluated (Dormann et al. 2008).

Results

Bee community composition

In total, 5477 bees were collected across all 29 sites. While rarefaction suggests additional species are likely present, sampling methods for the entire region were effective at capturing the diversity present throughout the city (Figure 2). From the specimens collected, 26 of the ~37 (~70%) bee genera previously recorded throughout Toronto were represented including a potentially new city record for a *Pseudopanurgus* species. Abundance across the entire study region was primarily dominated by members of the Apidae and Halictidae families. *Agapostemon, Apis, Bombus, Eucera*, and *Lasioglossum* constituted the top five most abundant genera with 1584, 705, 659, 342 and 649 individuals sampled, respectively (Supplemental Figure 1). Of the most abundant genera, the degree of abundance was largely driven by a single species. For instance, within the genera *Agapostemon* and *Bombus* the dominating species included *Agapostemon virescens* (86%; 1366/1584 individuals) and *Bombus impatiens* (40%; 263/659).

Overall, 164 species were identified from the collected material. The top five most abundant species displayed a similar but not exact trend to the most abundant genera with the top five species being *A. virescens*, *A. mellifera*, *E. pruinosa*, *B. impatiens,* and *A. sericeus* with 1366, 705, 342, 263, and 215 individuals collected, respectively. As with genera, the most abundant species were still dominated by the Apidae and Halictidae families. The families with the most species significantly represented were the Halictidae and Apidae families with 52 and 41 species identified, respectively (Kruskal-Wallis, X^2 = 83.36, *DF* = 4, *P* = 2.2^{-16}).

Landscape influence on bees

Total abundance of all bees sampled at low, medium, and high urban intensity was 1786, 2375, and 1316, respectively. Interestingly, intermediate urban intensity possessed the highest average number of collected individuals. Average abundance was highest for the medium urban intensity (237 ± 64.14) followed by low (180 ± 40.27) and high (146 ± 38.18) urban intensities, respectively. Despite medium urban intensity exhibiting the greatest average abundance, this did not statistically differ among the urban categories (ANOVA, *F* = 0.935, *DF* = 2, *P* = 0.405). Examining total abundance of bees collected at individual sites, two of the top five most abundant sites were of medium urban intensity (673, 492) while the remaining three sites belonged to the high (318, 348) and low (474) intensities (Supplemental Figure 2). With the medium urban intensity displaying the highest average abundance, the same can be said for species richness. Average species richness for low, medium, and high intensities was approximately 36 ± 3.95, 39 ± 15.01, and 32 ± 5.65 species, respectively. Interestingly, high intensity sites represented locations with the highest and lowest number of species with 15 and 70 species reported (Supplemental Figure 3). Species richness among the three urban categories, however, did not vary significantly (ANOVA, *F* = 0.59, *DF* = 2, *P* = 0.561).

Most of the individuals recorded throughout the study region belonged to the family Halictidae (n = 2329) and/or were native (n = 4352), solitary (n = 3180), polylectic (n = 4628), and ground-nesting (n = 3889) (Supplemental Figure 11a-e). Native, ground-nesting, and polylectic bees were significantly more abundant than nonnative, cavity-nesting, and oligolectic bees found throughout the study region (Origin: U test, W = 732, *P* = 1.32^{-06}, Lecty: U test, W = 53, 1.14^{-08}, Nesting: U test, W = 176, *P* = 1.48^{-04}). The families Halictidae and Apidae were significantly more abundant than all other families but not significantly different from each other (Table 2; Supplemental Figure 4e). Likewise, solitary and eusocial behaviour was significantly more abundant than all other behaviours but not from each other (Table 2; Supplemental Figure 4e). Bee richness followed a similar trend in which the average number of species among all sites were halictid (n = 13), solitary (n = 18), native (n = 30), ground nesting (n = 25), polylectic bees (n = 30). Bee richness of these groups showed the same trends as with abundance (Table 3; Figure 3a-e).

Subsocial bee richness was correlated with landscape variables. In fact, percent impervious surface appeared to have a significant negative correlation with subsocial abundance whereas tree cover had the opposite effect (Imp: Spearman, s = 4862.8, r = -0.42, *P* = 0.02, Tree: Spearman, s = 2923.2, r = 0.40, *P* = 0.03) (Table 4). Despite the slight correlation among these variables, regression analysis revealed no significance among % impervious and % tree cover (*F* = 1.83, *DF* = 26, R^2 = 0.056, *P* = 0.18). Additionally, urban landscape features also did not appear to be significantly associated with bee abundance or richness for other bee groups (Tables 4-6).

Despite there being no evident correlation among the urban landscape variables with any bee characteristics, bee community compositions did appear to be significantly affected by % impervious surface (ADONIS, *DF* = 1, R^2 = 0.057, *F* = 1.689, *P* = 0.022) and % tree cover (ADONIS, *DF* = 1, R^2 = 0.058, *F* = 1.716, *P* = 0.020) (Figure 4). While PCA analysis did not detect any distinct patterns among communities associated with each urban category, community weighted means revealed that such communities were driven by the functional traits origin, lecty, genus, and behaviour (PCA, Origin: R^2 =

0.202, $P = 0.046$, Lecty: $R^2 = 0.212$, $P = 0.042$, Genus: $R^2 = 0.274$, $P = 0.015$, Behaviour: $R^2 = 0.440$, $P = 0.001$). Further determination of which specific functional traits falling within these broader categories suggests that polylectic ($P = 2.2^{-08}$), native ($P = 1.2^{-06}$), and genera such as *Agapostemon* and *Apis* ($X^2 = 438.45$, $DF = 25$, $P < 2.2^{-16}$) are most likely to be driving community composition.

Plant influence on bees

None of the urban variables investigated in the study were correlated with plant richness (Table 6). Alternatively, nearly every bee variable, with the exception of cleptoparasitism, had a significant positive correlation with plant richness. Plant richness among collected samples significantly influenced both abundance (Linear regression, $t = 4.87$, $DF = 27$, $R^2 = 0.45$, $P = 4.29^{-05}$) and richness of bees (Linear regression, $t = 6.73$, $DF = 27$, $R^2 = 0.61$, $P = 3.15^{-07}$) (Figure 5).

Bee-Plant Interaction Networks

Overall, 3267 interactions were recorded across the entire study region (high = 753, low = 1227, medium = 1287). When strictly examining the top ten most visited plant families and genera across all sites, almost half belong to the family Asteraceae (n = 1279 interactions). Among the top visited genera include *Solidago* (275), *Symphyotrichum* (176), *Agastache* (139), *Salvia* (122), and *Trifolium* (108) (Table 9). The genera possessing some of the highest visitations are primarily the result of single plant species receiving the majority of visitations. For instance, *Solidago canadensis* (176), *Agastache foeniculum* (134), *Symphyotrichum novae-angliae* (117), and *Trifolium repens* (106) were the dominant plant species for their respective genera (Supplemental Figure 5).

Network and species-level indices for both plant and bee communities were determined for each urban category and for the entire study region broadly (Tables 7-9). Network and species-level analyses performed in conjunction with the construction of plant-bee networks (Figure 6, Supplemental Figures 6-8). Overall, 1195 unique interactions were observed for the entire network between 145 bee species and 182 plant genera. Connectance among each category and the full network was relatively low with the high urban intensity possessing the highest connectance (0.047). Every other category including the full network possessed a connectance of 0.046 (Table 7). WN remained consistent across the study region; however, across the three urban categories WN was highest for the lowest urban intensity (0.552). Interestingly, robustness for both plant and bee communities within each intensity and even the full network was relatively high with the full network possessing the highest robustness for both bees (0.835) and plants (0.805) (Table 7). Between the three urban categories, IE was also consistently low with IE being barely the highest for the overall network (0.625) despite the highest urbanization category having an IE of 0.624. The overall network exhibited greater interaction evenness however (0.626). Bee species were analyzed using the species level indices degree, ND, and PSI (pollinator service index) (Tucker and Rehan 2016). Plant genera within the full network were analyzed similarly with the exception of PSI. Bees with the highest degree at high, medium, and low urban intensity categories were *Apis mellifera* (37), *Apis mellifera* (39), and *Agapostemon virescens* (30), respectively (Table 8). *Agapostemon sericeus* (20) and *Bombus griseocollis* (20) as well as *Agapostemon virescens* (27) had the second highest degrees for high and medium urbanization, respectively. ND followed the same trend with the same species maintaining the highest values for their respective urban categories (0.38, 0.34, and 0.33, respectively). Species with the highest PSI somewhat varied depending on urban category. Species with the highest PSI were *Lasioglossum atwoodi, Lasioglossum obscurum, and Osmia caerulescens* (all 1.00) for the high intensity, *Lasioglossum oblongum* (1.00) for the medium intensity, and *Hylaeus punctatus* (0.60) for the low intensity. For plants, degree and normalized degree (N/ND) was highest for *Solidago* (23/0.23) in high, *Solidago* (23/0.19) in medium, and *Taraxacum* (27/0.21) in low urbanization categories.

Apis mellifera possessed the highest degree or number of unique interactions (68) within the full network with *Agapostemon. virescens* have the second highest degree (55) (Table 8). These two species also made up the largest number of interactions within the full network with 678 (21%) for *Apis mellifera* and 260 (0.08%) interactions for *Agapostemon virescens*. Unsurprisingly, ND was also highest for *A. mellifera.* PSI was highest for the specialist species *Chelostoma philadelphi* (0.57) (Table 8). For plant genera, *Solidago* had the highest degree (40) in addition to the highest number of raw bee visitations (275) (Table 9). *Solidago* also possessed the highest ND (0.24) with *Taraxacum* possessing the second highest (0.19). Despite *Symphotrichum* having the second most visitations (176), *Allium* and *Taraxacum* both received the second largest number of *unique* interactions within the full network (32) (Table 9). This consistency in visitation for plants such as *Solidago* however could highlight an important plant group for specific pollinators.

Discussion

Landscape effects on bees

Urban bee communities appear to respond to land use. Unlike many studies that have associated bee declines with urbanization, this study found neither bee abundance nor richness to vary among landscape variables. Wilson and Jamieson (2019) obtained a similar result where in their study across urban and rural landscapes in Michigan only species diversity and evenness was influenced by urbanization. While it may be noted that monitoring efforts only reported about half of the bees previously recorded in the region (164/~360; City of Toronto 2016), it is worth mentioning that the study area did not cover the entirety of the cityscape. As a result, unreported species likely exist in spaces that were unmonitored. Moreover, yearly variation could have also influenced the presence of bees captured during the field season. This highlights the benefit of repeated monitoring within locations in addition to surveying areas that, if feasible, effectively cover broad regions. Interestingly, the city may support uncommon bee species such as *Pseudopanurgus andrenoides* which, despite being sampled in surrounding locations such as Niagara (Onuferko et al. 2015), has not been previously observed in Toronto (City of Toronto, 2016).

Even though land use within the city may not appear to be affecting richness and abundance, it does not discredit the city's ability to alter the bee communities present within it (Wilson and Jamieson 2019). In fact, this study suggests factors such as percent impervious cover and percent tree cover can negatively contribute to species compositions. This partially corroborates the work done by Burdine et al. (2019), which found only impervious surface negatively affected bee diversity. Tree cover also negatively influenced bee abundance (Burdine et al. 2019). Other studies have found connections between tree cover and reduced bee richness due to the indirect effects of tree shading possibly influencing floral availability (Matteson et al. 2010).

This study reported a dominance of bees particularly within the Apidae and Halictidae families with *Apis, Bombus, Agapostemon,* and *Lasioglossum* accounting for over half of all collected material. Similar to this study, Tucker and Rehan (2016) also surveyed bees overwhelmingly belonging to both families despite monitoring occurring outside of an urban context in rural New Hampshire. Sivakoff et al. (2018) also reported *A. virescens* as the most abundant species in urban gardens and vacant lots in Ohio. These genera possess species that are predominantly polylectic, native, and ground nesting (*Apis* being the exception to the last two traits). It is not unexpected then that functional traits such as generalist foraging and bee family were contributing most to bee community assemblage. This pattern is consistent with other studies in Poland (Banaszak-Cibicka and Żmihorski 2012) and France (Geslin et al. 2013) also reporting an increased number of generalist species in urban landscapes. This result is expected given, as others have stated, the pervasiveness of non-native and ornamental plants throughout urban landscapes (Banaszak-Cibicka and Żmihorski 2012; Nolan et al. 2014).

Curiously, despite the bulk of literature indicating that ground nesting species are not particularly favoured in cities (Geslin et al. 2016; Cardoso and Gonclaves 2018; Baldock 2020; Pereria et al. 2021; Wenzel et al. 2021), this study seems to suggest otherwise in some instances as bee abundance and richness in the case of Toronto was dominated by ground nesting bees regardless of urban intensity. This is peculiar given that nesting availability for ground nesting species becomes increasingly limited in intensely urbanized areas extensively covered with impervious surface. As a result, the prevalence of ground nesting species within this study may suggest that nesting habitat within the city could be more accessible or of sufficient size for ground nesting species (Naeme et al. 2013) compared to other cities. It could also be speculated that such an observation could be linked with bee behaviour given ground nesting abundance was driven by social species such as *Bombus* as well as species such as *A. virescens* which both nest gregariously. Soil type may also influence nesting; however, this variable was not explicitly examined in this study.

