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Functional traits of wild bees in response to urbanization

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Abstract

Wild bees are vital for maintaining biodiversity and food security. However, bees are currently threatened by the conversion of their natural habitat into urban areas, among many other factors. Here, we examine how five wild bee species respond to increasing urbanization according to their functional traits across the most populous city in Canada, which is also the fourth largest in North America. We investigate the effect of urbanization on bee demography and morphology as measured by abundance, sex ratio, body size, and foraging efforts. We found more bees in medium-urbanized sites and larger bees in medium and high-urbanized sites for two species (*Eucera pruinosa* and *Ceratina calcarata)*. We found higher wing wear in low and medium-urbanization sites. Our data suggests that urbanization potentially affects these wild bee species' abundance, body size, and foraging efficiency. We further discuss these findings according to the ecology of urbanization and the biology of each species.

Implications for insect conservation Human activity can significantly alter natural habitats, causing adverse effects on wild bees and ultimately affecting their survival. Considering the crucial role bees play in pollinating numerous crop and wild plant species, which, in turn, sustains biodiversity and food security, it is crucial to assess their response to the increasing levels of urbanization.

Keywords Abundance · Body size · Foraging · Fourth-corner analysis · Bumble bees · Sweat bees

Introduction

Wild bees play a crucial role in pollinating crops and wild plants, making them essential for conserving biodiversity and maintaining food security (Potts et al. 2010, 2016). Notwithstanding, wild bees are currently threatened due to various factors, including converting their natural habitat into agricultural and urban areas (McKinney 2002; Cameron et al. 2011; Potts et al. 2016). Urbanization is one of the most significant drivers of global environmental change, having profound effects on biodiversity and ecosystem functioning and potentially reducing available food and nesting sites for bees as a result of habitat loss (McKinney 2002; McDonnell and Hahs 2008; Seto et al. 2012; Normandin et al. 2017). Thus, understanding how bees respond to urban environments is crucial for managing urban landscapes and conserving bee populations.

Increasing urbanization can alter floral resources for pollinators in many ways. For example, native plants may be replaced by non-native or ornamental species that are better suited to urban conditions, impacting on the availability of nectar and pollen (Morales and Traveset 2009; Threlfall et al. 2015). Fragmentation caused by buildings, roads, and other infrastructure can disrupt the natural flow of pollinators and make it harder for them to find floral resource (Stenhouse 2004; Hadley and Betts 2011; but see Warzecha et al. 2016), and some urban areas may feature large monocultures of a single plant species, such as lawns, limiting the diversity of floral resources available to bees (Lanner et al. 2020). All these processes expose wild bees to new stressors and changes in resources they rely on, often translating into decrease in abundance, significant population decline or local extinction (Cameron et al. 2011; Goulson et al. 2015; Potts et al. 2016).

Functional traits are key characteristics that determine how organisms interact with their environment, can explain the coexistence of species, help identify how different

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species respond to habitat change, and how organisms obtain and use resources in their environment (Cadotte et al. 2011; Wilson and Jamieson 2019; Buchholz and Egerer 2020). Depending on their functional traits (e.g., body size, diet breadth, sociality, nesting behavior, and flight season), a species might respond differentially to increasing urbanization (Wilson and Jamieson 2019; Buchholz and Egerer 2020; Theodorou et al. 2020; Fortuin and Ghandi 2021). Urban areas may affect intraspecific variation in body size, favoring larger-bodied bees in contrast to smaller bees given their usual larger foraging ranges, often translating into the ability to better navigate between flowering patches (Greenleaf et al. 2007; Gunnarsson and Federsel 2014; Ferrari and Polidori 2022, but see Castilla et al. 2017; and Hofmann et al. 2020 for small solitary bees). Body size has also been correlated to the amount of pollen a bee can carry, with smaller bees often able to adhere and carry less pollen and nectar (Cullen et al. 2021), probably impacting the provisioning of brood cells and the survival of offspring. Food provisioning under higher urbanization has also explained a shift towards a male-biased sex ratio in bees, given that under depletion of food resources, the male sex seems to present higher fitness (Tepedino 1982; Kim 1999).

Nesting opportunities can also be more limited in highly urbanized sites, given the higher amount of impervious surface that reduces available nesting, especially for ground-nester bees, highly reliant on bare ground (Cane 2006; Geslin et al. 2016). Additionally, the urban environment can significantly impact the foraging effort of bees, which refers to the amount of time and energy that a bee spends searching for food (Cartar 1992). As cities expand, the increment of concrete creates fragmented patches of available food resources for bees, often forcing them to increase efforts in foraging. A potential consequence of higher foraging efforts in bees is increasing wing wear, given that bees that forage more often and for longer periods are likely to experience greater wing wear (Cartar 1992). Adverse consequences of wing wear include changes in flight speed and performance, changes in foraging behavior, and increasing risk of mortality (Cartar 1992; Haas and Cartar 2008; Foster and Cartar 2011). Additionally, local landscape changes have overly affected solitary bees instead of social bees at small scales (Steffan-Dewenter et al. 2002). This is also partially explained by the difference in foraging efficiency between social and solitary bees, where the latter is reported to be less efficient (Ratnieks 2000; Zurbuchen et al. 2010).

Urban green spaces (e.g., parks and community gardens) often support generalist (polylectic) pollinators compared to specialist (oligolectic) as floral species are primarily dominated by exotic and ornamental plants, mostly generalists' preference (Thompson et al. 2003; Frankie et al. 2009; Threlfall et al. 2015). In fact, the majority of the studies have revealed a pattern of reducing the diversity of oligolectic bees in cities (Cane et al. 2006; Banaszak-Cibicka and Zmihorski 2012; Twerd and Banaszak-Cibicka 2019; but see Banaszak-Cibicka et al. 2018; Hamblin et al. 2018). Urban gardens and green spaces are often well-maintained and may include non-native or ornamental plants that bloom later in the season (Thompson et al. 2003; Frankie et al. 2009; Threlfall et al. 2015). This can provide a continuous food source for bees when natural wildflowers have finished blooming. Besides, phenology mismatches between flowering plants and bees are likely to occur in a warmer climate scenario, disproportionally harming bees limited by one reproducing cycle within one season of the year (i.e., univoltine species). Across Canada, plants have experienced flowering changes as a result of warming temperatures, with the first bloom of temperate and boreal plants occurring early in the season (Gonsamo et al. 2013). Hence, bivoltine species (i.e., two reproducible cycles per year) might experience a wider assortment of flowering options as a result of their season window length.

