

Title: Assessing the impacts of urban beehives on wild bees using individual, community, and population-level metrics

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Abstract

Several species of wild bees are in decline globally and the presence of managed honey bees is one of many proposed stressors on wild bee populations. However, there is limited knowledge of the impacts of honey bee hives on wild bees, especially in urban landscapes. We performed a field study to assess the associations between honey bees and wild bees within the Greater Toronto Area in Ontario, Canada. We measured relative abundance of honey bees, wild bee metrics (abundance, community composition, functional diversity, and body size), and floral resources (floral density and richness); we also calculated impervious surface at 500m and 1km for each of our sites. Our main findings were that increasing honey bee abundance was correlated with decreases in wild bee species richness and functional diversity, as well as two wild bee species' abundances and one wild bee species body size, out of many assessed. This research adds to the growing body of literature aiming to evaluate whether honey bees are a stressor on wild bees in urban landscapes, which will be valuable for informing conservation management practices and future research.

Key words: urban ecology; *Apis mellifera*; wild bees; competition; Canada; honey bees

Introduction

Bees are among the most efficient pollinators for many crops and wildflowers (Fontaine et al. 2006; Winfree et al. 2008) and pollination services are estimated to increase annual global crop production by USD \$235-577 billion (Lautenbach et al. 2012). Alarming, many bee species abundances are in steep decline globally, including in Canada (Colla and Packer 2008; Potts et al. 2010a). There are numerous proposed reasons as to why some native bee species are declining, including climate change, pesticides, habitat loss and fragmentation (e.g., increased urbanization), lack of suitable forage, diseases and pests, and even the increase in non-native pollinators (Potts et al. 2010a; Winfree 2010; Thomson 2016). Honey bees, which are non-native to North America, are often the focus of conservation initiatives, including in urban areas (Colla and MacIvor 2017). However, there is evidence that: the introduction of non-native honey bees may negatively impact wild bee species (Thomson 2004; Lindström et al. 2016; Cane and Tepedino 2017), honey bee hive reductions are not a good proxy for native bee declines (Wood et al. 2020), and that honey bees are not at-risk of extinction (IUCN 2020).

There are two main hypotheses for how the presence of managed honey bees might harm native bees: pathogen spillover and floral resource competition. Pathogen spillover from domesticated hosts has been documented in a variety of taxonomic groups and can lead to drastic declines among the exposed wild species, for example the Ethiopian wolf, red squirrels in the UK, and orange-bellied parrots (Haydon et al. 2002; Rushton et al. 2006; Randall et al. 2006; Woodroffe et al. 2012; Peters et al. 2014). Pathogen spillover from managed bees to wild bees is a relatively new field of research and has mainly been documented in bumble bees (Colla et al. 2006; Cameron et al. 2011) and honey bees (Graystock et al. 2013; Alger et al. 2019; Gusachenko et al. 2020). Floral resource competition has been studied more intensively

(Mallinger et al. 2017). Honey bees have the potential to strongly compete with wild bees over floral resources (i.e. pollen and nectar) for a variety of reasons related to their natural history, management, and behaviour (Visscher and Seeley 1982; Beekman and Ratnieks 2000; Al-Ghamdi and Hoopingarner 2004). Honey bees have very large colonies, with the number of workers often varying between 15,000-60,000, creating large demand for pollen and nectar (DeGrandi-Hoffman et al. 1989; Al-Ghamdi and Hoopingarner 2004); whereas most wild bees are solitary (Batra 1984; Michener 2000a). It is crucial for solitary bees to have floral resources within a short distance from their nests because of they often have small foraging ranges, usually within just a few hundred meters (Wright et al. 2015); however, foraging range is related to body size (Greenleaf et al. 2007). Honey bees can forage up to several kilometers from their hive, meaning they have more choice when it comes to floral resource selection compared to smaller bee species (Visscher and Seeley 1982; Beekman and Ratnieks 2000). Honey bees store food to consume through the winter while most wild bees in temperate regions enter diapause (Santos et al. 2019), and thus more resources are extracted from the environment to keep honey bees hives active over the entire year. Finally, honey bees' ability to store honey helps colonies when floral resources are scarce, whereas wild bees in temperate regions have no form of long-term food storage and therefore need resources to be available throughout their flight season (Wcislo and Cane 1996; Williams et al. 2014).