Plant influence on bees

Despite cities displaying a relatively high degree of floral richness driven greatly the prevalence of non-native and ornamental species, many studies have not detected any increases in bee abundance or richness attributed to flower richness (Prendergast et al. 2022). This could be due to other variables in the urban landscape such as UHI undermining the potential positive impacts of increased plant richness and abundance (Hamblin and Youngsteadt 2018). Some studies, however, have noted an increase in bee richness and abundance in response to floral abundance and spatial arrangement but not floral richness (Plascencia and Philpott 2017; Choate et al. 2018; Stewart et al. 2018). This may be a result of many floral resources available in urban spaces being undesirable to bees (Salisbury et al. 2015; Garbuzov et al. 2017; Lowenstein et al. 2019). Regardless, some studies consistent to this one, have found positive associations between increased floral richness and bee richness and abundance (Wilson and Jamieson 2017; Egerer et al. 2020; Gerner and Sargent 2022). As a result, increases in plant richness in specific urban contexts may be beneficial to bees especially if such additions include attractive plant species and extend floral resource availability. Ultimately, the inconsistency in results observed throughout the literature reaffirms the importance of continuing studies to evaluate how floral resources can be manipulated in urban spaces in the hopes of enhancing bee biodiversity.

Bee-plant interaction networks

Plant-pollinator networks and their network statistics remained fairly consistent across all urban intensities and revealed interesting observations about the interactions occurring throughout the study region. Compared to other studies, weighted nested, while somewhat low, was higher than that reported in less urban contexts (Tucker and Rehan 2016). Therefore, urban generalist and specialist bees may overlap in floral resource usage more so in non-urban environments perhaps as a result of increased floral diversity present throughout the cityscape. Despite this, low nestedness could be detrimental especially for specialist plant and bee species. Connectance, or the proportion of all realized interactions within the entire network, was surprisingly low which is consistent with Tucker and Rehan (2016) which found similar trends in rural New England. Whereas Tucker and Rehan (2016) speculate that low connectance could indicate an unrobust network, this study interestingly found robustness for both plant and bee communities to be reasonably high across all urban gradients. Within urban contexts, other studies have reported connectance comparable between urban and rural environments (Olsen et al. 2021) and within cities this connectance can be relatively low (Stewart and Waitayachart 2020). Robustness for both bee and plant communities were only slightly lower for the largest intensity which could suggest that intensely urbanized areas may be more sensitive to species losses. Similar results have been found in residential gardens in Australia where robustness was lower than that found in bushland (Prendergast and Ollerton 2021). Interaction evenness contrasts previous research while corroborating others. Whereas interaction evenness in previous studies either decreased with increasing urbanization (Udy et al. 2020) or increased with urbanization (Geslin et al. 2013). Interaction evenness in the context of this study corroborated Fisogni et al. (2022) that found evenness to be consistent across an urban gradient. This could indicate that despite many interactions occurring between various plant and bee species throughout the network, not as many interactions are occurring more broadly compared to other cities (Geslin et al. 2013).

Species-level indices provide more insight into plants and bees that may be contributing most or least to networks. Unsurprisingly, the bee species with the highest degree tended to be species with greater abundances (Tucker and Rehan 2016). While *A. virescens* was the most abundant bee in every urban intensity, *A. mellifera* in the case for the overall network exhibited the most generalist diet. It is unsurprising that the honey bee was one of the most abundant generalist bees found throughout the city as hive density in Toronto can be as high as 6.5 hives/km^2 (Ropars et al. 2019; MacKell 2021). Due to their dominance; however, it is important to determine whether the presence of honey bees is pernicious to wild bee communities as developing research have indicated competitive interactions (Ropars et al. 2019; Harrison and Winfree 2015) and pathogen spillover (Tehel et al. 2016) may be concerns for native species. Regardless, native bees such as *A. virescens* and *Ceratina calcarata* can also display quite wide foraging preferences which could be important for maintaining network stability and robustness should more vulnerable species be lost from the network. With that said, PSI highlighted different bee species depending on urban intensity. For the entire network, however, the specialist bee species *Chelostoma philadelphi* appeared to be an especially important pollinator. *C. philadelphi* is the only native species of *Chelostoma* in southern Ontario and is a specialist on flowers in the mock-orange genus, *Philadelphus* (Messinger and Wilson 2021). This result may emphasize the importance of specialist species within urban networks as their services can be essential to the plants that depend on them.

The Asteraceae family is one of the largest plant families worldwide (Mandel et al. 2019), therefore, it is not unexpected that plants from this group made up a significant portion of all bee visits. Specifically, *Solidago* (goldenrod) had the highest number of unique bee interactions in every urban category aside from the low intensity where degree was highest for *Taraxacum* (dandelion). *Solidago* is a genus possessing over 100 late-season species (Werner et al. 1980). Most species are native to North America and commonly grow in open fields and roadsides alike (Newcomb 1977). Their efficient proliferation, dispersal, and ability to inhabit polluted environments (Krolak 2021) may explain goldenrod's prominence in the urban environment and, as a result, their use by various bee species such as *Bombus* and *Apis* (Werner et al. 1980). Additionally, *Solidago* was found to be associated with bee abundance and was a substantial flowering plant in plant-pollinators created in Quebec (Martins et al. 2017).

Additional genera such as *Taraxacum*, which only included the species *T. officinale*, appeared important in specific urban contexts. Dandelion was particularly important in low urban intensity. This is potentially due to a number of low intensity sites being highly managed parks. Park management, in particular mowing, as a result could have reduced floral availability (Lerman et al. 2018) to a few select species which tend to cope well against such disturbances. *Agastache* (giant hyssops) and *Symphyotrichum* (asters) were other highly visited genera throughout the urban environment with *Symphyotrichum* attracting the most bee visitors at the intermediate urban intensity. Overall, this could indicate the usefulness of some plant genera to pollinators in varying urban environments. It should be noted, however, that other factors could be responsible for a plant's particular attractiveness in certain urban settings. For instance, the abundance of plants may vary from one space to another and, as a result, vary in their ability to ability to attract an abundance of pollinators (Wilson and Jamieson 2019). Additionally, the presence of other perhaps more favourable genera such as *Solidago* could be drawing interactions away from other plant species (Hennig and Ghazoul 2011). As a result, more work should be done to investigate factors contributing to floral preferences especially in urban landscapes.

Conclusions

Overall, this study in urban Toronto illustrates the variability of bee response to land use and emphasizes the importance of conducting regional studies when attempting to corroborate generalizable patterns to urbanization. As different areas of the world urbanize at varying rates, understanding urbanization impacts on bees and other pollinators will be essential to mitigating their losses and further declines. In this study, landscape features such as impervious surface and tree cover shaped communities dominated particularly by polylectic, native, ground-nesting bees—a contrasting result to previous studies (Matteson et al. 2008; Geslin et al. 2016; Cardoso and Gonclaves 2018). Additionally, plant richness rather than urban landscape variables had an influence on bee richness and abundance. In particular, plant genera such as *Solidago* may be especially effective at attracting an abundance and diversity of bees comprising various functional traits. As a result, enhancing appropriate green spaces with an increased richness of especially attractive plant species may be useful in thwarting detrimental effects of urbanization in certain contexts.

Future work investigating the potential impacts of urbanization at different landscape scales could be beneficial and additional plant-pollinator networks should be investigated to continue determining plants of interest to specific bees within urban contexts (Egerer et al. 2017). These networks could be applied to urban seed mixes or used to evaluate the efficacy of projects conducted by non-profit organizations and city governments alike. Such information may aid such groups to establish landscapes better suited to support local pollinator communities.

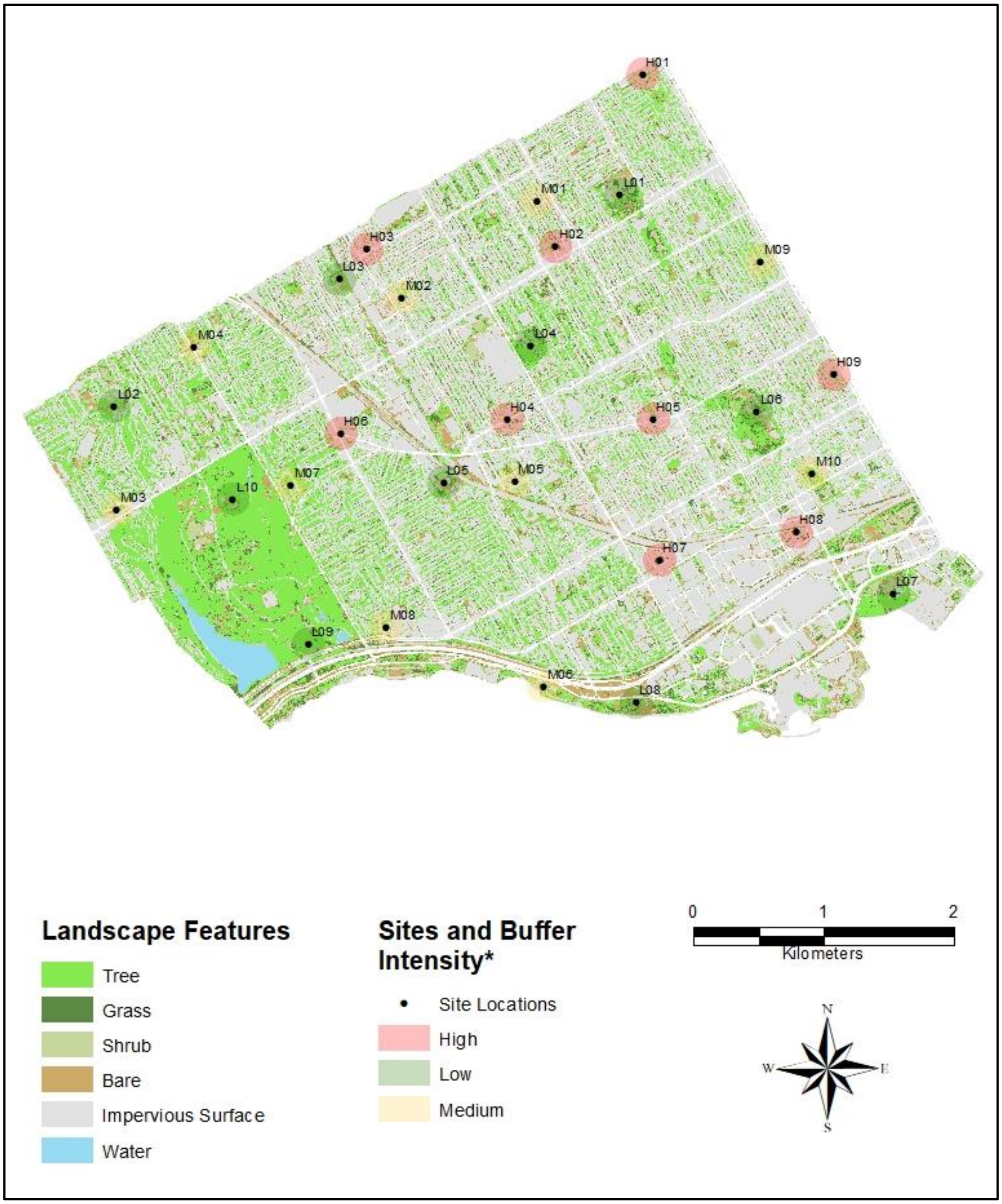

Figure 1. Southern Toronto study region displaying monitoring site locations varying in urbanization intensity. Unique Site IDs also indicated for each site with the first letter of each site ID corresponding to urban intensity ("H" = High, "M" = Medium, "L" = Low).