Here, we examine how five bee species representing five functional traits (body size, diet, nesting, social behavior, and voltinism) respond to increasing urbanization in the most populous city in Canada. Toronto is located in southern Ontario and has a population estimate of 2.7 million inhabitants, being currently among the fourth largest cities in North America (Statistics Canada 2021). The population density of Toronto is 4427 inhabitants per km^2, with a prediction of continued increasing density in coming decades (Vaz and Arsanjani 2015; Statistics Canada 2021). Nevertheless, Toronto holds a large park system, including more than 1,600 parks throughout the city and other green spaces such as golf courses and sports fields, greenways, and community allotment gardens, reaching up to 8,000 hectares and representing 13.6% of the total land area of the city (City of Toronto 2017, 2019). These contrasting features position the city as opportune to understand distinctive levels of urbanization affecting different bee species. This study has the following aims: (1) to investigate if different levels of urbanization (low, medium, and high) affect wild bee demography as measured by abundance and sex ratio; and (2) to examine the impact of urbanization on bee foraging effort and on bee morphology measured as body size; and (3) to investigate if the relationship between urbanization and functional traits in bees, and how functional traits are related to one another. We predict that highly urbanized sites will host lower bee abundance and a male-biased sex ratios, as well as larger bees with greater wing wear and that urbanization is filtering bees according to their functional trait.

Methods

Sampling and mapping

Sampling was conducted in Toronto, Canada, from May to October 2021 (Fig. 1). Sample sites were spaced throughout the city, covering twenty-two km^2 and three levels of urbanization: low, medium, and high. The sites were classified based on the percentage of impervious surface using the Ontario Land Cover Compilation v.2.0 (OLCC, Land Information Ontario 2019) in ArcMap v.10.7.1. From this compilation, we also calculated the percentage of shrubs, grass, and trees, although only the percentage of impervious surface was used to determine the levels of urbanization. Low urbanized sites (n=10) presented less than 25% of impervious surfaces, medium urbanized sites (n=10) had between 25% and 75% of the impervious surfaces, and high urbanized sites (n=9) had more than 75% of impervious surfaces (Birdshire et al. 2020; Ayers and Rehan 2023). Additionally, for each sampling point, we also recorded and identified every flowering plant species from which bees were collected using Newcomb's Wildflower Guide (Newcomb 2011) (Table S1). All sites were located at least 250 m apart to meet the maximum foraging distance for the majority of bees (Greenleaf 2007). In each site, we sampled bees using three approaches: pan traps (New Horizons Support Services Inc.; water with blue Dawn™ dish detergent), blue vane traps (BanfieldBio™), and sweep netting (Bioquip™).

Study species

Based on all twenty-nine sampling points, we ranked the most abundant species with a minimum abundance of 150 individuals. Five species satisfied these criteria. *Agapostemon sericeus* Foster (Halictidae), the silky-striped sweat bee, is a small (average body length, x̄ = 9 mm) solitary ground-nester bee, with a single adult bee per nest and a bivoltine phenology, where two generations are produced by year. This species is widespread across North America (Roberts 1969; Eickwort 1981; Janjic and Packer 2003). *Bombus griseocollis* DeGeer (Apidae), the brown-belted bumble bee, is a large social bee (x̄ = 15 mm), bivoltine, widespread across North America (Williams et al. 2014). This species nests below ground in abandoned rodent nests or on the surface in tufts of grass, old bird nests, rock piles, or cavities in dead trees (Hatfield et al. 2015), and has no dietary specialization, although it may preferably collect pollen from milkweed, thistle, sunflower, and sumac (Williams et al. 2014). *Bombus impatiens* Cresson (Apidae), the common eastern bumble bee, is widespread across North America (Hurd 1979; Williams et al. 2014). This large species (x̄ = 14 mm) also has social colony behavior, is bivoltine with two generations per year, and is polylectic with no dietary specialization (Williams et al. 2014). Both *Bombus* species present eusocial castes (queen, worker, and males) with body size differentiation. Only males and workers were collected and included in this study. *Ceratina calcarata* Robertson (Apidae) is a small (x̄ = 7 mm) carpenter bee widely distributed across eastern North America (Shell and Rehan 2018). This species has a subsocial behavior with
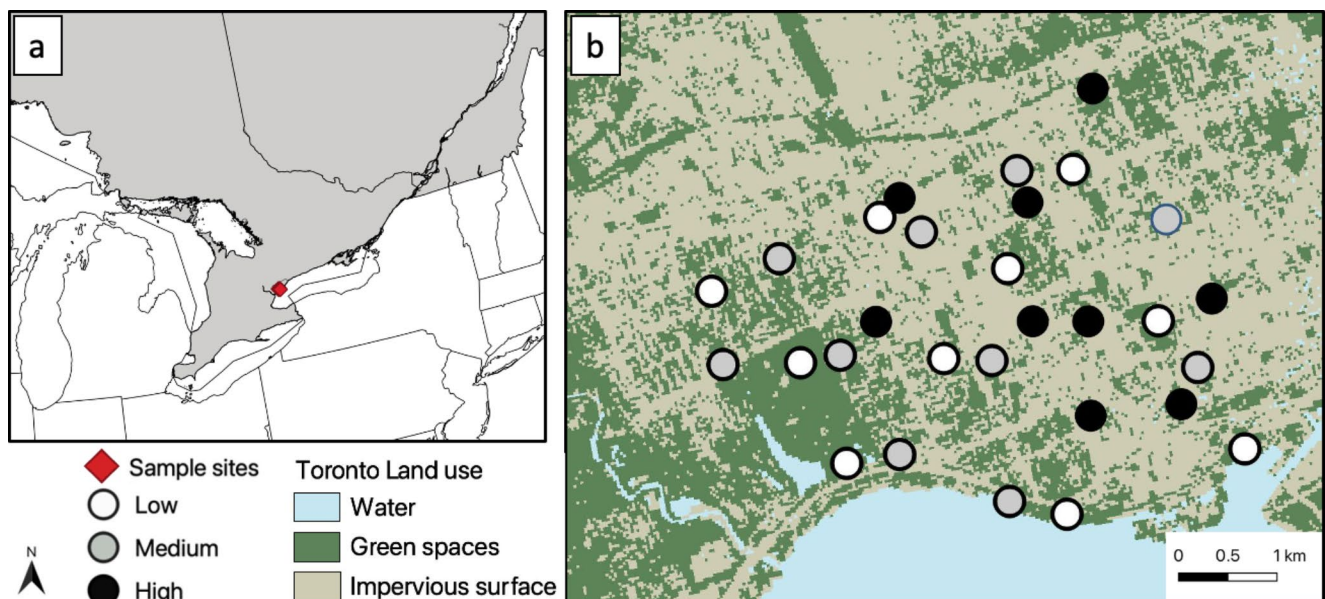
Fig. 1 Map of sampling points. (A) Location of sampling points in Toronto, Canada. (B) Distribution of the 29 selected points according to the percentage of impervious surface