Previous studies have shown that honey bees may have a negative impact on native bees at the individual, population, and community levels. These effects include decreased floral visitation rates (Aizen and Feinsinger 1994; Dupont et al. 2004; Carneiro and Martins 2012), abundance (Thomson 2016), diversity (Badano and Vergara 2011), body size (Goulson and Sparrow 2009b), and fecundity (Thomson 2004; Paini and Roberts 2005). Body size (e.g. thorax

width) is often used as a proxy for resources available at the larval stage (Goulson and Sparrow 2009b). This makes body size a measure for generational impacts as most bee species are solitary (Batra 1984) and are provisioned with food as an egg before they emerge the following year. Smaller bumble bees are also less efficient foragers (Goulson et al. 2002), which may subsequently reduce their food supply and impact their colony's ability to produce reproductive offspring. Another wild bee community metric that is important to assess in terms of competition is functional diversity since it has been shown to impact ecosystem functioning and sustainability (Loreau 1998; Díaz and Cabido 2001). However, functional diversity has not been investigated in terms of honey bee competition to date. Considering there are multiple metrics to assess competition, it is important to continue to study the various ways that honey bees could be impacting wild bees at the individual, population, and community levels.

A recent review found approximately half of the current honey bee and wild bee competition studies so far have found negative impacts with increased honey bee abundance, whereas about a quarter were non-significant, and the last quarter had mixed impacts with increased honey bees (Mallinger et al. 2017). Additionally, there are few studies investigating competition between native bees and honey bees in urban areas (Brant et al. 2022; Mallinger et al. 2017). Only five studies have investigated honey bee and native bee competition within urban landscapes. Three out of the five studies stated hive densities in the landscape assessed, and two found that there was evidence of competition with relatively high hive density (6.5 hives/km² and 19 hives/km²) (Ropars et al. 2019; Weissman et al. 2021), while the other found no signs of competition with relatively low hive density (0.32 – 0.48 hives/km²) (McCune et al. 2020). The other two studies found different trends between honey bees and wild bees depending on the year and floral interactions (Prendergast et al. 2021) and high honey bee abundances were correlated

with reduced wild bee visitations in an urban garden (Renner et al. 2021). Within urban landscapes, the most common factors known to have impacts on bee abundance and community composition are: floral resources (Fitch et al. 2019; McCune et al. 2020), proportion of impervious surface as a proxy for urbanization (Ahrné et al. 2009; Burdine and McCluney 2019), and temperature (Hamblin et al. 2018). In order to conserve wild bee abundance and diversity within urban landscapes, it is crucial to better understand the factors that may have negative impacts on them, including honey bee abundance and/or density.

Here we investigate whether floral resource competition between native bees and honey bees is occurring within the Greater Toronto Area (GTA), Ontario, Canada. Toronto is the largest city in Canada, in terms of area and human population size; it is a hotspot for native bee biodiversity as well, with over 350 species within the GTA, making it an important area for biodiversity conservation (City of Toronto 2016). The approximate hive density for the City of Toronto and Toronto Region was 1.0 hives/km² for 2019 and 0.93 hives/km² for 2018 (OMAFRA 2021, personal communication). We assessed impacts of increased honey bee abundance on wild bees (abundance, community and trait composition, and body size), while taking into consideration other possible explanatory factors (amount of impervious surface and floral resources). We predict that if floral resource competition is occurring between native bees and honey bees, then we will find a negative relationship between honey bee abundance and the following wild bee parameters: abundance, diversity (at the community and functional levels), and body size.