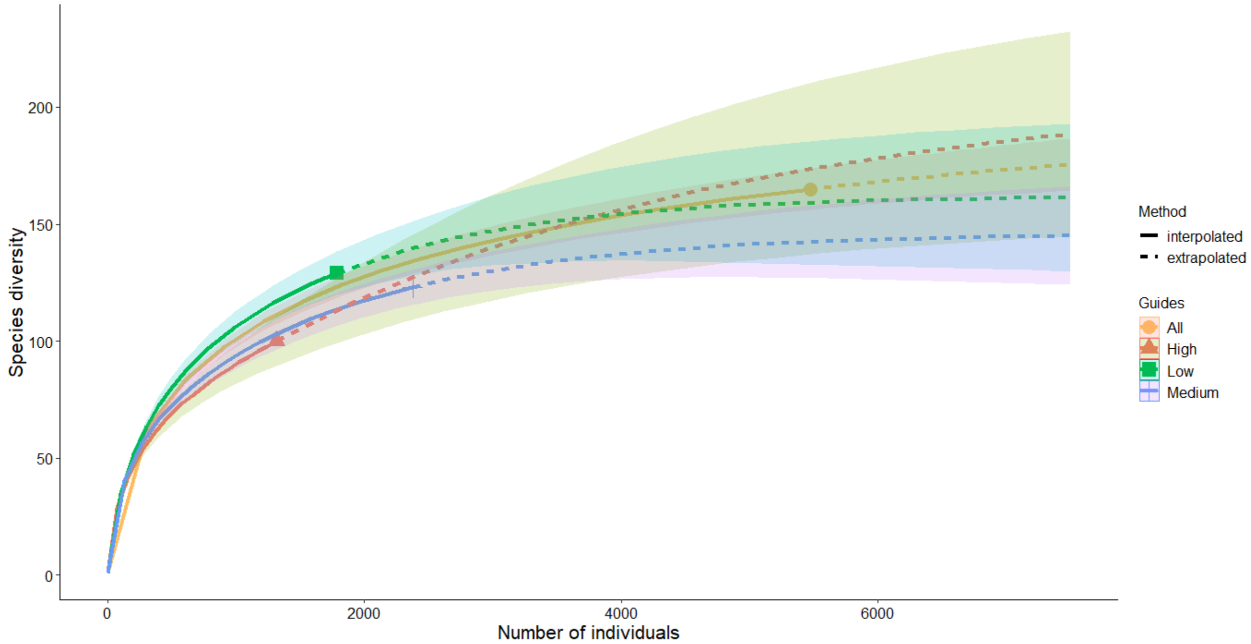

Figure 2. Rarefaction curves displaying the sampling efficiency recorded for each of the urban categories and overall.

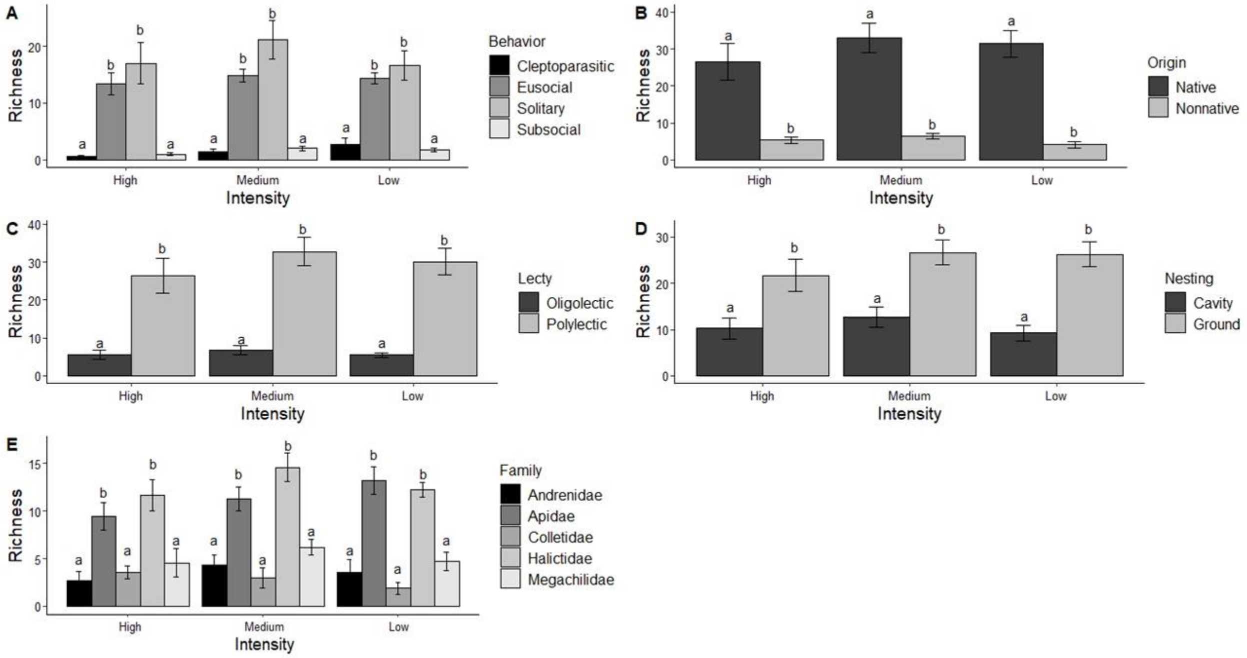

Figure 3. Average richness (± SE) of bee functional trait groups at each urbanization category. a - Nesting, b - Behavior, c - Family, d – Origin, e – Lecty.

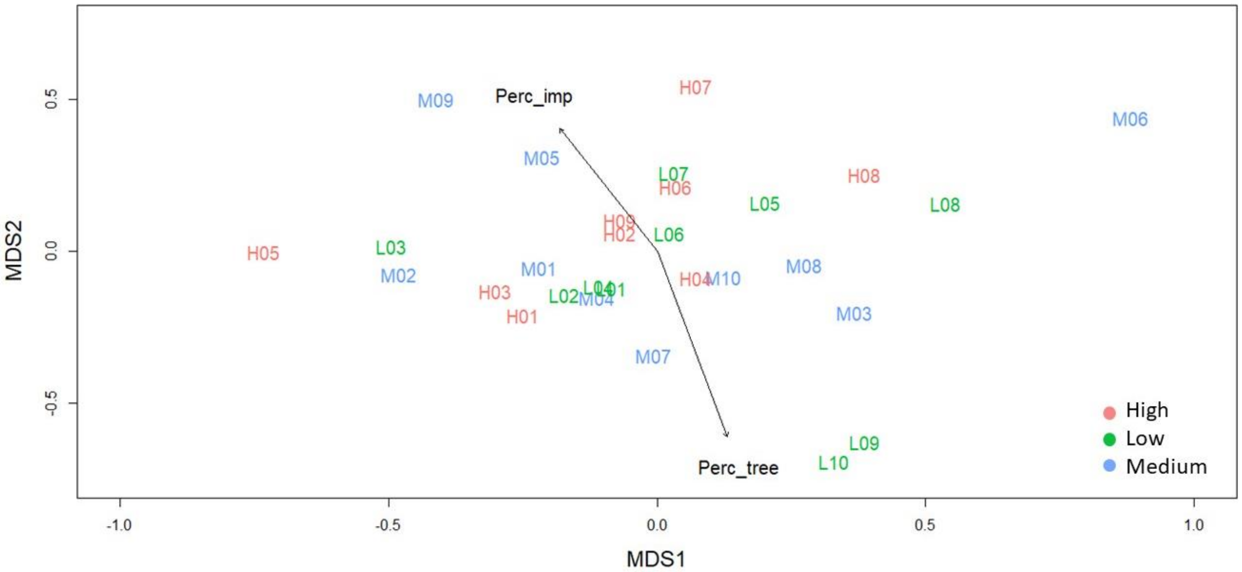

Figure 4. Nonmetric multidimensional scaling (NMDS) results displaying significant (< 0.05) urban landscape variables overlayed over species communities at each site location. k = 3, stress = 0.139. High, medium, and low intensity sites are indicated with site ID codes starting with “H”,”M”, and “L”, respectively.

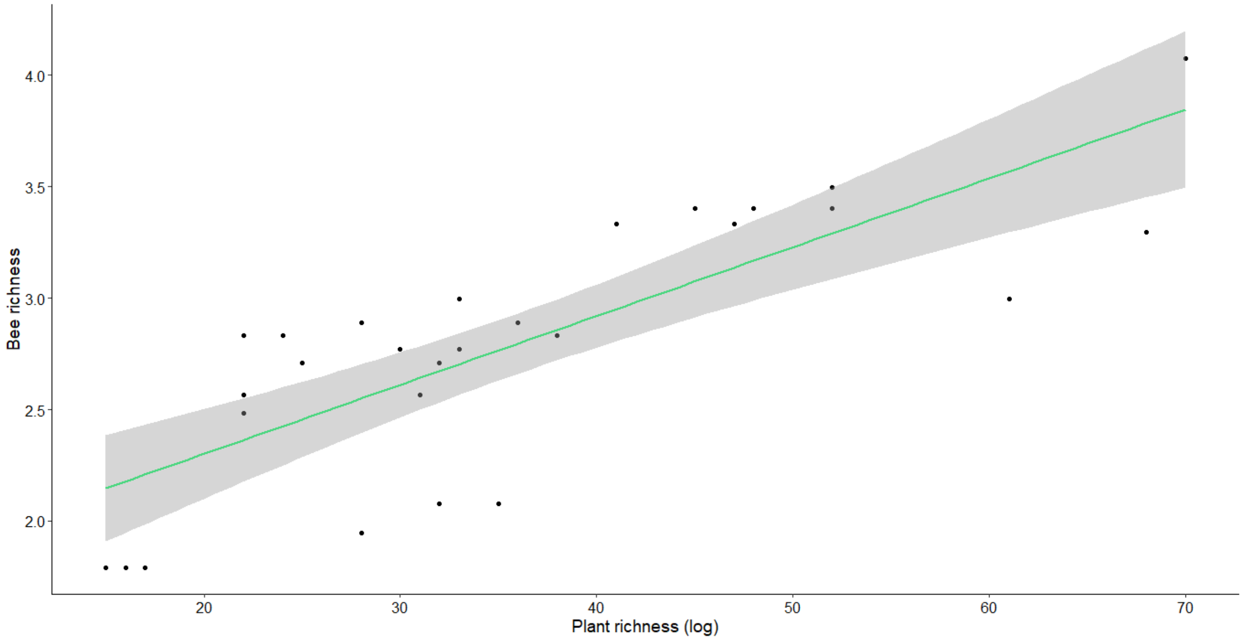

Figure 5. Bee richness response to plant richness (log) across all sites. Bee richness significantly increased with an increase to plant richness (t = 6.73, df = 27, $r^2 = 0.61$, p = 3.15e-07).

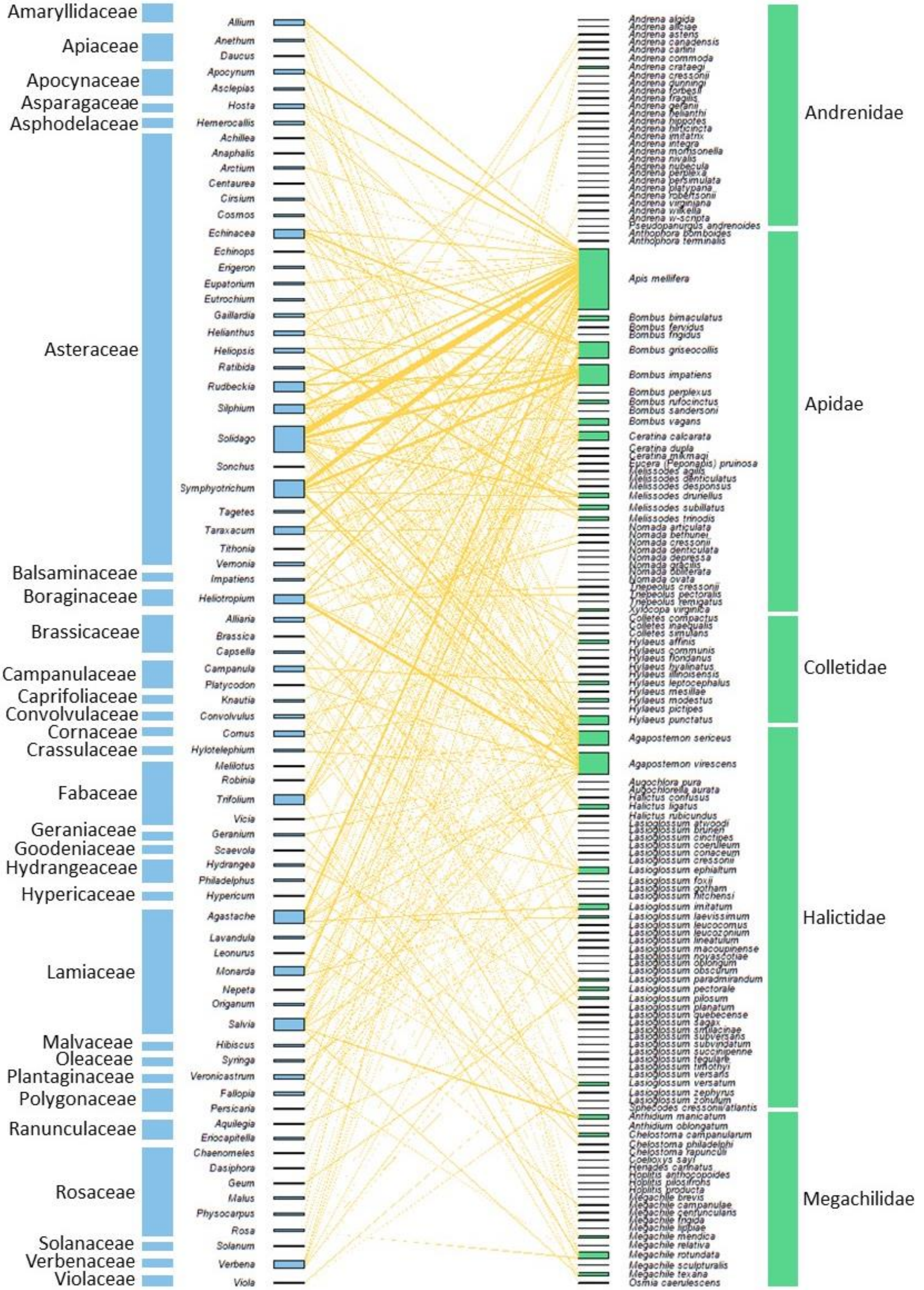

Figure 6. Plant-pollinator network for the entire study region. Network only includes plant genera with more than 10 interactions. Plant and bee families denoted for species and genera represented. For full list of plant genera and bee species see Tables 8 and 9.