prolonged parental care and mother-offspring interaction (Rehan 2020). Is a generalist pollinator collecting pollen from diverse floral species, is univoltine, and nests aboveground, preferably in the cavities of broken stems of raspberry (*Rubus sp.*) and sumac (*Rhus sp.*) (Lawson et al. 2016; Shell and Rehan 2018). *Eucera pruinosa* Say (formerly *Peponapis pruinosa*) is widely distributed from the Atlantic coast to southwestern North America. This species is a large ($\bar{x} = 13$ mm) solitary, ground-nesting bee that is oligolectic and collects pollen only from cultivated species of squash and pumpkin (Hurd et al. 1974). These five species present a variety of functional traits, differing in size, sociality, diet specialization, nesting biology, social behavior, and seasonality. Summarized information about functional traits for each species is available in Table S3.

Bee functional traits

We selected six functional traits widely known for their relation to bees' response to increasing urbanization and for their important role in bee ecology and adaptation (Michener 2000; Moretti et al. 2009; Ayers and Rehan 2021): (1) body size (small or large), (2) diet (oligolectic or polylectic), (3) nesting biology (cavity or ground), (4) social behavior (solitary or eusocial), (5) voltinism (univoltine and bivoltine), and (6) wing wear (a proxy for foraging effort). We also recorded the sex for each bee. Body size was measured according to the distance between each tegulae in millimeters (intertegular distance, ITD, Cane 1987) using a stereo microscope (Nikon SMZ1270). We grouped the entire data to categorize the body size clines and ranked the percentiles. Small bees were classified according to the 1st and 50th percentile values. The species comprising this small size interval were *Ceratina calcarata* and *Agapostemon sericeus*. The large species comprising ITD values between the 51st and 100th percentile were *Eucera pruinosa*, *Bombus griseocollis*, and *Bombus impatiens*. Traits for diet, nesting, social behavior, and voltinism were assigned for each bee species based on primary literature on their natural history (Hurd et al. 1974; Hurd 1979; Abrams and Eickwort 1980; Rehan and Richards 2010; Williams et al. 2014). Wing wear was measured by classifying the damages on wing margins on a scale from zero to five, where zero represents no damage, and five denotes the wing outer margin is entirely worn (Mueller and Wolf-Mueller 1993).

Statistics

To investigate aim 1, we tested if the ratio for each urbanization level in each species significantly varied from the observed and expected proportions (1:1) using Chi-square tests, and tested any differences in the abundance according to urbanisation levels using a two-sample t-test. To test the effect of urbanization on bee body size and foraging effort (aim 2), we used ANOVA in R (v 4.2.1). Results with a significant p-value were further analyzed by a Tukey *posthoc* test. We used the fourth-corner method to test the association of urbanization and functional traits across all species (aim 3) (Legendre et al. 1997; Dray and Legendre 2008). The methods' approach is to fit a predictive model (GLM-based) to associate the species' functional traits to environmental variables according to their relative abundance (Brown et al. 2014). For this, we created three matrices: a matrix with the percentage of impervious surface as a three-level factor, plant species richness, and the percentage of shrub, grass, and tree for each sampling point (R); a matrix with functional traits for each species (Q), and a matrix with species count for each site (L) (Tables S2–S4). Finally, fourth-corner analysis was conducted using a general linear model (GLM, negative binomial family) as a function of traits and environmental variables in the R package *mvabund* (Wang et al. 2012). As a result, the test provides coefficient scores that quantify the significance and strength of negative or positive interactions between functional traits and environmental variables, where the strength of the association is related to the likelihood of that trait existing in that environmental condition. We tested model fit using the ANOVA function (Wald, n = 1000 bootstraps), giving a deviance table with likelihoods and p-values for every relationship. Given that many traits and environment variables did not show a strong relationship (see Table S8), we reduced the number of predictors by adding a LASSO penalty to our variables using the method *glm1path* in R package *mvabund*. LASSO (Least Absolute Shrinkage and Selection Operator) is a machine learning tool that optimizes the model's accuracy by automatically reducing non-significant interactions to zero (Hastie et al. 2009). Results were plotted as heatmaps using the R package *lattice* (Sarkar et al. 2015). We also used a two-sample t-test with unequal variance to test if body size and wing wear were affected by any functional traits. For bivoltine species, we also tested if abundance, body size, and wing wear differentiated between seasons by performing a two-sample t-test and used a one-sample t-test to check for increasing or decreasing patterns within each season. All analyses were performed in R 4.0.2 (R Core Team 2020).