Methods

Site selection

Ten sites across the GTA were sampled (refer to Figure 1). Seven of the ten sites were in public parks, two were at university campuses (York University, Keele Campus and University of Toronto, Scarborough Campus), and one of the sites was at a botanical garden. The number of sites was limited due to requiring approval from land managers and beekeepers, and by capacity for sampling methods described below. Sites were chosen as “matching pairs” with one site being an area with estimated high hive density (at least known 5 hives within 2km of the site) and the other with estimated low hive density (0 known hives within 2km of the site) (Shavit et al. 2009). Note, estimated hive density was based on limited geographical knowledge of hives in the GTA; we were mainly aware of organizations that have been beekeeping for several years, which were more likely to be registered hives. For high hive density sites, we chose sites that have had honey bee hives for multiple years to better understand the impacts of long-term beehives on native bees. Other similar studies chose specific sites to make a gradient of no honey bee hives to close to known honey bee hives or manipulated the number of honey bees in an area (Thomson 2004; Shavit et al. 2009). However, there is not enough publicly available information about honey bee hive locations in the GTA to do this.

Fig. 1 Map of the ten study sites across the GTA

Bee sampling

Sites were sampled every 7-10 days on warm, sunny days from May to August in 2019 to measure bee abundance and community composition by using standard pan trapping and sweep

netting methods (Droege 2015; Packer and Darla-West 2021). Pan traps were put out for 8 hours a day (approximately 8am to 4pm), and sweep netting was done for 30 minutes, 3x a day (approximately 8am, 1pm, and 4pm). Thirty pan traps (96 mL from New Horizons Support Services, Maryland, USA) filled with soapy water (10 white, 10 blue, and 10 yellow) were put out at each site in a line spanning 30m, with one meter between each trap. Dawn Ultra® blue was used as a surfactant in the traps. Pan traps were deployed on the ground, along edges of grass and dense vegetation (e.x. trees, shrubs and/or long grass) so they would be visible and away from high human traffic areas to avoid damage. All bees were collected and identified to species (when possible) in the lab using identification keys. Bee genera that are commonly cited as being difficult to identify were verified by experts. We sampled honey bees at our sites to assess if our sites reflected our estimated categories of low and high hive density as well. Bee specimens are currently stored at York University, except *Tripeolus* specimens that are stored at the Canadian Museum of Nature. Refer to Online Resource 1 for identification methods to species for each genus.

Body size measurements

In order to determine whether body size was associated with relative honey bee abundances, all bee species with at least 50 specimens per females and/or males had their heads and thoraxes measured. This was done that assuming that honey bee relative abundance has not fluctuated much from the previous year. The threshold of 50 specimens was chosen to ensure a large enough sample size to capture variation within sites and between sites. Thorax width is the most common metric for bee body size, but we chose to also measure head width because it has

also been used as a proxy for body size instead of thorax width for some solitary bee species, particularly sweat bees (Cane 1987a; Rust 1991; Davison and Field 2017; Nooten and Rehan 2019). All other species had five specimens' thoraxes measured only for use in our trait analysis described below. All measurements were taken using a digital Vernier caliper (Goulson and Sparrow 2009b). Only worker body sizes were used when analyzing impacts of honey bees on body size for eusocial species. Queens were not used in our analysis due to the large variation in body size between them and workers. For head width, maximum distance between lateral margins of the eyes was measured and for thorax width, the maximum distance between the lateral margins of their tegulae was measured. We decided to include tegulae into our measurements, unlike other studies that use intertegular distance (Cane 1987b; Goulson and Sparrow 2009b), because we found that this made it easier to measure smaller bees accurately. However, we only measured body size for all bee species with an average of over 1.8mm thorax width as we found that it was hard to precisely measure after this point.

Floral resource assessment

Floral density (number of flowers per m²) and richness (number of flowering species at a site) were measured at each site on a biweekly basis. Floral density and richness were measured by tossing a 0.58m² circular quadrat ten times within 7.5m of the entire row of pan traps and counting the number of open flowers or florets in inflorescence within each quadrat. The number of florets within an inflorescence were counted individually, as opposed to being counted as one whole, since it has been found that the number of bees visiting an inflorescence is positively associated with the number of florets (Willson and Bertin 1979). Floral density and richness

were measured within 7.5m of pan traps to account for flowers that were found at the edges of grass and dense vegetation, as well as logistically the furthest we could walk into the denser vegetation. For floral richness, pictures were taken of each flower within the quadrats to be identified to species. Flower species were identified mainly using expert-level identification on iNaturalist, however some common species were identified on the spot (e.g. dandelion, white and red clover). For these analyses we report floral density as the average flower density per sampling day averaged over the season, and floral richness is the number of flower species per site per sampling day averaged over the season.