Table 1. Network and species level indices used for bipartite analysis of plant-bee interactions.

Network level indices	**Definition**	**References and application**
Connectance (C)	Proportion of all possible interactions within a network that are achieved.	Dormann et al. 2008; Gresty et al. 2018; Tucker and Rehan 2016
Weighted nestedness (WN)	Specialist species interaction with a subset of species generalists interact with	Dormann et al. 2008; Tucker and Rehan 2016
Robustness (R)	Fraction at which total network loss is >50% after species removal	Dormann et al. 2008; Dunne 2002
Interaction evenness (IE)	Analysis of how equal the number of interactions is among species	Dormann et al. 2008; Tylianakis et al. 2007
Species level indices		
Degree (D)	Number of links or unique interactions per species	Dormann et al. 2008; Martin Gonzalez et al. 2010
Normalized degree (ND)	Degree divided by the number of all possible interactions between species	Dormann 2008; Prendergast and Ollerton 2021
Pollinator Service Index (PSI)	Indicator of a pollinators importance in maintaining ecosystem functions	Dormann et al. 2008; Tucker and Rehan 2016

Table 2. Non-parametric comparisons (with associated post hoc tests) of the average abundance between functional trait categories across the entire study region.

Variable	**Statistical Test**	**Post hoc test**	**Test statistic**	**P-value**
Behaviour	Kruskal-Wallis		$X^2 = 83.21$	<2.2e-16*
Cleptoparasitic vs Subsocial		Dunn's	z = -1.64	0.12
Eusocial vs Cleptoparasitic		Dunn's	z = -6.81	2.89e-11*
Eusocial vs Solitary		Dunn's	z = -0.67	0.50
Eusocial vs Subsocial		Dunn's	z = 5.17	3.57e-07*
Solitary vs Cleptoparasitic		Dunn's	z = -7.49	4.25e-13*
Solitary vs Subsocial		Dunn's	z = 5.84	1.03e-08*
Family	Kruskal-Wallis		$X^2 = 86.28$	<2.2e-16*
Andrenidae vs Colletidae		Dunn's	z = -0.08	1.00
Andrenidae vs Megachilidae		Dunn's	z = -1.92	0.08
Apidae vs Andrenidae		Dunn's	z = -6.52	6.98e-10*
Apidae vs Colletidae		Dunn's	z = 6.44	3.87e-10*
Apidae vs Halictidae		Dunn's	z = 0.05	1.00
Apidae vs Megachilidae		Dunn's	z = 4.60	8.38e-06*
Colletidae vs Megachilidae		Dunn's	z = -1.84	0.08
Halictidae vs Andrenidae		Dunn's	z = -6.47	4.97e-10*
Halictidae vs Colletidae		Dunn's	z = -6.39	4.11e-10*
Halictidae vs Megachilidae		Dunn's	z = 4.55	9.0e-06*
Lecty	Mann-Whitney U		W = 53	1.14e-08*
Nesting	Mann-Whitney U		W = 176	1.48e-04*
Origin	Mann-Whitney U		W = 732	1.32e-06*

Table 3. Non-parametric comparisons (with associated post hoc tests) of the average richness between functional trait categories across the entire study region.

Variable	Statistical Test	Post hoc test	Test statistic	P-value
Behaviour	Kruskal-Wallis		$X^2 = 86.04$	<2.2e-16*
Cleptoparasitic vs Subsocial		Dunn's	z = -0.49	0.62
Eusocial vs Cleptoparasitic		Dunn's	z = -6.48	1.88e-10*
Eusocial vs Solitary		Dunn's	z = -0.612	0.65
Eusocial vs Subsocial		Dunn's	z = 5.98	3.29e-09*
Solitary vs Cleptoparasitic		Dunn's	z = -7.09	8.16e-12*
Solitary vs Subsocial		Dunn's	z = 6.59	1.28e-10*
Family	Kruskal-Wallis		$X^2 = 83.36$	<2.2e-16*
Andrenidae vs Colletidae		Dunn's	0.54	0.59
Andrenidae vs Megachilidae		Dunn's	z = -1.56	0.15
Apidae vs Andrenidae		Dunn's	z = -5.67	3.59e-08*
Apidae vs Colletidae		Dunn's	z = 6.21	1.82e-09*
Apidae vs Halictidae		Dunn's	z = -0.75	0.50
Apidae vs Megachilidae		Dunn's	z = 4.11	6.68e-05*
Colletidae vs Megachilidae		Dunn's	z = -2.10	0.05
Halictidae vs Andrenidae		Dunn's	z = -6.42	6.83e-10*
Halictidae vs Colletidae		Dunn's	z = -6.96	3.51e-11*
Halictidae vs Megachilidae		Dunn's	z = 4.86	2.38e-06*
Lecty	Mann-Whitney U		W = 2	7.69e-11*
Nesting	Mann-Whitney U		W = 73	6.57e-080*
Origin	Mann-Whitney U		W = 841	6.16e-11*

Table 4. Spearman correlation results between bee variable richness and urban landscape variables; p-values (r values) shown for each comparison.

Bee variable	% Impervious	% Tree	% Bare	Plant richness
Richness				
Richness	0.20 (-0.24)	0.51 (0.13)	0.84 (0.04)	7.5e-08 (0.81)*
Functional traits				
Lecty				
Polylectic	0.16(-0.27)	0.41 (0.16)	0.10 (0.31)	1.8e-08 (0.83)*
Oligolectic	0.46 (-0.14)	0.77 (0.06)	0.93 (0.02)	4.5e-03 (0.51)*
Origin				
Native	0.10 (-0.31)	0.28 (0.21)	0.90 (0.25)	1.9e-07 (0.80)*
Nonnative	0.43 (0.15)	0.17 (-0.26)	0.61 (0.10)	7.6e-05 (0.67)*
Behaviour				
Solitary	0.43 (0.15)	0.64 (0.09)	0.66 (-0.08)	3.1e-06 (0.75)*
Subsocial	0.02 (-0.42)*	0.03 (0.40)*	0.73 (-0.07)	8.4e-03 (0.48)*
Eusocial	0.26(-0.22)	0.72 (0.07)	0.15 (0.28)	7.9e-09 (0.78)*
Cleptoparasitic	0.07 (-0.34)	0.14 (0.28)	0.89 (0.03)	0.05 (0.37)
Nesting				
Ground	0.40 (-0.16)	0.24 (0.23)	0.85 (0.04)	3.8e-06 (0.74)*
Cavity	0.07 (-0.34)	0.89 (-0.03)	0.89 (-0.03)	7.0e-08 (0.82)*
Family				
Andrenidae	0.25(-0.22)	0.22 (0.24)	0.30 (-0.20)	7.4e-03 (0.49)*
Apidae	0.10 (-0.31)	0.57 (0.11)	0.13 (0.29)	1.6e-04 (0.64)*
Colletidae	0.37 (0.13)	0.23 (-0.23)	0.71 (-0.07)	1.3e-03 (0.57)*
Halictidae	0.57 (-0.11)	0.60 (0.10)	0.68 (-0.08)	2.0e-04 (0.64)*
Megachilidae	0.31 (-0.19)	0.75 (0.06)	0.59 (0.10)	1.1e-09 (0.87)*

Table 5. Spearman correlation results between bee variable abundances and urban landscape variables; p-values (r values) shown for each comparison.

Bee variable	% Impervious	% Tree	% Bare	Plant richness
Abundance				
Abundance	0.48 (-0.14)	0.77 (0.06)	0.25 (0.22)	1.8e-04 (0.64)*
Functional traits				
Lecty				
Polylectic	0.25 (-0.22)	0.55 (0.12)	0.10 (0.31)	2.5e-04 (0.63)*
Oligolectic	0.89 (-0.03)	0.99 (0.002)	0.64 (-0.09)	0.02 (0.44)*
Origin				
Native	0.46 (-0.14)	0.69 (0.08)	0.29 (0.21)	1.3e-03 (0.527)*
Nonnative	0.54 (-0.12)	0.97 (0.01)	0.15 (0.28)	3.8e-05 (0.69)*
Behaviour				
Solitary	0.70 (-0.08)	0.91 (0.02)	0.59 (-0.11)	2.4e-03 (0.54)*
Subsocial	0.30 (-0.20)	0.14 (0.28)	0.16 (-0.27)	1.3e-03 (0.57)*
Eusocial	0.10 (-0.31)	0.38 (0.14)	0.05 (0.37)	7.6e-06 (0.73)*
Cleptoparasitic	0.10 (-0.32)	0.17 (0.26)	0.96 (-0.01)	0.04 (0.39)*
Nesting				
Ground	0.40 (-0.16)	0.69 (0.08)	0.16 (0.27)	2.6e-03 (0.54)*
Cavity	0.35 (-0.18)	0.50 (0.13)	0.58 (0.11)	2.0e-06 (0.76)*
Family				
Andrenidae	0.10 (-0.31)	0.22 (0.24)	0.62 (-0.10)	2.7e-04 (0.63)*
Apidae	0.23 (-0.23)	0.55 (0.12)	0.34 (0.19)	2.7e-05 (0.70)*
Colletidae	0.43 (0.15)	0.30(-0.20)	0.45 (-0.15)	1.3e-03 (0.57)*
Halictidae	0.80 (-0.05)	0.91 (0.02)	0.04 (0.39)	2.0e-02 (0.43)*
Megachilidae	0.62 (-0.10)	0.88 (-0.03)	0.76 (0.06)	1.2e-05 (0.72)*

Table 6. Spearman correlation results between plant richness and bee richness and abundance vs percent impervious surface, tree cover, and bare ground.

Variable	% Impervious	% Tree	% Bare
Richness and abundance			
Richness	0.379 (-0.007)	0.998 (-0.04)	0.824 (-0.036)
Abundance	0.393 (-0.009)	0.942 (-0.04)	0.305 (0.003)
Plant Richness			
	0.08 (-0.33)	0.32 (0.19)	0.64 (-0.09)

Table 7. Network statistics for each urban intensity and for the overall study region. Asterisks indicate the largest value per category

Network level indices	High	Medium	Low	All
Connectance	0.047*	0.046	0.046	0.046
Weighted nestedness (WN)	0.511	0.455	0.552*	0.626
Robustness (Bee)	0.799	0.775	0.808*	0.835
Robustness (Plant)	0.777*	0.724	0.743	0.805
Interaction evenness (IE)	0.624*	0.607	0.596	0.626

Table 8. Bee species abundance counts and associated species-level statistics for bees caught throughout the entire study region. NAs either represent species that were not collected from flowers (†) or cleptoparasitic species for which PSI was not calculated for (‡).