Results

Abundance, sex ratio, and urbanization

We collected 1185 individuals belonging to five species. *Eucera pruinosa* was the most abundant species (n = 342,

29% of the total specimens collected), followed by *Bombus impatiens* (n = 263, 22%), *Agapostemon sericeus* (n = 213, 18%), *Bombus griseocollis* (n = 194, 16%) and *Ceratina calcarata* (n = 173, 15%, Table S4). Overall, medium urbanized areas had the highest bee abundance (n = 564), followed by low (n = 338) and high (n = 283). The most abundant species in medium and high-urbanized was *E. pruinosa*, and *B. impatiens* was the most abundant species in low-urbanized sites (Fig. 2). Low-urbanized sites hosted a male-biased sex ratio for *B. griseocollis* (71% male, χ2 = 16.044, p = 0.001) and *A. sericeus* (74%, χ2 = 12.519, p = 0.001). Medium urbanized sites had a female-biased sex ratio for *C. calcarata* (26% male, χ2 = 13.067, p < 0.001) and male-biased for *E. pruinosa* (72%, χ2 = 38.337, p < 0.001, Table S5). High urbanized sites had male-biased sex ratios for *(A) sericeus* (64%, χ2 = 4.245, p = 0.04) and female-biased for *(B) impatiens* (2%, χ2 = 46.08, p < 0.01; Table S5).

## Body size, foraging efforts, and urbanization

Across all five species, only *E. pruinosa* and *C. calcarata* significantly varied in body size by urbanization. *E. pruinosa* males displayed a higher body size in medium urbanized sites (ANOVA with Tukey's, F = 6.64, p = 0.001, Fig. 3), and *C. calcarata* females in high urbanized sites (ANOVA with Tukey's, F = 7.09, p = 0.01, Fig. 3). Across all urbanization levels, we found that variation in body size (predictor) was significant on bivoltine species *(A) sericeus*, *(B) impatiens* and *B. griseocollis* (x̄ = 3.23, ± 1.27; t-test, t = 28.77, p < 0.001), social bumble bees (x̄ = 3.20, ± 1.42; t-test, t = 22.98, p < 0.001), ground-nesting species (x̄ = 2.83, ± 1.21; t-test, t = -41.60, p < 0.001), and polylectic

species (x̄ = 2.82, ± 1.99; t-test, t = 16.74, p < 0.001, Table S6).

Urbanization only significantly affected wing wear in *E. pruinosa* and *C. calcarata*. Males of *E. pruinosa* and *C. calcarata* had higher wing wear in low (ANOVA with Tukey's, F = 6.87, p = 0.001, Fig. 4) and medium (ANOVA with Tukey's, F = 6.58, p = 0.002, Fig. 4) urbanization sites, respectively. Using wing wear as a predictor and the other functional traits as a response variable, we found a significant wing wear only in social bees *B. impatiens* and *B. griseocollis* (x̄ = 2.46, ± 1.36; t-test, t = 9.94, p < 0.001), and not in the univoltine species *C. calcarata* and *E. pruinosa* (x̄ = 2.14, ± 1.46; t-test, t = -0.90, p = 0.18), cavity-nesting *C. calcarata* (x̄ = 2.18, ± 1,92; t-test, t = 0.66, p = 0.25), or on oligolectic *E. pruinosa* (x̄ = 2.11, ± 1.50; t-test, t = -0.35, p = 0.36). No seasonality effect on body size or wing wear was found for any of the five species (Table S7).