Impervious Surface

Previous studies have found that bee abundance and community composition is related to urbanization intensity, which is most commonly measured as proportion of impervious surface (Ahrné et al. 2009; Burdine and McCluney 2019). We calculated the proportion of impervious surface per site by using landscape data from Southern Ontario Land Resource Information System (SOLRIS) 3.0 (Ontario Ministry of Natural Resources and Forestry 2019). We defined impervious surface as the combination of transportation areas (highways and roads) and built-up impervious areas (residential, industrial, commercial, and civic areas). We calculated the proportion of impervious surface area with a radius of 500m and 1km from the middle of the pan trap line, which were the middle of our sites (Ahrné et al. 2009; Fortel et al. 2014; Geslin et al. 2016; Glaum et al. 2017). This analysis was done on QGIS 3.4.13 GRASS 7.6.1 using the LecoS – Landscape Ecology Statistics plugin (Jung 2013).

Data Analysis

Two out of our five sites that were initially identified as low hive density actually had high relative abundance of honey bees compared to sites that were initially labelled as high hive density. We likely missed smaller apiaries at the sites with more honey bees than expected. Therefore, we alternatively chose to base our analysis on relative honey bee abundance instead of site-specific hive density because our estimated categories of hive density were not reflective of how many honey bees were actually visiting our sites. Relative honey bee abundance was calculated as the total number of honey bees at a site divided by the total number of all bees at that site. Honey bee relative abundance was used instead of numerical honey bee abundance to reflect the likelihood of competition between honey bees and wild bees at each site, as relative abundance is more representative of interactions between species than numeric abundance.

Generalized linear models (GLMs) were used to assess whether abundance, community and trait composition, and body size have an association with relative honey bee abundance. For all GLMs, the best model was selected starting with flower density, flower diversity, relative abundance of honey bees, impervious surface area at 1km, impervious surface at 500m as predictors, in this particular order. The best model was determined using either Akaike Information Criterion corrected for small sample size (AIC_c) (Burnham and Anderson 2002) or quasi- AIC_c values (for overdispersed models) (Fitch et al. 2019). R package *AICcmodavg* was used for calculating AIC_c for models that were not overdispersed and the *MuMIn* package was used for calculating quasi- AIC_c for overdispersed models. A stepwise reduction was conducted, beginning with removing the predictor that had the least explanatory power (i.e. the lowest absolute value of z-value or t-value) (Fitch et al. 2019). This stepwise procedure was done until AIC_c increased or $\Delta AIC_c < 2$ (Burnham and Anderson 2002). In addition to understand whether

there were any possible confounding interactions between predictors, a Spearman's correlation matrix was performed using all predictor variables. The correlation matrix was done using the *rcorr* function in the *Hmisc* package. All data analyses were conducted in R (R Core Team, 2020 version 4.0.3).

We first conducted a GLM with the abundance of wild bees at each site as the response variable to investigate whether honey bees impact overall abundance of wild bees. Then to assess whether certain species or genera had significant associations with relative honey bee abundance, a redundancy analysis (RDA) for all genera was first completed to assess which genera were likely to have a negative or positive association; GLMs were then conducted based on findings from the RDA. Prior to running the RDA, the data were checked for collinearity using the variance inflation factor (VIF) using the *vifcor* function in the *usdm* package (Naimi et al. 2014). If variables were identified as collinear, then the variable with the higher VIF was taken out. Also, the Hellinger transformation was used on all genera counts to account for the double-zero effect (i.e. the *decostand* function in *vegan* package) (Legendre and Gallagher 2001). The genera that were identified as being negatively or positively associated with honey bees in the RDA were then further investigated with GLMs. GLMs were conducted with each identified genus, and species within those genera, when there were at least 50 specimens of the genus or species and there was presence at a reasonable number of sites (at least 5), including after taking out outliers that were identified by assessing relationships with relative honey bees and wild bee abundance to see if any site alone was driving trends and was not representative of the overall relationship. These GLMs were either Poisson distributed, or quasi-Poisson distributed (depending on results from the overdispersion test from the *AER* package) with a log-link function and went through the same stepwise model selection as described above. The p-values

for all abundance models were adjusted using false discovery rate (FDR) to take into consideration the increased probability of a false positive when conducting simultaneous hypothesis testing (Benjamini and Yekutieli 2001); the *p.adjust* function was used to calculate the adjusted p-values.