Bee family	Bee species	Abundance	Degree	ND	PSI
Andrenidae	*Andrena algida*	3	2	0.01	0.13
	Andrena aliciae	2	1	0.01	0.02
	Andrena asteris	7	2	0.01	0.02
	Andrena canadensis	5	2	0.01	0.01
	Andrena carlini	11	5	0.03	0.04
	Andrena commoda	34	10	0.05	0.44
	Andrena crataegi	30	6	0.03	0.56
	Andrena cressonii	6	4	0.02	0.08
	Andrena dunningi	6	5	0.03	0.08
	Andrena forbesii	2	2	0.01	0.14
	Andrena fragilis	5	3	0.02	0.16
	Andrena geranii	7	3	0.02	0.51
	Andrena helianthi	12	1	0.01	0.26
	Andrena hippotes	4	2	0.01	0.07
	Andrena hirticincta	7	3	0.02	0.01
	Andrena imitatrix	3	2	0.01	0.07
	Andrena integra	7	1	0.01	0.10
	Andrena miserabilis †	3	0	NA	NA
	Andrena morrisonella	1	1	0.01	0.02
	Andrena nasonii †	1	0	NA	NA
	Andrena nivalis	2	1	0.01	0.08
	Andrena nubecula	2	1	0.01	0.01
	Andrena perplexa	2	1	0.01	0.06
	Andrena persimulata	1	1	0.01	0.02
	Andrena platyparia	1	1	0.01	0.02
	Andrena robertsonii	5	3	0.02	0.05
	Andrena virginiana	1	1	0.01	0.02
	Andrena wheeleri †	1	0	NA	NA
	Andrena wilkella	20	6	0.03	0.15
	Andrena w-scripta	1	1	0.01	0.01
	Pseudopanurgus andrenoides	1	1	0.01	0.00
Apidae	*Anthophora bomboides*	1	1	0.01	0.01
	Anthophora terminalis	25	11	0.06	0.11
	Apis mellifera	705	68*	0.37*	0.34
	Bombus bimaculatus	53	26	0.14	0.15
	Bombus borealis †	1	0	NA	NA
	Bombus fervidus	11	1	0.01	0.25
	Bombus frigidus	1	1	0.01	0.05
	Bombus griseocollis	197	45	0.25	0.23
	Bombus impatiens	263	40	0.22	0.20
	Bombus perplexus	1	1	0.01	0.01
	Bombus rufocinctus	50	23	0.13	0.11
	Bombus sandersoni	3	1	0.01	0.02
	Bombus vagans	79	31	0.17	0.09
	Ceratina calcarata	173	51	0.28	0.15
	Ceratina dupla	17	5	0.03	0.06

Bee family	Bee species	Abundance	Degree	ND	PSI
	Ceratina mikmaqi	7	3	0.02	0.03
	Eucera (Peponapis) pruinosa	342	3	0.02	0.14
	Melissodes agilis	17	6	0.03	0.04
	Melissodes denticulatus	3	1	0.01	0.01
	Melissodes desponsus	61	8	0.04	0.13
	Melissodes druriellus	71	8	0.04	0.09
	Melissodes subillatus	67	13	0.07	0.22
	Melissodes trinodis	84	14	0.08	0.08
	Nomada armatella †	3	0	NA	NA
	Nomada articulata ‡	10	2	0.01	NA
	Nomada bella †	1	0	NA	NA
	Nomada bethunei ‡	4	1	0.01	NA
	Nomada cressonii ‡	9	3	0.02	NA
	Nomada denticulata ‡	2	2	0.01	NA
	Nomada depressa ‡	3	1	0.01	NA
	Nomada gracilis ‡	2	1	0.01	NA
	Nomada integerrima ‡	1	1	0.01	NA
	Nomada luteoloides †	1	0	NA	NA
	Nomada maculate †	2	0	NA	NA
	Nomada obliterate ‡	1	1	0.01	NA
	Nomada ovata ‡	4	2	0.01	NA
	Triepeolus cressonii ‡	1	1	0.01	NA
	Triepeolus pectoralis ‡	5	4	0.02	NA
	Triepeolus remigatus ‡	1	1	0.01	NA
	Xylocopa virginica	28	11	0.06	0.07
Colletidae	*Colletes compactus*	2	1	0.01	0.01
	Colletes inaequalis	7	2	0.01	0.51
	Colletes simulans	7	1	0.01	0.03
	Hylaeus affinis	34	21	0.12	0.10
	Hylaeus communis	1	1	0.01	0.01
	Hylaeus floridanus	17	10	0.05	0.25
	Hylaeus hyalinatus	12	8	0.04	0.11
	Hylaeus illinoisensis	4	3	0.02	0.06
	Hylaeus leptocephalus	31	19	0.10	0.13
	Hylaeus mesillae	5	4	0.02	0.05
	Hylaeus modestus	36	19	0.10	0.12
	Hylaeus pictipes	2	2	0.01	0.01
	Hylaeus punctatus	94	24	0.13	0.26
Halictidae	*Agapostemon sericeus*	215	40	0.22	0.19
	Agapostemon splendens †	1	0	NA	NA
	Agapostemon texanus †	1	0	NA	NA
	Agapostemon virescens	1366*	55	0.30	0.24
	Augochlora pura	4	3	0.02	0.09
	Augochlorella aurata	9	6	0.03	0.12
	Halictus confuses	21	9	0.05	0.09
	Halictus ligatus	48	15	0.08	0.08
	Halictus rubicundus	9	7	0.04	0.31
	Lasioglossum acuminatum †	2	0	NA	NA
	Lasioglossum admirandum	3	2	0.01	0.23
	Lasioglossum atwoodi	3	3	0.02	0.21

Bee family	Bee species	Abundance	Degree	ND	PSI
	Lasioglossum bruneri	3	1	0.01	0.01
	Lasioglossum cinctipes	8	2	0.01	0.03
	Lasioglossum coeruleum	3	2	0.01	0.04
	Lasioglossum comagenense †	1	0	NA	NA
	Lasioglossum coriaceum	11	3	0.02	0.12
	Lasioglossum cressonii	3	2	0.01	0.01
	Lasioglossum ephialtum	111	54	0.30	0.20
	Lasioglossum foxii	2	2	0.01	0.03
	Lasioglossum gotham	4	3	0.02	0.01
	Lasioglossum hitchensi	13	12	0.07	0.24
	Lasioglossum imitatum	88	34	0.19	0.17
	Lasioglossum laevissimum	30	19	0.10	0.11
	Lasioglossum leucocomus	4	1	0.01	0.02
	Lasioglossum leucozonium	5	5	0.03	0.06
	Lasioglossum lineatulum	17	10	0.05	0.15
	Lasioglossum lionotum ‡	1	1	0.01	NA
	Lasioglossum macoupinense	10	8	0.04	0.16
	Lasioglossum novascotiae	1	1	0.01	0.09
	Lasioglossum oblongum	6	5	0.03	0.09
	Lasioglossum obscurum	5	5	0.03	0.15
	Lasioglossum oenotherae	5	2	0.01	0.27
	Lasioglossum paradmirandum	37	23	0.13	0.15
	Lasioglossum pectoral	48	20	0.11	0.16
	Lasioglossum pilosum	44	23	0.13	0.14
	Lasioglossum planatum	22	13	0.07	0.11
	Lasioglossum quebecense	3	1	0.01	0.05
	Lasioglossum sagax	9	7	0.04	0.10
	Lasioglossum smilacinae	3	2	0.01	0.13
	Lasioglossum subversans	2	1	0.01	0.01
	Lasioglossum subviridatum	9	6	0.03	0.12
	Lasioglossum succinipenne	2	2	0.01	0.07
	Lasioglossum tegulare	22	9	0.05	0.21
	Lasioglossum tenax †	2	0	NA	NA
	Lasioglossum timothyi	1	1	0.01	0.03
	Lasioglossum versans	2	1	0.01	0.04
	Lasioglossum versatum	81	32	0.18	0.19
	Lasioglossum viridatum	1	1	0.01	0.13
	Lasioglossum zephyrus	22	12	0.07	0.05
	Lasioglossum zonulum	1	1	0.01	0.04
	Sphecodes clematidis †	2	0	NA	NA
	Sphecodes cressonii ‡	2	1	0.01	NA
	Sphecodes mandibularis †	1	0	NA	NA
Megachilidae	*Anthidium manicatum*	57	14	0.08	0.19
	Anthidium oblongatum	6	2	0.01	0.13
	Chelostoma campanularum	54	13	0.07	0.30
	Chelostoma philadelphi	15	3	0.02	0.57*
	Chelostoma rapunculi	46	7	0.04	0.17
	Coelioxys moestus †	1	0	NA	NA
	Coelioxys sayi ‡	5	3	0.02	NA
	Heriades carinatus	7	3	0.02	0.47

Bee family	Bee species	Abundance	Degree	ND	PSI
	Hoplitis anthocopoides	2	1	0.01	0.10
	Hoplitis pilosifrons	1	1	0.01	0.08
	Hoplitis producta	5	3	0.02	0.08
	Megachile brevis	1	1	0.01	0.06
	Megachile campanulae	8	5	0.03	0.07
	Megachile centuncularis	8	5	0.03	0.13
	Megachile frigida	9	6	0.03	0.18
	Megachile lippiae	6	5	0.03	0.05
	Megachile mendica	30	21	0.12	0.06
	Megachile relativa	2	2	0.01	0.04
	Megachile rotundata	79	32	0.18	0.14
	Megachile sculpturalis	2	1	0.01	0.03
	Megachile texana	34	15	0.08	0.11
	Osmia atriventris †	1	0	NA	NA
	Osmia caerulescens	8	5	0.03	0.09
	Osmia distincta †	1	0	NA	NA
	Osmia lignaria †	1	0	NA	NA
	Osmia pumila †	4	0	NA	NA

Table 9. Flower genera counts with associated species-level statistics for plants involved with bee-plant interactions occurring throughout the entire study region

Flower	Common name	Bee spp. associations	Bee abundance	Normalized degree (ND)
Adoxaceae				
Viburnum	Viburnum	1	1	0.01
Aizoaceae				
Carpobrotus	Ice plant	1	1	0.01
Lampranthus	Ice plant	1	1	0.01
Mesembryanthemum	Ice plant	2	2	0.01
Amaranthaceae				
Chenopodium	Goosefoot	1	1	0.01
Gomphrena	Globe amaranth	6	8	0.04
Amaryllidaceae				
Allium	Chive	32	69	0.19
Apiaceae				
Anethum	Dill	6	26	0.04
Coriandrum	Coriander	3	3	0.02
Daucus	Carrot	8	11	0.05
Pastinaca	Parsnip	3	5	0.02
Apocynaceae				
Apocynum	Dogbane	6	42	0.04
Asclepias	Milkweed	13	31	0.08
Asparagaceae				
Hosta	Hosta	14	46	0.08
Ornithogalum	Star-of-Bethlehem	1	1	0.01
Asphodelaceae				
Hemerocallis	Daylily	7	27	0.04
Asteraceae				
Achillea	Yarrow	7	12	0.04
Anaphalis	Pearly everlasting	7	10	0.04
Arctium	Burdock	11	23	0.07
Bechium	Ironweed	2	5	0.01
Bidens	Beggartick	1	3	0.01
Carduus	Plumeless thistle	2	2	0.01
Centaurea	Knapweed	8	13	0.05
Cichorium	Chicory	5	5	0.03
Cirsium	Plume thistle	12	28	0.07
Coreopsis	Tickseed	1	1	0.01
Cosmos	Cosmos	10	22	0.06
Echinacea	Coneflower	21	89	0.13
Echinops	Globe thistle	7	10	0.04
Erigeron	Fleabane	17	31	0.10
Eupatorium	Boneset	10	26	0.06
Eurybia	Wood aster	3	4	0.02
Eutrochium	Joe-pye weed	9	22	0.05

Flower	Common name	Bee spp. associations	Bee abundance	Normalized degree (ND)
Farfugium	Leopard plant	2	2	0.01
Gaillardia	Indian blanket	8	32	0.05
Galinsoga	Gallant soldier	3	3	0.02
Helianthus	Sunflower	15	47	0.09
Heliopsis	False sunflower	15	45	0.09
Hieracium	Hawkweed	4	5	0.02
Lactuca	Lettuce	1	1	0.01
Leucanthemum	Shasta daisy	3	4	0.02
Liatris	Blazing star	5	6	0.03
Matricaria	Mayweed	3	6	0.02
Ratibida	Prairie coneflower	9	24	0.05
Rudbeckia	Black-eyed susan	27	94	0.16
Silphium	Cup plant	13	87	0.08
Solidago	Goldenrod	39*	275*	0.24*
Sonchus	Sow thistle	11	16	0.07
Symphyotrichum	Aster	22	176	0.13
Tagetes	Marigold	11	21	0.07
Tanacetum	Tansy	4	4	0.02
Taraxacum	Dandelion	32	87	0.19
Tithonia	Mexican sunflower	6	12	0.04
Vernonia	Ironweed	11	25	0.07
Zizia	Golden alexander	1	1	0.01
Balsaminaceae				
Impatiens	Touch-me-not	7	22	0.04
Bignoniaceae				
Campsis	Trumpet vine	2	8	0.01
Boraginaceae				
Heliotropium	Heliotrope	16	99	0.10
Hydrophyllum	Waterleaf	3	4	0.02
Myosotis	Forget-me-not	2	2	0.01
Symphytum	Comfrey	1	1	0.01
Brassicaceae				
Alliaria	Garlic mustard	29	55	0.18
Brassica	Field mustard	10	17	0.06
Capsella	Shepherd’s purse	13	19	0.08
Cardamine	Bittercress	1	1	0.01
Diplotaxis	Diplotaxis	2	3	0.01
Erucastrum	Dogmustard	2	3	0.01
Hesperis	Dame’s rocket	1	1	0.01
Sinapis	Mustard	3	3	0.02
Thlaspi	Pennycress	2	2	0.01
Campanulaceae				
Campanula	Bell flower	19	51	0.12
Lobelia	Lobelia	3	3	0.02
Platycodon	Balloon flower	6	10	0.04
Caprifoliaceae				
Diervilla	Bush honeysuckle	2	2	0.01
Knautia	Knautia	8	22	0.05
Linnaea	Twin flower	1	1	0.01