Functional traits and urbanization

The fourth-corner analysis revealed some strong trait-urbanization associations (Fig. 5). The strongest positive association was found between polylectic and trees percentage (IC = 0.29, Wald = 18.06, p = 0.05, Fig. 5A), and polylectic and grass percentage (IC = 0.27, Wald = 17.25, p = 0.19). The two strongest negative associations were found between ground-nesters and trees percentage (IC = -0.25, Wald = 22.10, p = 0.15) and between univoltine bees and grass percentage (IC = -0.20, Wald = 18.31, p = 0.27). After applying the GLM-LASSO penalty, which reduces false interactions and keeps only significant predictions, the maximum likelihood supported the higher probability of finding polylectic bees at sites with low impervious surfaces
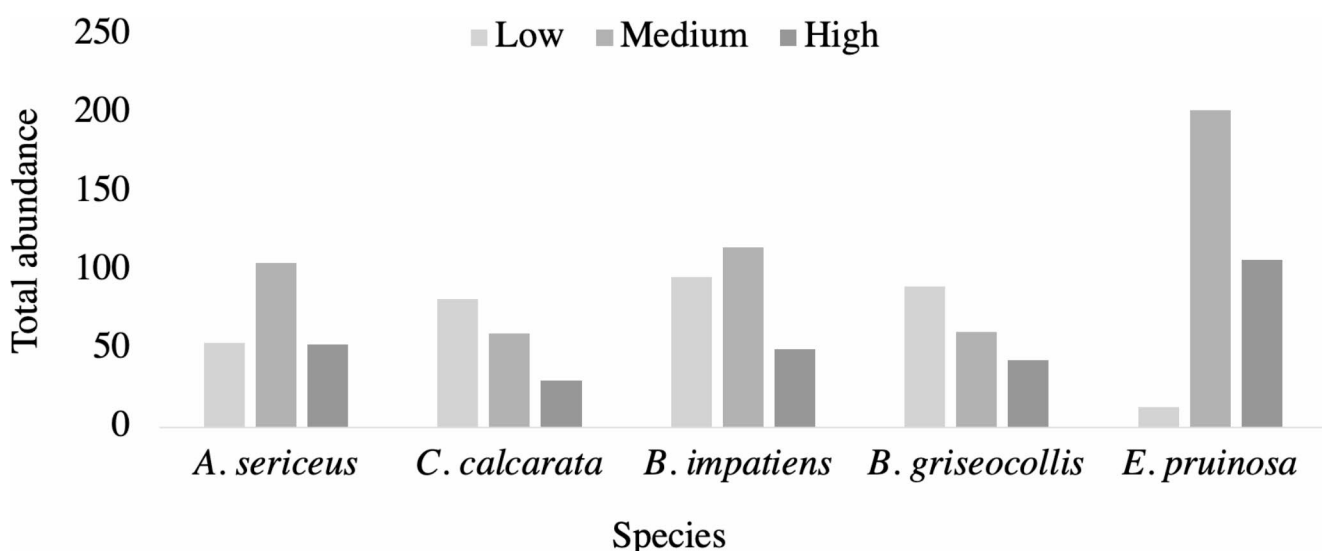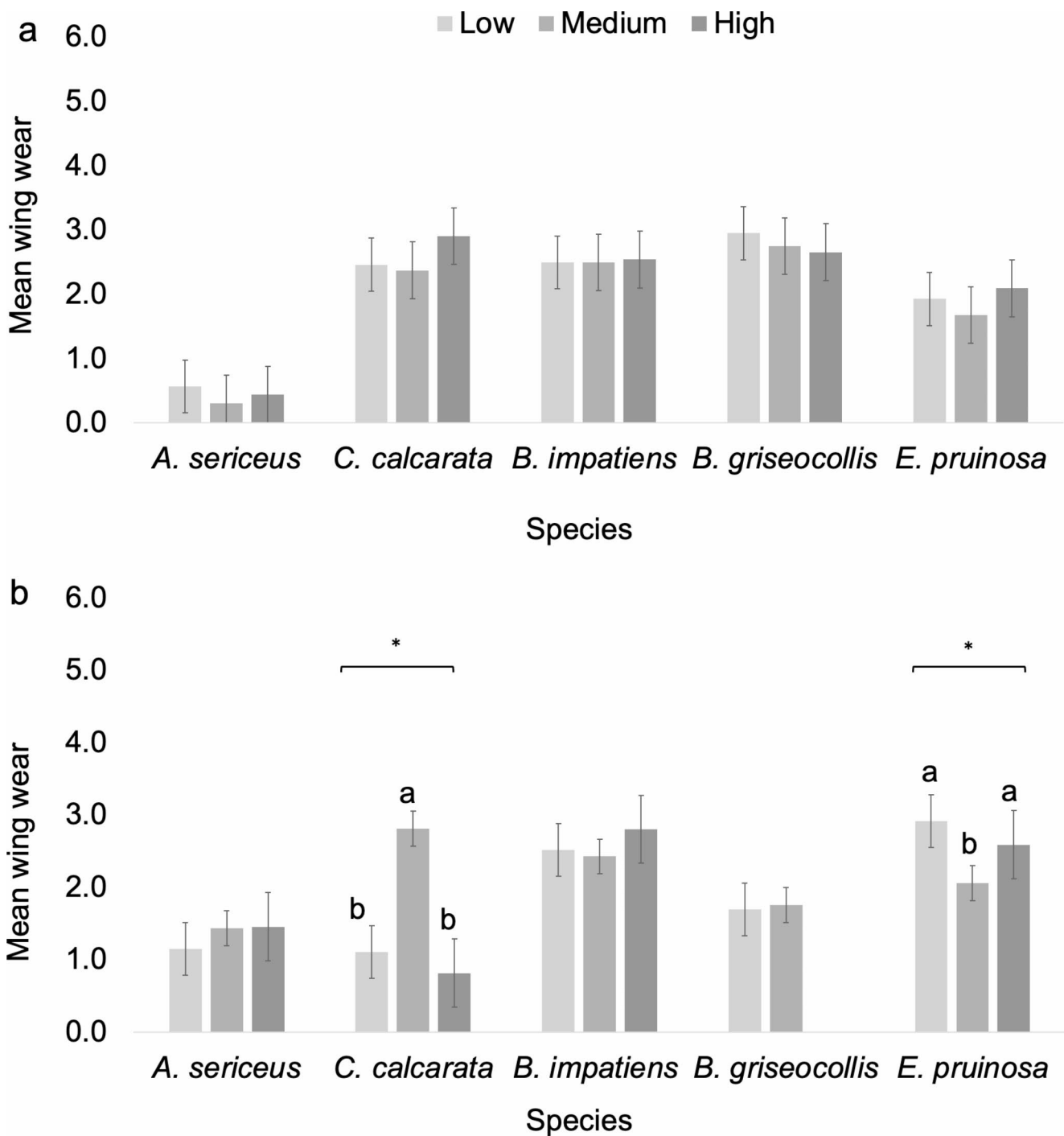