Genus and species richness, and Shannon diversity index at the genus and species levels were calculated per site. The Shannon diversity index was calculated using the *diversity* function in the *vegan* package. Then GLMs (with a quasi-Poisson or Poisson distribution, dependent on overdispersion) were conducted with a log-link function to assess whether richness was associated with relative honey bee abundance. GLMs with Gaussian distribution with an identity link function were also used to assess whether the Shannon diversity index had any association with relative abundance of honey bees (Buchholz et al. 2020).

A database of eight life history traits was compiled for all species collected in order to assess impacts on trait composition (Table 1). These eight traits were specifically chosen because they are known to impact the functional roles of bees in their ecosystems (Forrest et al. 2015; Normandin et al. 2017; Tonietto et al. 2017; Hung et al. 2019). Trait composition for each site, specifically weighted functional dispersion (FDis) as a measure for functional diversity, was calculated from our trait database and relative abundance data of all species at each our 10 sites. Weighted FDis was chosen because this parameter represents the mean distance of each species to the centroid of all other species within trait space and takes into consideration the relative abundance of each species at each site (Laliberte and Legendre 2010). FDis was calculated for all traits (i.e. total FDis) and each trait individually to better understand which trait may cause the total functional dispersion to have specific relationships with predictors. FDis was calculated using the *fdisp* function from the *FD* package in R. Then a GLM with a Gaussian distribution

and an identity link (Buchholz et al. 2020) was conducted with FDis as the explanatory variable to assess whether relative honey bee abundance impacts trait composition. All community and trait composition GLMs went through the same selection process as previously mentioned.

GLMs (with a log-link function) were performed with only one of the following response variables at a time: female head width, female thorax width, male head width, or male thorax width. These models were done to investigate whether there are any associations between body size of wild bees and relative abundance of honey bees. Models were separated by sex and species since both factors can cause large variations in body size. Also, GLMs were only done for sexes that had at least 50 specimens and at least 5 sites after outliers removed (same as abundance models above). Models also went through the same selection process as above. The p-values for all body size models were adjusted using FDR, as described previously for the abundance models (Benjamini and Yekutieli 2001).

Table 1 Life history trait database used in analysis of FDis, including sources for trait information. Refer to Online Resource 1 for all trait information per species

Trait	Trait Type	Description	Data Source
Body Size	Continuous	Mean thorax width of five randomly selected female specimens or taken from other papers when only male specimens were available	Our dataset and (Forrest et al. 2015; Normandin et al. 2017; Kendall et al. 2019; MacInnis et al. 2020)

Diet	Categorical (3 categories)	Oligolectic (specialized preference for pollen resources) Polylectic (non-specialized preference for pollen resources) Parasitic (social or brood parasite)	(Michener 2000b; Normandin et al. 2017; Hung et al. 2019)
Sociality	Categorical (3 categories)	Solitary (solitary or communal) Social (eusocial or cooperative breeding) Parasitic (social or brood parasite)	(Packer et al. 2007; Gibbs et al. 2012; Fortel et al. 2014; Normandin et al. 2017)
Seasonality	Categorical (6 categories)	All Season Spring Summer Spring & Summer Summer & Fall	(Mitchell 1960, 1962; Forrest et al. 2015; Normandin et al. 2017)
Type of nesting site	Categorical (3 categories)	Aboveground Belowground Parasitic (social or brood parasite)	(Krombein 1967; Packer et al. 2007; Hung et al. 2019)
Tongue Length	Categorical (2 traits)	Short or Long – based off bee family morphology	(Michener 2000b; Biesmeijer et al. 2006; Fortel et al. 2014; Cariveau et al. 2016)
Nest Building	Categorical (3 categories)	Excavate (actively constructing nests) Rent (utilizes already existing spaces/cavities) Parasitic (occupying nests of host bees)	(Mitchell 1960, 1962; Krombein 1967; Michener 2000b; Sheffield et al. 2011; Forrest et al. 2015; Hung et al. 2019)