Flower	Common name	Bee spp. associations	Bee abundance	Normalized degree (ND)
Lonicera	Honeysuckle	4	4	0.02
Weigela	Weigela	2	2	0.01
Caryophyllaceae				
Silene	Catchfly	1	1	0.01
Cercidoideae				
Cercis	Redbud	1	1	0.01
Convolvulaceae				
Convolvulus	Bindweed	15	27	0.09
Ipomoea	Morning glory	5	9	0.03
Cornaceae				
Cornus	Dogwood	24	52	0.15
Crassulaceae				
Hylotelephium	Orpine	12	22	0.07
Phedimus	Phedimus	3	5	0.02
Sedum	Stonecrop	5	5	0.03
Cucurbitaceae				
Cucumis	Cucumber	1	1	0.01
Ericaceae				
Berberis	Barberry	1	1	0.01
Rhododendron	Rhododendron	2	3	0.01
Vaccinium	Blueberry	1	1	0.01
Fabaceae				
Lotus	Trefoil	3	3	0.02
Medicago	Medick	2	6	0.01
Melilotus	Sweet clover	9	14	0.05
Phaseolus	Wild bean	1	1	0.01
Robinia	Locust	3	10	0.02
Trifolium	Clover	16	108	0.10
Vicia	Vetch	8	18	0.05
Geraniaceae				
Geranium	Geranium	9	26	0.05
Pelargonium	Geranium	1	1	0.01
Goodeniaceae				
Scaevola	Fan flower	4	10	0.02
Hydrangeaceae				
Deutzia	Deutzia	1	1	0.01
Hydrangea	Hydrangea	14	20	0.08
Philadelphus	Mock orange	8	20	0.05
Hypericaceae				
Hypericum	St. John’s wort	9	18	0.05
Iridaceae				
Iris	Iris	2	2	0.01
Lamiaceae				
Agastache	Giant hyssop	26	139	0.16
Ajuga	Bugleweed	1	1	0.01
Hyssopus	Hyssop	5	6	0.03
Lamium	Deadnettle	3	3	0.02
Lavandula	Lavender	7	22	0.04
Leonurus	Leonurus	5	11	0.03

Flower	Common name	Bee spp. associations	Bee abundance	Normalized degree (ND)
Melissa	Melissa	2	2	0.01
Mentha	Mint	2	2	0.01
Monarda	Beebalm	18	91	0.11
Nepeta	Catnip	5	10	0.03
Origanum	Oregano	10	18	0.06
Physostegia	Obedient plant	2	5	0.01
Pycnanthemum	Mountain mint	6	8	0.04
Salvia	Sage	25	122	0.15
Teucrium	Germander	2	2	0.01
Thymus	Thyme	1	1	0.01
Liliaceae				
Lilium	Lily	2	2	0.01
Tulipa	Tulip	3	3	0.02
Lythraceae				
Lythrum	Loosestrife	3	4	0.02
Malvaceae				
Alcea	Hollyhock	2	5	0.01
Hibiscus	Hibiscus	4	23	0.02
Malva	Mallow	4	5	0.02
Oleaceae				
Ligustrum	Privet	3	7	0.02
Syringa	Lilac	15	20	0.09
Onagraceae				
Chamaenerion	Fireweed	2	3	0.01
Circaea	Circaea	6	6	0.04
Oenothera	Evening-primrose	5	5	0.03
Orobanchaceae				
Euphrasia	Eyebright	1	1	0.01
Oxalidaceae				
Oxalis	Wood sorrel	7	8	0.04
Papaveraceae				
Chelidonium	Celandine	2	2	0.01
Corydalis	Corydalis	2	2	0.01
Lamprocapnos	Bleeding-heart	1	1	0.01
Phytolaccaceae				
Phytolacca	Pokeweed	1	1	0.01
Plantaginaceae				
Angelonia	Angelonia	1	1	0.01
Antirrhinum	Snapdragon	4	4	0.02
Bacopa	Waterhyssop	4	5	0.02
Chelone	Chelone	1	1	0.01
Penstemon	Beardtongue	4	8	0.02
Plantago	Plantain	1	1	0.01
Veronicastrum	Culver’s root	17	37	0.10
Polemoniaceae				
Phlox	Phlox	3	3	0.02
Polygonaceae				
Fallopia	Buckwheat	5	27	0.03
Persicaria	Knotweed	7	10	0.04

Flower	Common name	Bee spp. associations	Bee abundance	Normalized degree (ND)
Polygonum	Knotweed	2	2	0.01
Primulaceae				
Primula	Primrose	1	1	0.01
Ranunculaceae				
Anemone	Anemone	4	4	0.02
Aquilegia	Columbine	11	15	0.07
Clematis	Leather flower	2	8	0.01
Eriocapitella	Eriocapitella	6	15	0.04
Ranunculus	Ranunculus	6	9	0.04
Rhamnaceae				
Ceanothus	Jersey tea	1	1	0.01
Rosaceae				
Argentina	Argentina	2	4	0.01
Aronia	Chokeberry	1	3	0.01
Chaenomeles	Flowering quence	5	12	0.03
Cotoneaster	Cotoneaster	2	2	0.01
Dasiphora	Cinquefoil	13	16	0.08
Fragaria	Strawberry	6	8	0.04
Geum	Avens	8	10	0.05
Malus	Apple	9	22	0.05
Physocarpus	Ninebark	9	31	0.05
Potentilla	Cinquefoil	5	5	0.03
Prunus	Cherry	3	3	0.02
Rosa	Rose	13	26	0.08
Rubus	Brambles	6	7	0.04
Sibbaldiopsis	Three-leaved cinquefoil	5	5	0.03
Spiraea	Spiraea	6	8	0.04
Rubiaceae				
Galium	Bedstraw	2	3	0.01
Sapindaceae				
Aesculus	Horse chestnut	3	4	0.02
Saxifragaceae				
Heuchera	Coral bell	4	4	0.02
Scrophulariaceae				
Buddleja	Butterfly bush	4	5	0.02
Verbascum	Mullein	1	1	0.01
Solanaceae				
Nicotiana	Tobacco	1	1	0.01
Solanum	Nightshade	7	13	0.04
Talinaceae				
Talinum	Fameflower	1	1	0.01
Tropaeolaceae				
Tropaeolum	Nasturtium	4	4	0.02
Verbenaceae				
Verbena	Vervain	21	91	0.13
Violaceae				
Viola	Violet	8	10	0.05

General Discussion

Successful conservation initiatives are reliant upon an in-depth understanding of the communities they are attempting to protect. Although urban pollinator research has expanded greatly within the last couple of decades and has even made significant strides towards the better understanding of pollinator response to urban change, urban research still lags behind work conducted in agricultural landscapes. Additionally, much of this research is especially lacking outside of Europe, Brazil, and North America (Wenzel et al. 2020). As a result, multiple knowledge gaps remain that may limit the efficacy of current conservation measures. This is especially pertinent considering habitat loss, predominantly resulting from both urbanization and agriculturalization, is one of the largest contributors to species declines (Goulson et al. 2015; Cariveau and Winfree 2015). What's more, bee response to urbanization may be regionally specific, often as a by-product of cities being idiosyncratic in their compositions of both local and landscape features (Ayers and Rehan 2021). Therefore, conservation strategies may vary across different urban regions. The first chapter of this thesis synthesized current knowledge of bee response to urbanization while emphasizing areas where future research should be directed. The second chapter uses the city of Toronto as a case study to empirically investigate bee community and plant interaction response along a gradient of urbanization. By illuminating the influence urban landscapes exert on local bee communities, enhancements to city spaces may be made to foster an integration between humans and biologically diverse plant and animal communities.

The first chapter of this thesis addressed bee response to urbanization and investigated the drivers contributing to bee community response in urban landscapes. Bee response appears to be ultimately dependent on the composition of the heterogenous landscapes they are present within (Sattler et al. 2010; Tommasi et al. 2004). Cities possess a series of local and landscape features that interact with one another to create complex and unique urban environments (Beninde et al. 2015; Quistburg et al. 2016; Egerer et al. 2017; Ballare et al. 2019). As a result, the effects of urbanization on bees are not entirely generalizable (Cariveau and Winfree 2015; Buchholz and Egerer 2020). Urban areas are extensively covered in impervious surfaces such as buildings, roads, and sidewalks which ultimately restricts ground cover that can be used either for nesting or supporting floral communities. Consequentially, many studies report a homogenization of bee communities in which some functional traits are more dominant than others as a result of resource availability determined by the urban matrix (Deguines et al. 2016; Knop 2016). Multiple studies have noted, for example, a prevalence of polylectic or generalist foraging, cavity nesting, and social species which may be more resilient to urbanization than other functional traits that possess stricter resource requirements (Cane et al. 2006; Matteson et al. 2008; Banaszak-Cibicka and Zmihorski 2012; Geslin et al. 2016; Cardoso and Gonclaves 2018). Unfortunately, other functional traits such as body size and behaviour (ie degree of sociality) have yielded inconsistent results (Martins et al. 2017; Banaszak-Cibicka et al. 2018) and therefore require additional study.

Green space quality may vary greatly from one green space to the next and understanding which of these spaces are best supporting bees and other pollinators is essential considering they represent some of the most important urban habitats for bees (Tonietto et al. 2011; Baldock et al. 2019; Dylewski et al. 2019). Multiple factors such as management intensity (Aronson et al. 2017; Lerman et al. 2018), floral patch size and quality (Werrell et al. 2009; Matteson and Langellotto 2010; Martins et al. 2017), and green space size (Beninde et al. 2015) may influence pollinator assemblages; however, understanding how such characteristics are affecting bees is an ongoing research topic. For instance, it is unclear what size is necessary to sufficiently support pollinating species and this answer may vary depending on the species present within a particular region. Furthermore, as urban landscapes possess a disproportionate amount of nonnative plant species, research is still needed to understand their full effect on the environment and on native bee species. Investigating these topics and continuing urban ecological studies are necessary if cities are to establish landscapes that sufficiently support healthy pollinator communities.

To determine how urbanization may be influencing bee communities and their plant interactions, the second chapter of this study monitored twenty-nine sites categorized into three urban categories (low, medium, high). Unexpectedly, urbanization did not exert a significant influence on bee abundance or richness (Wilson and Jamieson 2019); however, urban characteristics such as the percent impervious surface and tree cover may still influence overall bee community composition. This is likely a result of how such variables limit nesting and floral resource availability within city spaces (Matteson et al. 2010; Burdine et al. 2019). Additionally, plant richness appeared to significantly affect bee richness and abundance across the entire study region. While some studies have reported contrasting results, this could indicate the importance of enhancing urban spaces with a variety of plant species in some cities like Toronto (Plascencia and Philpott 2017; Choate et al. 2018; Stewart et al. 2018). Bees within the Halictidae and Apidae families as well as bees that were polylectic, ground nesting, native, solitary and eusocial were pervasive throughout the study region. Depending on the functional trait, this result either complimented or contradicted prior research conducted in other cities which could indicate that Toronto has its own distinctive influence on bees (Banaszak-Cibicka and Żmihorski 2012; Geslin et al. 2013; Wenzel et al. 2020).

Plant-pollinator networks generally remained consistent across the urban gradient regarding connectance, weighted nestedness, robustness, and interaction evenness. This could potentially suggest urbanization, in the case for Toronto, may either negatively affect aspects of plant-pollinator networks like connectance broadly or not have a strong impact on plant-pollinator interactions generally. Regardless, re-examining such networks at broader or narrower spatial scales may provide additional insight as the current scale may not have been able to detect such changes (Egerer et al 2017). Plant-pollinator interactions also highlighted major players within the urban landscape. This study generally found *Apis mellifera* and *Agapostemon virescens* to be among the most abundant species and therefore it was unsurprising that such species played a significant role in plant-pollinator networks. Likewise, plant genera such as *Solidago* were widely visited by various hosts including both specialists and generalists alike. This potentially underlines the practicality of using such networks in the context of accessing plant quality for pollinators.

The observed impact of Toronto's landscape features on its bee communities could be the result of multiple factors. Toronto itself is an interesting case study in that it possesses several characteristics which could make it favourable to bees and other pollinators. For instance, Toronto has restricted the use of pesticides on public and private property since 2003 through the introduction of by-law No. 456-2003 (City of Toronto 2003). Within the following four years of introducing the legislature, the number of residents reporting the application of pesticides on private property fell by 57% and has since continued to drop (McKeown 2009). Additionally, non-profit organizations such as Project Swallowtail and grants provided by the City of Toronto have been established with the aim of specifically promoting pollinator diversity through the planting of native plants (City of Toronto 2022b). Aside from providing foraging and nesting resources for bees, the development of these plantings may also enhance habitat connectivity which can facilitate the mobility of species between green spaces (Braaker et al. 2014).