Fig. 2 Total abundance for *(A) sericeus, C. calcarata, (B) impatiens, B. griseocollis* and *E. pruinosa* within each level of urbanization (low, medium and high)
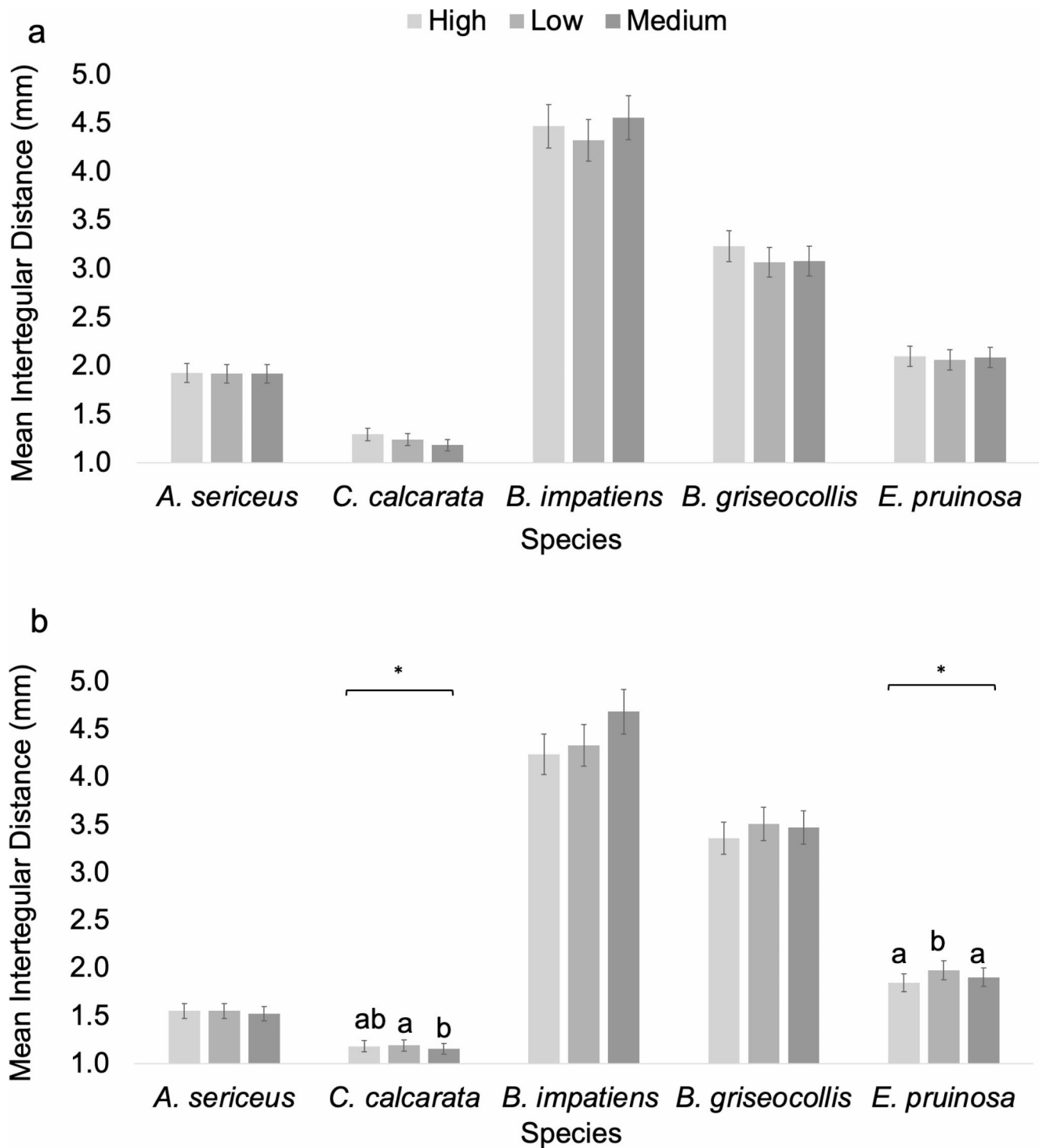
Fig. 3 Mean Intertegular Distance (a proxy for body size) for *(A) sericeus, C. calcarata, (B) impatiens, B. griseocollis* and *E. pruinosa* within each level of urbanization. (a) Female mean body size in low, medium and high urbanization. (b) Male mean body size in low, medium and high urbanization. Error bars correspond to standard errors. Asterisk and letters indicate significant differences according to the Tukey test

Fig. 4 Mean wing wear for *(A) sericeus, C. calcarata, (B) impatiens, B. griseocollis* and *E. pruinosa* within each level of urbanization. (a) Female mean wing wear in low, medium and high urbanization. (b) Male mean wing wear in low, medium and high urbanization. Error bars correspond to standard error. Asterisk and letters indicate significant differences according to Tukey test
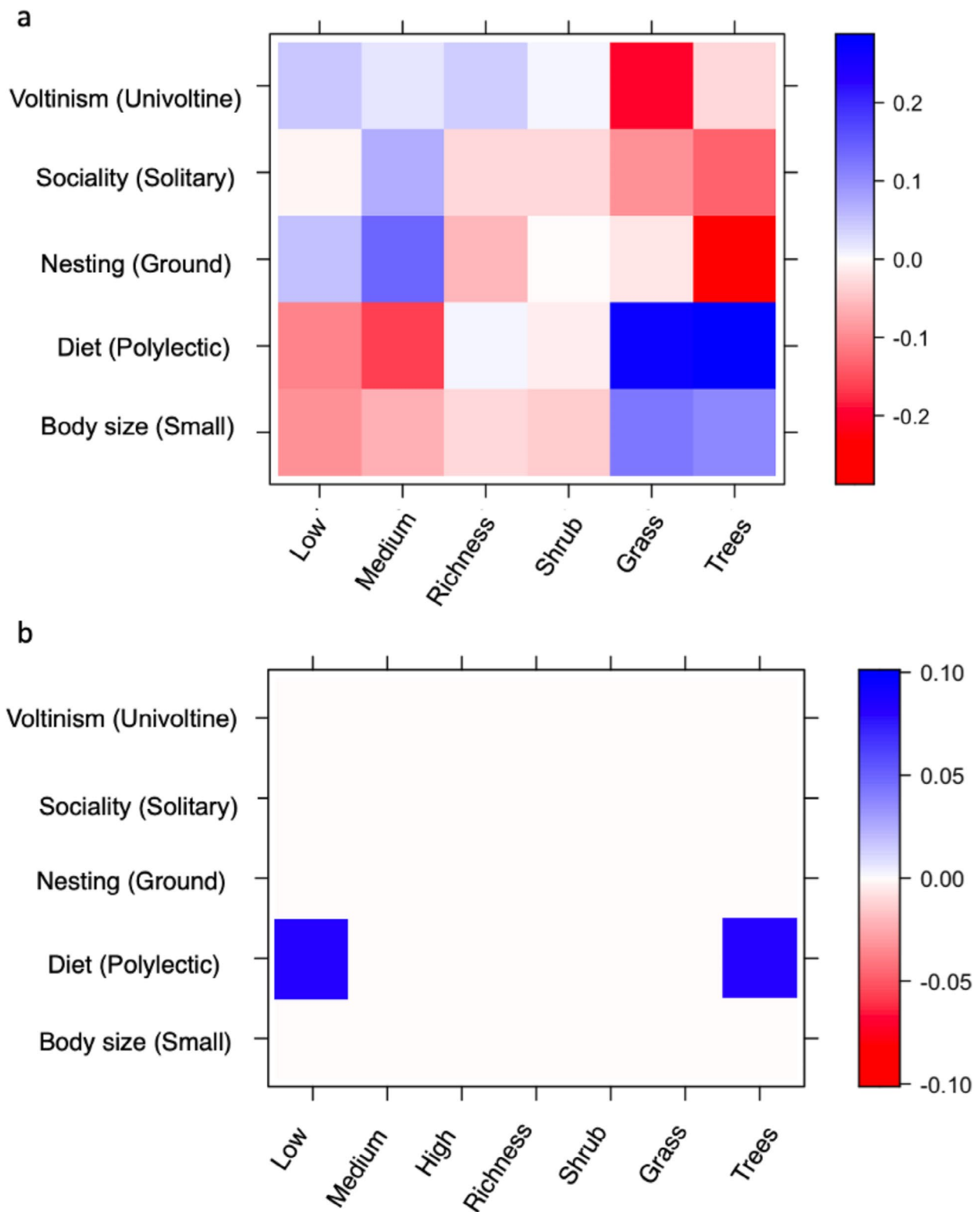
Fig. 5 Heatmap of Standardized coefficients quantifying the strength of the relationship between environmental variables (urbanization, plant richness, percentage of shrub, grass and trees) and bee functional traits (voltinism, sociality, nesting, diet and body size) as estimated by fourth-corner method. (a) Associations estimated by Generalized Lin- ear Model using all variables, and (b) Significant associations cross- validated after LASSO penalty addition. Blue squares represent posi- tive correlation estimates and red squares represent negative estimates. Brighter colors show stronger associations