Pollen Strategy	Categorical (6 categories)	Accidental (does not actively pollinate - limited to parasitic species) Corbiculae (specialized pollen baskets on legs) Crop (pollen storage within their crop) Legs Leg & Body Underside (underside of abdomen)	(Mitchell 1960, 1962; Michener 2000b; Normandin et al. 2017)
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Results

In total, 9,389 bees, 32 genera, and 195 species were collected from all ten sites in the Greater Toronto Area. The top five most abundant genera were: *Apis* (19.4%), *Bombus* (15.9%), *Ceratina* (11.4%), *Lasioglossum* (9.8%), and *Andrena* (9.2%). All bees were identified to genus and most to species; however, we could not identify 276 (3%) bees to species, either because of missing body parts or lack of suitable identification keys and expertise. Most sites were sampled 17 days throughout the season; however, Downsview Park and Northwood Park were sampled for 15 days and Maloca Gardens and G Ross Lord Park were sampled for 16 days. The discrepancy between the number of sampling days was due to inclement weather. A list of flowering plant species found at each site can be found in Online Resource 2. Finally, refer to Table 2 for correlations between predictor variables.

Table 2. Spearman's correlation matrix coefficients for all predictor variables.

	Relative Abundance of Honeybees	Impervious surface at 500m	Impervious surface at 1km	Flower Density	Flower Richness
Relative Abundance of Honeybees		-0.19	-0.36	-0.33	-0.63 ^N
Impervious surface at 500m			0.78**	0.2	0.3
Impervious surface at 1km				0.37	0.48
Flower Density					0.69*

Significance levels: ^N near significant, p = between 0.05 and 0.1, *p < 0.05, **p < 0.01, ***p < 0.001

Abundance

The genera that were identified for further investigation with associations with relative honey bee abundance from the RDA were: *Agapostemon*, *Andrena*, *Anthidium*, *Calliopsis*, *Coelioxys*, *Colletes*, *Halictus*, *Lasioglossum*, *Nomada*, *Osmia*, *Sphecodes*, *Stelis*, *Triepeolus*, and *Xylocopa*. Out of these identified genera (and therefore species), nine genera and 18 species had over 50 specimens and consequently a total of 27 GLMs were conducted to assess correlations between their abundances and relative honey bee abundance.

Out of these 27 GLMS, two species were found to be negatively associated with relative honey bee abundance (*Lasioglossum hitchensi* Gibbs and *Nomada bethunei* Grote and Robinson) (Figure 2a and 2b, respectively) and no genera were negatively associated with relative honey bee abundance. No genera or species were positively associated with relative honey bee abundance. In addition, the number of bees at each site was not found to be associated with any predictors (quasi-Poisson GLM, $F(8) = 697.22$, $t = -1.381$, $p = 0.159$). Impervious surface at 1km

was the only predictor included in the final model for number of bees at each site after the stepwise reduction procedure was completed. Refer to Online Resource 3 for the: RDA biplot, RDA1 and RDA2 values for all genera investigated, and all genera and species GLM results.

The predictor that most commonly had a significant relationship with species/generic abundance was impervious surface at 500km. Two genera (*Lasioglossum* and *Osmia*) and five species (*Lasioglossum imitatum* Smith, *L. hitchensi*, *L. paradmirationum* Knerer and Atwood, *L. weemsi* Mitchell, and *Osmia conjuncta* Cresson) had negative relationships with impervious surface at 500m. However, *Nomada bethunei* and *Andrena cressonii* Robertson had a positive relationship with impervious surface at 500m. One species (*Nomada bethunei*) had a negative relationship with impervious surface at 1km and two species (*Lasioglossum hitchensi*, and *L. paradmirationum*) had a positive relationship with impervious surface at 1km. One genera (*Osmia*) and three species (*Lasioglossum hitchensi*, *L. paradmirationum*, and *L. weemsi*) had a significantly negative relationship with flower richness, but two species (*Halictus ligatus* Say and *Halictus rubicundus* Christ) had a positive relationship with flower richness. Finally, only *Lasioglossum imitatum* had a positive relationship with flower density.