The reduced exposure of pesticides and creation of flowering patches throughout the city may enhance the quality of habitats for Toronto's bees (Goulson et al. 2015). This represents an essential first step in promoting bee diversity within the city. The results from this study provides additional insight into the varying effects of urbanization on bees and their plant interactions. Additionally, the use of plant-pollinator interactions may have practical regional implications by providing information that can be used to enhance the quality of local city green spaces in particular by indicating which floral genera or species could be included in pollinator plantings. By continuing to engage in urban ecological studies and therefore continuing to expand the existing understanding of urbanization's impact on wildlife, appropriate conservation initiatives can be developed for organisms such as bees that can most effectively promote healthy community compositions in human dominated landscapes.

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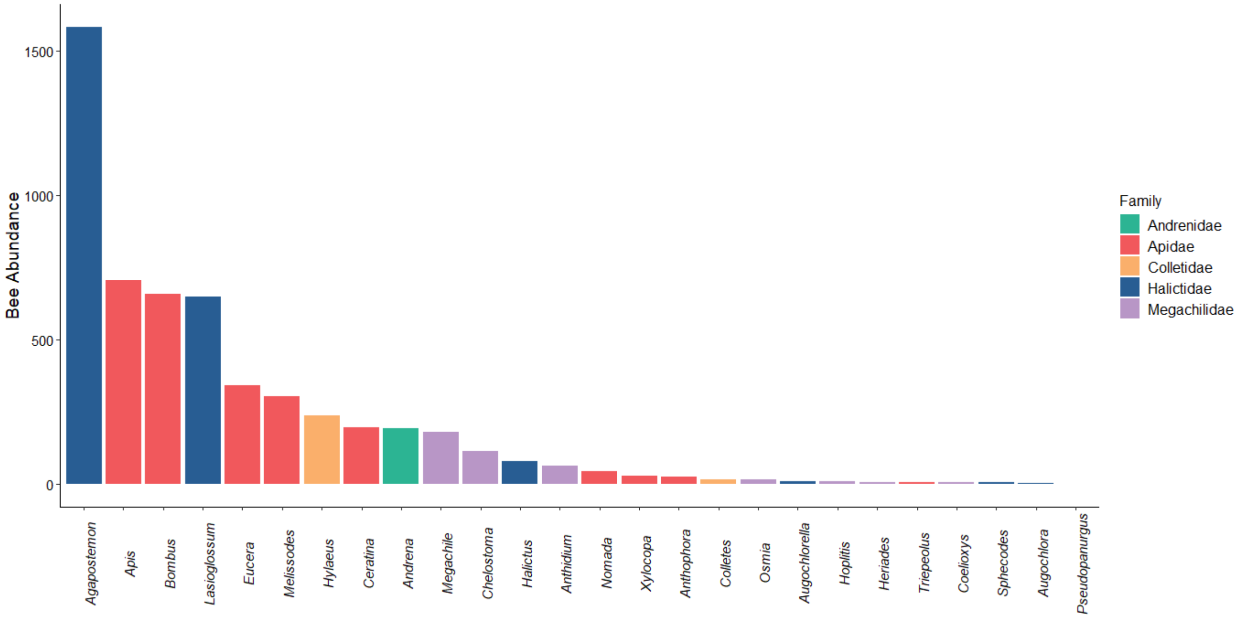
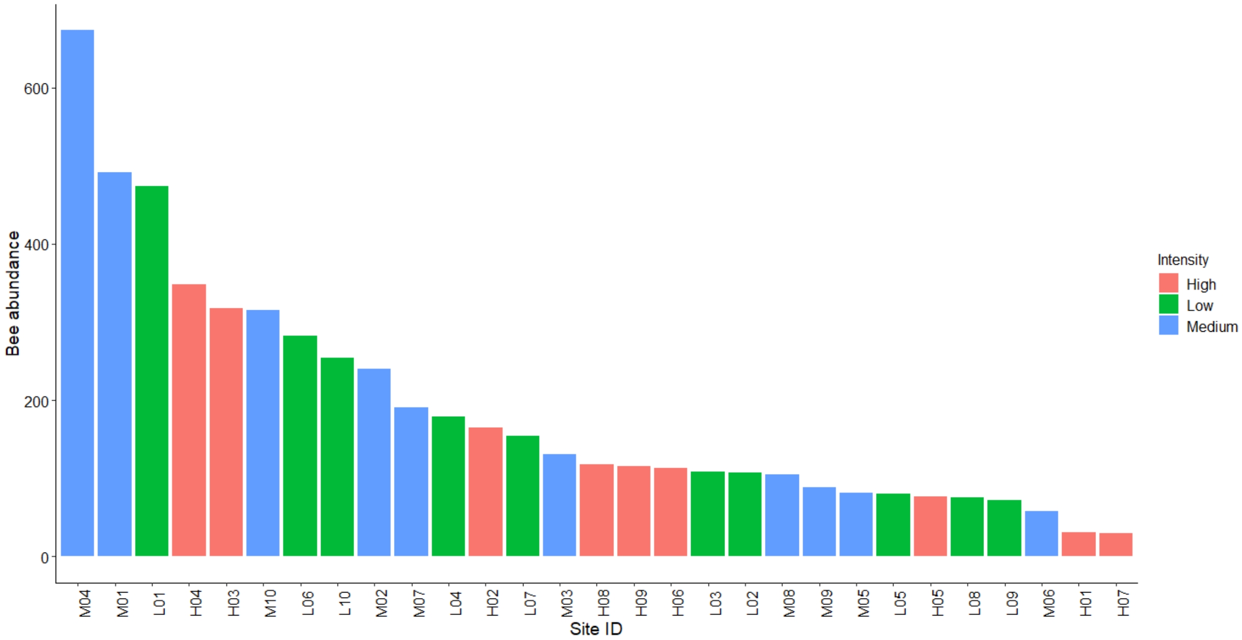
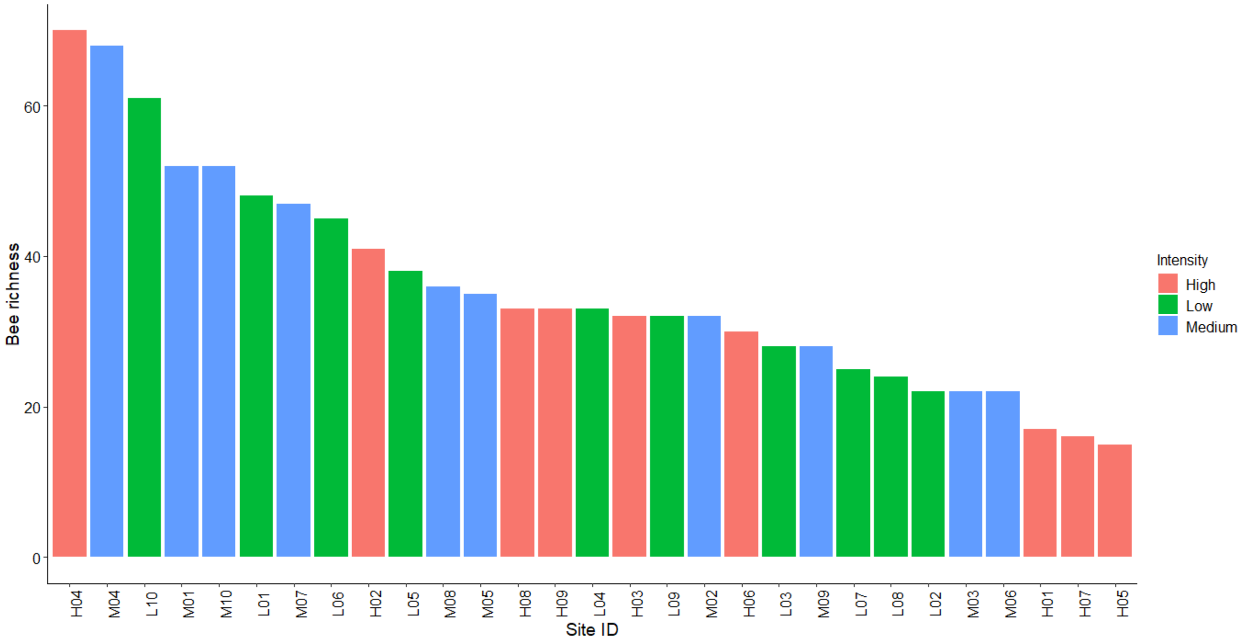
Appendix A: Chapter II Supplementary Material



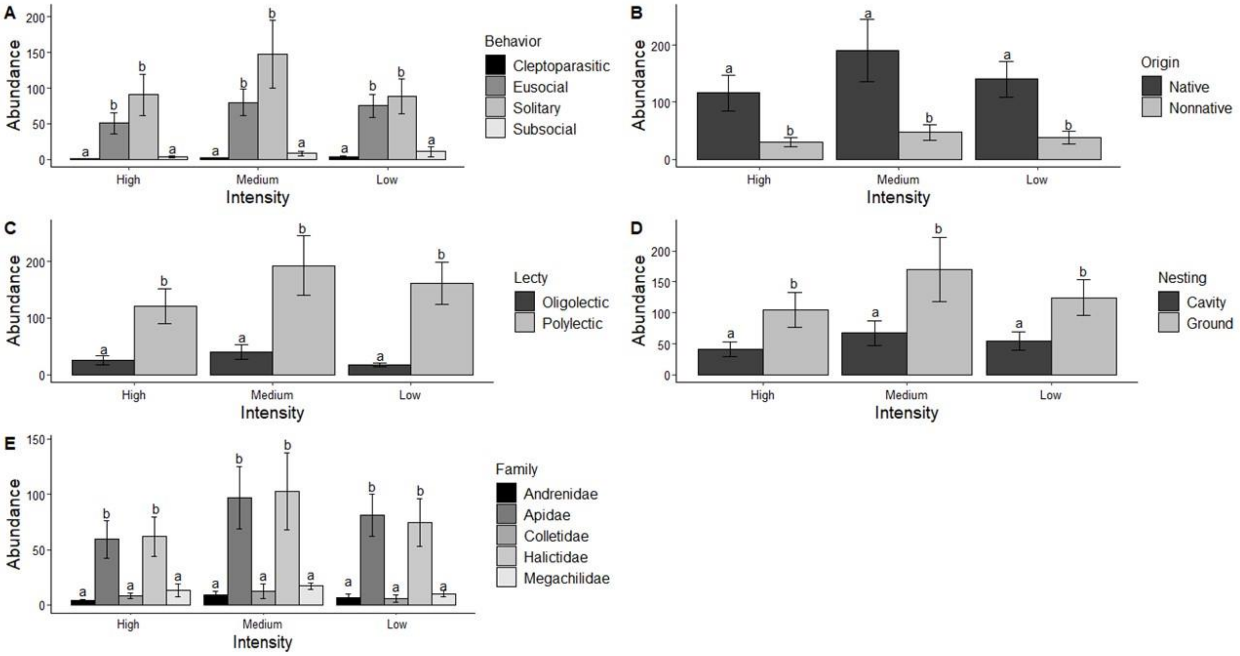
Supplemental Figure 1. Total abundance of all bee genera collected across all the entire study region.



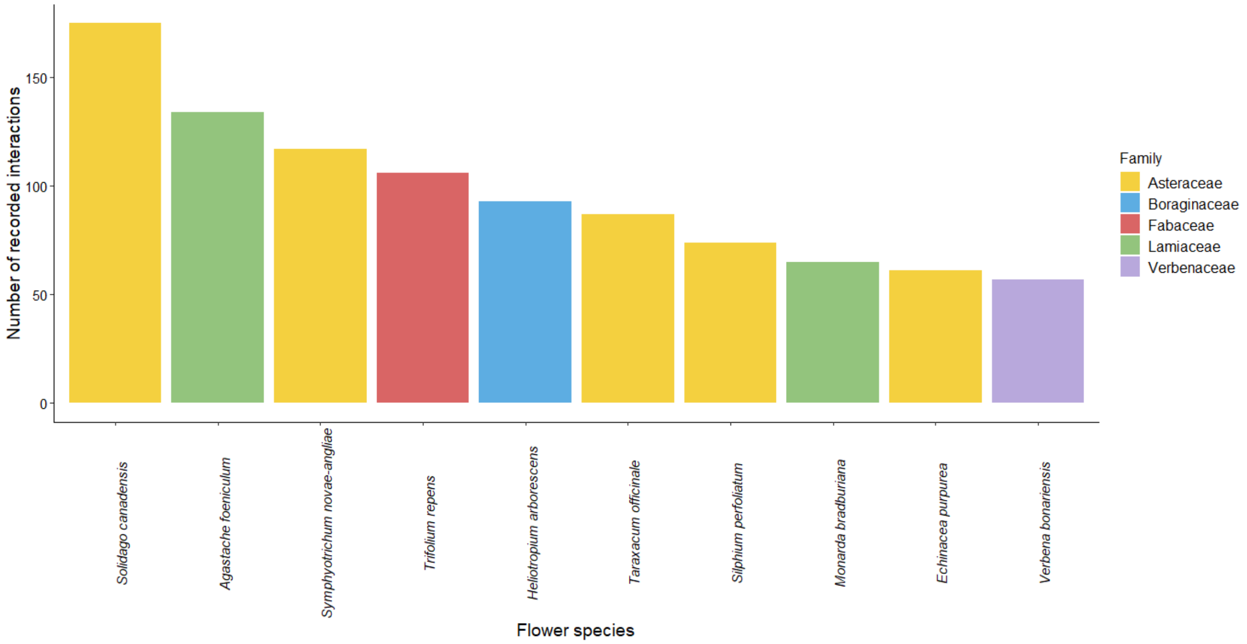
Supplemental Figure 2. Total abundance of bees recorded at each study site. Intensity refers to urban intensity category of sites.