(IC = 0.10) and higher tree percentage (IC = 0.08, Fig. 5B). See Table S8 for all coefficients.

Discussion

We evaluated the effects of different urbanization levels on wild bee demography, morphology and foraging efforts across five wild bee species. We predict finding lower bee abundance, male-biased sex ratios, larger bees, and greater wing wear in highly urbanized sites. We found a higher abundance in medium-urbanized sites but did not find a consistent urbanization-related sex ratio. We found larger body sizes in medium and high urbanized sites for males of two species (*E. pruinosa* and *C. calcarata*) and greater wing wear in low (*E. pruinosa*) and medium (*C. calcarata*) urbanization sites. We also predicted that urbanization is filtering bees according to their functional trait. Our fourth-corner analysis revealed that polylectic bees are more likely to occur in low levels of urbanization and habitats with higher percentages of trees. Our findings suggest a potential effect of urbanization on foraging efficiency, body size, and diet breadth for these wild bee species.

Abundance and sex-ratio

Higher bee abundance was found in medium-urbanized sites. Specifically, we found higher abundance in three species: *A sericeus*, *B. impatiens*, and *E. pruinosa*. Similar results were observed by a study across France, where the intermediate proportion of urbanization held higher species diversity (Fortel et al. 2014), and a study in California, USA, where butterfly species peaked their richness at moderately urbanized areas (Blair and Launer 1997). A pattern of increase in insect richness has been found comparing low to medium urbanization in thirteen studies worldwide (McKinney 2008). These findings can be attributed to the diverse habitats and ecological niches that moderate levels of human disturbance can create within cities, leading to increased biodiversity and promoting the coexistence of species and individuals (Blair and Launer 1997; Bendix et al. 2017). This has been corroborated by a study investigating a plant-pollinator community where a diverse set of floral traits sustained a larger number of pollinator individuals within a non-overlapping niche (Junker et al. 2013). The mosaic of different land use in urban areas creates diverse habitats such as residential areas, industrial zones, parks, and green spaces, each of which provides unique habitats (Rebele 1994; McKinney 2008). This is true for gardens and other green spaces within a conventionally resource-poor city, which can be a highly rewarding resource for bees (McFrederick and LeBuhn 2006; O'Connell et al. 2021).

Thus, these habitats seem to display some possible advantages in providing sufficient resources for these bees.

We did not find distinct trends for sex-ratio associated with urbanization. Across species, we had diverse results, including male-biased in low, medium, and high sites (*B. griseocollis, E. pruinosa*, and *A. sericeus*, respectively). A similar finding was documented across low, medium, and high resource availability of the leaf-cutting bee *Megachile rotundata*, where no consistent relationship between sex ratio and resource availability was found (Peterson and Roitberg 2006). Importantly, we found a deviation from equality in sex ratio (1:1; Fisher 1930) for every species, meaning that, for this urbanized study system, maternal sex allocation may not be highly influenced by the overall availability of food resources. Yet, additional ecological conditions might be affecting investment decisions.

Body size and foraging efforts

We investigated whether there is a relationship between bee body size and urbanization. We found larger male bees in medium (*E. pruinosa*) and high (*C. calcarata*) urbanized sites. In a prior investigation conducted in Toronto, Canada, it was also observed a significant intraspecific variation in bees, where male *Agapostemon virescens* exhibited larger sizes in areas with moderate levels of urbanization, and females were larger in high urbanized sites (Brasil et al. 2023a). Larger-bodied bees would benefit from the medium and high urbanization given the patchily distributed suitable habitat that is typical of these sites. Another example is the buff-tailed bumblebee, *Bombus terrestris*, which exhibits a larger body size in heavily urbanized cities marked by a fragmented landscape (Theodorou et al. 2020). Urban areas often have a different mix of flowering plants compared to natural environments, thus promoting a more abundant and diverse array of flowers, which can lead to bees accessing richer nectar and pollen sources. This increased resource availability can support larger body sizes. Also, human activities associated with urbanization, such as landscaping and gardening, can introduce cultivated plant species that provide abundant resources for bees, further influencing body size dynamics (McFrederick and LeBuhn 2006; O'Connell et al. 2021). Specifically for *E. pruinosa* and *C. calcarata*, such flowering options could be represented by *Cucurbita* and *Rubus sp.* (Hurd et al. 1974; Tepedino 1981; Lawson et al. 2016).