Community and trait composition

Species richness had a significantly negative association with relative honey bee abundance, and only included relative honey bee abundance as a predictor (Poisson GLM, $\chi^2(8) = 10.323$, $z = -3.533$, $p < 0.001$; refer to Figure 2c). In addition, total functional diversity (i.e. FDis with all traits) was found to have a significantly negative association with relative abundance of honey bees (Gaussian GLM, $\chi^2(8) = 0.003$, $t = -2.523$, $p = 0.012$; refer to Figure 2d) and only

relative abundance of honey bees was included in the final model after model selection. For the individual trait FDis models, tongue length had a significantly negative relationship with relative abundance of honey bees (Gaussian GLM, $\chi^2(8) = 0.013$, $t = -2.024$, $p = 0.043$). Diet had a significantly negative relationship with both relative honey bee abundance (Gaussian GLM, $\chi^2(8) = 0.018$, $t = -2.024$, $p = 0.010$) and impervious surface at 1km. Seasonality had a significantly negative relationship with relative honeybee abundance (Gaussian GLM, $\chi^2(8) = 0.016$, $t = -8.768$, $p = 0.004$), impervious surface at 1km, and floral richness, but had a significantly positive relationship with floral density. Nesting had a significantly negative relationship with floral density. Refer to Online Resource 4 for all FDis model results.

The final model for generic richness only included relative honey bee abundance as a predictor, but did not have a significant relationship with relative honey bee abundance (Poisson GLM, $\chi^2(8) = 3.012$, $z = -1.501$, $p = 0.134$). Flower density was the only predictor included in the final model for genus-level Shannon index and there was no significant relationship between flower density and genus-level Shannon index (Gaussian GLM, $\chi^2(8) = 0.001180$, $t = 1.079$, $p = 0.281$). Similarly, species level Shannon index did not have a significant relationship with impervious surface at 1km, which was the only predictor in the final model (Gaussian GLM, $\chi^2(8) = 0.440$, $t = -0.962$, $p = 0.336$).

Body Size

Forty-six GLMs were performed to assess wild bee body size associations with relative honey bee abundance. Fifteen species had their female thorax widths and head widths assessed and eight species had their male thorax and head widths assessed; these GLMS included 16

species in total (one species had only male body size assessed) and 46 GLMs in total. Body size of one species (*Augochlorella aurata* Smith) was negatively associated with relative abundance of honey bees and one species was positively associated with honey bee abundance (*B. rufocinctus* Cresson) (refer to Table 3). For the models that had significant associations for flower density, two had negative associations (*Andrena imitatrix* Cresson and *A. nasonii* Robertson). Impervious surface at 500m had one species with positive relationships (*Andrena nasonii*) and two with negative (*Bombus griseocollis* and *B. impatiens*). Three species had a significantly positive association (*Agapostemon virescens* Fabricius, *Augochlorella aurata*, and *Nomada bethunei*) with impervious surface at 1km. Finally, two species were negatively associated (*Bombus griseocollis* and *B. impatiens*) with flower richness. Finally, refer to Online Resource 4 for all GLM results, including non-significant models.

Fig. 2 (a) *Lasioglossum hitchensi* was negatively associated with relative honey bee abundance (Poisson GLM, $\chi^2(7) = 439.02$, $z = -6.577$, $p < 0.001$). When the outlier was taken out the relationship between relative honey bee abundance and *L. hitchensi* became further negative and the p-value went down by three orders of magnitude (Poisson GLM, $\chi^2(6) = 28.170$, $z = -6.651$, $p < 0.001$). **(b)** *Nomada bethunei* was negatively associated with relative honey bee abundance (Poisson GLM, $\chi^2(8) = 57.265$, $z = -6.621$, $p < 0.001$). **(c)** Species richness was negatively associated with relative honey bee abundance ($p < 0.001$). **(d)** Total functional dispersion (FDis) was negatively associated with honey bee relative abundance ($p = 0.012$). Lines represent least-squares means.