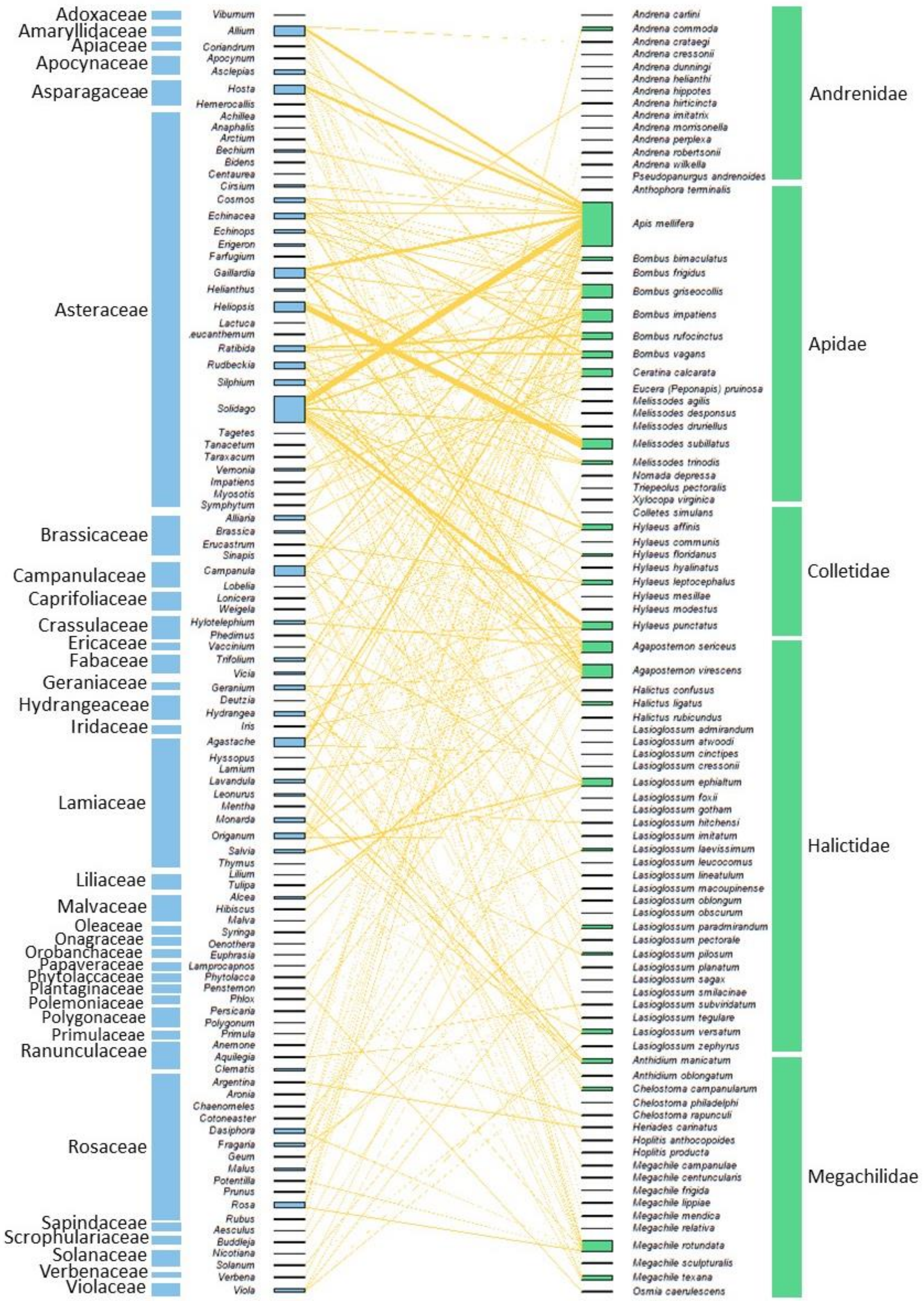
Supplemental Figure 3. Number of bee species recorded at each study site. Intensity refers to urban intensity category of sites.



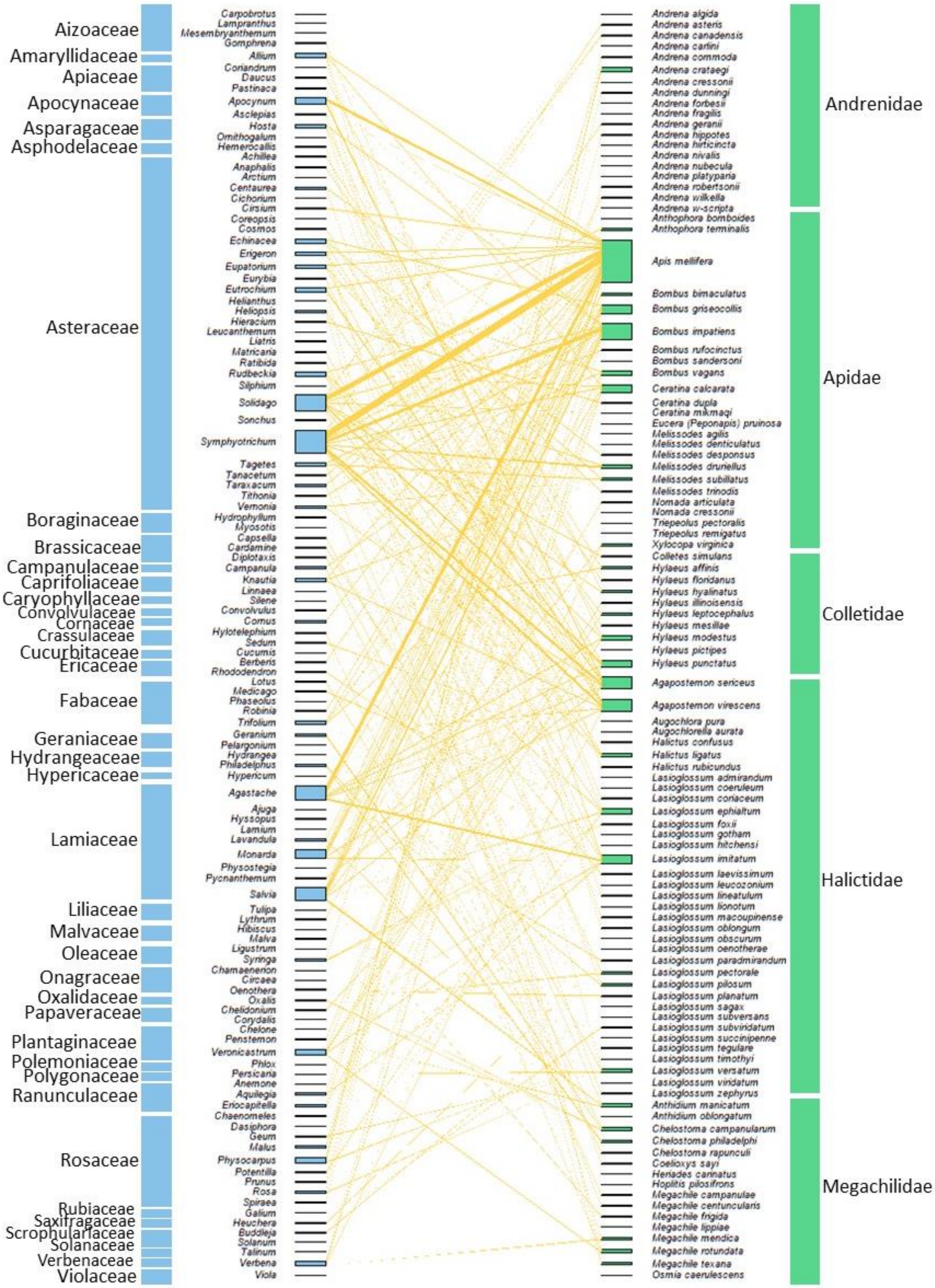
Supplemental Figure 4. Average abundance (± SE) of bee functional trait groups at each urbanization category. a - Nesting, b - Behavior, c - Family, d – Origin, e – Lecty.



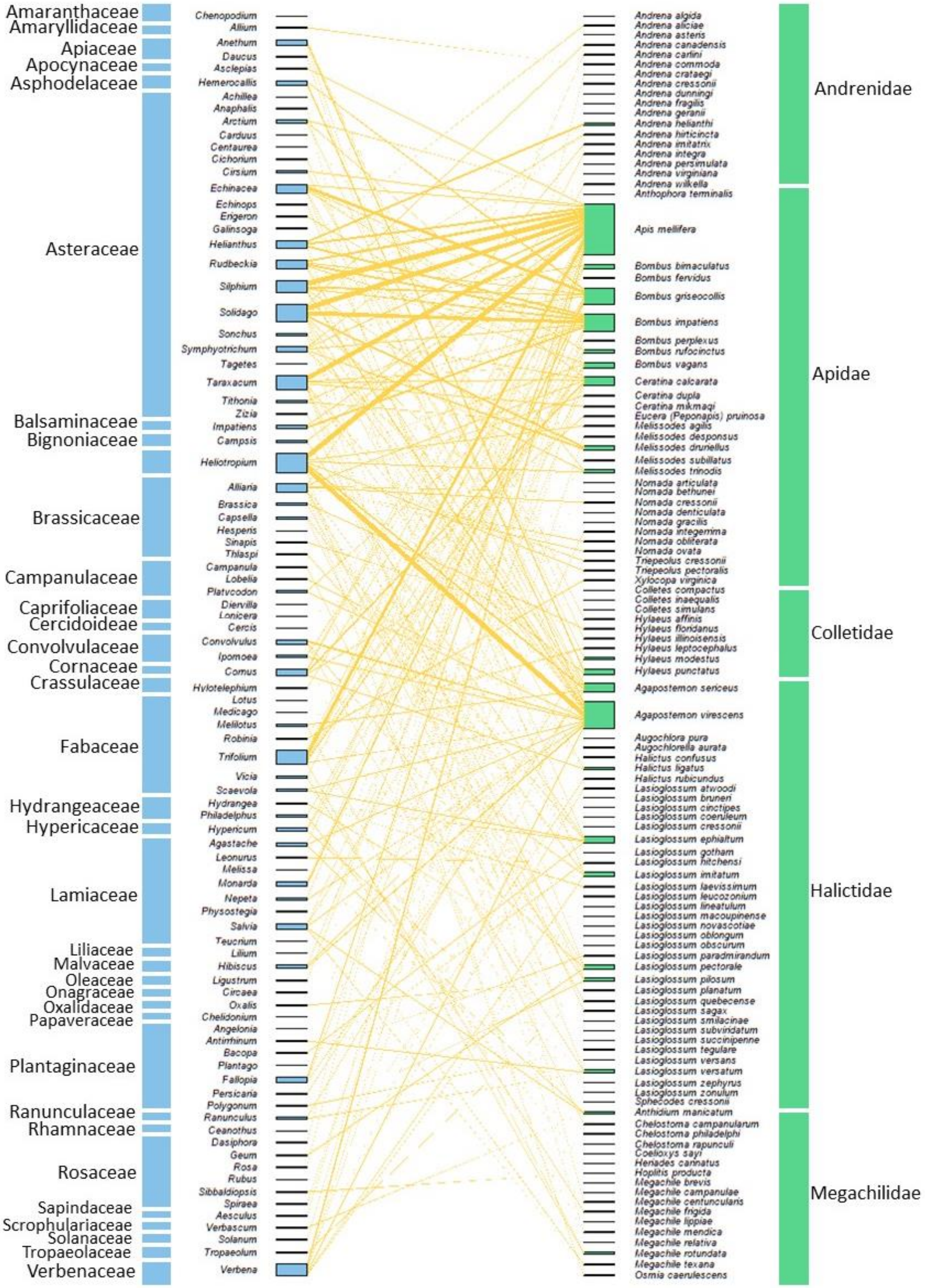
Supplemental Figure 5. Top ten most visited flower species across all sites.



Supplemental Figure 6. Plant-pollinator network at high intensity urbanization.



Supplemental Figure 7. Plant-pollinator network at medium intensity urbanization.



Supplemental Figure 8. Plant-pollinator network at low intensity urbanization.