We found higher wing wear in low and medium urbanized sites. Interestingly, this result was only found in *E. pruinosa* and *C. calcarata males*. A unique suite of factors might explain this result. Firstly, males (as opposed to females) are not central-place foragers, meaning they do not travel from a home base to a certain location. Rather, they are

simply randomly traveling (Orians and Pearson 1979). This random dispersal could mean increasing foraging efforts, as non-central-place foragers tend to spend more energy due to the extra time spent foraging (Houston 1985). Also, male *E. pruinosa* are efficient pollinators responsible for most visits to *Cucurbita* flowers compared to females (Hurd et al. 1974; Tepedino 1981). Moreover, male bees tend to patrol longer distances to encounter potential mates. For example, investigations on gregarious bee species revealed that male bees searched for virgin females in different nest aggregations (Alcock et al. 1978; Eickwort and Ginsberg 1980). *E. pruinosa* presented higher wing wear in low urbanized sites. This species is obligately oligolectic for the genus *Cucurbita* (squashes, pumpkins, gourds; Hurd and Linsley 1964; Hurd et al. 1974). As the flora composition changes, according to the percentage of impervious surfaces, with the number of trees being higher at low impervious surfaces (Yan et al. 2019), we would expect that cultivated crops such as *Cucurbita* would then be decreased, being more abundant in residential yards or community gardens. Thus, *E. pruinosa* may find it more difficult to locate available resources at low urbanization levels. Indeed, we found more bees associated with *Cucurbita* in high urbanization sites for this study (Table S1). We also found higher wing wear in medium urbanized sites, exclusively in *C. calcarata*. This species has previously been reported to have higher wing wear in medium urbanized sites in Toronto, Canada (Brasil et al. 2023b). Our plant richness data demonstrated a higher abundance of *Rubus sp.* in high and low urbanization sites, with only two recorded at medium. *C. calcarata* nests and uses pollen preferentially from *Rubus sp.* (Lawson et al. 2016). Thus, decreased preferential food and nesting resource is potentially driving higher wing wear in *C. calcarata* at medium urbanization levels.

Functional traits and urbanization

According to our fourth-corner method results, polylectic bees were the most positively influenced by low levels of urbanization and number of trees. Although it is essential to consider that the impact of urbanization on polylectic behavior can vary among bee species and regions, it is also important to stress that being a generalist may represent a higher tolerance and less pressure on these species dwelling in a continuously changing habitat. Previous studies in Montreal and Quebec City, Canada, have shown that polylectic bees were more abundant in urban habitats, which could be explained by their success in using a broad resource and their higher tolerance to a change in plant resources (Normadin et al. 2017).

Across all levels of urbanization, we also investigated if body size and foraging efforts (predictors) were associated with other functional traits. We found a significantly higher body size in bivoltine, social, polylectic bees, and ground-nesters, indicating that cities can act as filters for functional traits in this system. Two brood cycles produced in a year seems to be an advantage for *B. impatiens*, *B. griseocollis*, and *(A) sericeus* in an urbanization scenario, given that these bees experience a longer foraging and mating window throughout the year, encountering a wider variety of flowering and mating possibilities. The same rationale applies to social and polylectic bees, here represented by *(B) impatiens* and *B. griseocollis*, that, under a fragmented urbanized scenario, can benefit from the increasing foraging efficiency of many individuals foraging within a colony and being able to collect pollen and nectar from a wider variety of flowers (Ratnieks 2000; Steffan-Dewenter et al. 2002; Thompson et al. 2003; Frankie et al. 2009; Zurbuchen et al. 2010).

Ground-nesters can be unwittingly favored by the bare soil that urban parks and community gardens can provide (Lanner et al. 2020). Our study comprised four ground-nesting species, except for *C. calcarata*, a cavity-nester. Soil nesters represented 86% of the total number of specimens recorded in a study across an urbanization gradient spanning 58 cities in France (Fortel et al. 2014). Additional land use change, such as agricultural intensification has been reported to positively affect social, polylectic and ground-nesting bee species with later flight seasons (Forrest et al. 2015). Reproductive performance of social bees such as *B. impatiens* and *B. griseocollis* might also be enhanced in urban areas. In fact, findings from the National Bumblebee Nest Survey in the United Kingdom suggested that the density of bumble bee nests and colony growth were higher in gardens and country habitats compared to woodland and grassland (Osborne et al. 2008). This is partly explained by a city's highly available domestic garden habitat (e.g., fence lines and hedgerows), favoring bumble bee nesting (Osborne et al. 2008). Using wing wear as a predictor, we also found a significant association of sociality and foraging effort, with social bumble bees showing higher foraging effort. Indeed, under a food scarcity scenario, the bumble bee *Bombus vosnesenskii* tends to increase its foraging distances, reaching up to a 60-fold increase (Pope and Jha 2018).

This study presents unique findings on the effects of urbanization on wild bee demography, morphology and foraging efforts, emphasizing the importance of investigations on the effects of urban environments on pollinating insects, particularly when considering how individual species respond to these environments, and providing a heterogeneous habitat even within highly urbanized landscapes. Our findings suggest an effect of urbanization on foraging efficiency, body size, and diet breadth for these wild bee species. Our results can be further used to provide strategies

for understanding the impact of urbanization on wild bees. Specifically, as higher abundance was found in medium urbanized sites and large bodied bees were found in medium and high urbanized sites, these areas should be carefully managed, needing long-term monitoring for remediation to support wild bees. Rapid urbanization requires thoughtful planning for large cities, such as Toronto, to create and maintain habitats to sustain wildlife biodiversity.

Declarations

Competing interests The authors declare no competing interests.

Ethical approval Not applicable.

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