Table 3 Body size GLM results that found significance or near significance associations with relative abundance of honey bees. F is for female, M is for Male, T is for thorax, and H is for head. Light grey indicates a significantly positive association, and darker grey indicates a significantly negative association. Res. Dev. Stands for Residual Deviance, Est. stands for Estimate, and R.A. stands for Relative Abundance

Species	F/ M	T/ H	Flower Density			Flower Diversity			Relative Apis			Imp.Surface.1000			Imp.Surface.500		
			Res. Dev	t	Est.	Res. Dev	t	Est.	Res. Dev	t	Est.	Res. Dev	t	Est.	Res. Dev	t	Est.
<i>Augochlorella aurata</i>	F	T	2.692	0.65 1	0.001				2.576	0.43 0	0.205 ^N	2.53 9	2.63 9	0.90 0	2.44 2	-2.265	-0.671 ^N
<i>Augochlorella aurata</i>	F	H	1.016	- 4.34 0	-0.001				0.896	- 5.24 6	- 0.780* **	0.83 7	3.02 6	0.38 7*			
<i>Bombus griseocollis</i>	M	T				9.79 6	1.80 3	0.05 9	8.964	2.56 7	1.669 ^N						
<i>Bombus rufocinctus</i>	F	H	23.212	1.62 5	0.000				22.866	2.30 5	0.325 ^N						
<i>Bombus rufocinctus</i>	M	T							28.694	3.59 9	1.879* *	28.4 95	2.08 1	2.75 1	27.9 07	-1.909	-1.580
<i>Bombus rufocinctus</i>	M	H							7.116	2.27 1	0.594 ^N	7.03 6	1.17 1	0.77 5	7.00 1	-0.928	-0.384
<i>Nomada bethunei</i>	F	T	7.146	1.76 3	0.004	7.02 6	2.15 7	0.45 2	6.376	- 2.12 5	- 0.917 ^N	2.31 7	2.16 7	5.77 9 ^N			

Significance levels: ^N near significant, p = between 0.05 and 0.1, *p < 0.05, **p < 0.01, ***p < 0.001.

Discussion

Associations between honey bees and wild bees

We found that increasing abundance of honey bees was negatively associated with total wild bee functional diversity, species richness, two species' abundances out of 23 genera and species assessed (*Lasioglossum hitchensi* and *Nomada bethunei*), and one species body size out of 14 species assessed (*Augochlorella aurata*). This is the first study to investigate whether increasing honey bee abundance has a relationship with bee functional diversity, and abundance at the species and genus levels for a wild, urban bee community. Most studies considering the impact of honey bees either included the wild bee community as a whole or a subset of the wild bee community (e.g. bumble bees) (Mallinger et al. 2017). This has limited our understanding of how the presence of honey bee hives may impact specific groups of the bee community, including rare and understudied species (e.g. *Nomada*) (Mallinger et al. 2017). It is important to investigate honey bee impacts on the community as a whole, but also investigate which species or genera may be more affected by them so that conservation efforts can be focused, if needed. Honey bees have the potential to impact bee genera and/or species in different ways depending on various traits. For example, bee species that are active from the spring to fall may have more interactions with honey bees leading to higher chances of pathogen transfer or direct displacement interactions. Larger bee species may also be more greatly impacted by honey bees because they require more forage; this is supported by multiple studies showing negative impacts of honey bees on bumble bees (Goulson and Sparrow 2009b; Elbgami et al. 2014; Thomson 2016). Our results show that urban beehives may impact bee groups in different ways, but there are negative associations with richness and diversity as well.

However, when looking at overall bee abundance, negative associations with honey bees were not found. This may be due to Toronto having a hive density that is between the low hive density of McCune *et al.* (2020) (0.32 – 0.48 hives/km²) and the relatively high hive density of Ropars *et al.* (2019) (6.5 hives/km²), which are the only other studies that have included hive density while investigating impacts of urban beekeeping on wild bees. In 2019, the estimated hive density for the City of Toronto and Toronto Region was 1.00 hives/km² (OMAFRA 2021, personal communication). Since McCune *et al.* (2020) did not find any negative associations with wild bee abundance and Ropars *et al.* (2019) found that overall wild bee abundance was negatively correlated with honey bee hive density, our study results may represent a lack of impact on wild bee total abundances due to a relatively moderate hive density. It is also important to note that both these studies only included subsets of the wild bee community; McCune *et al.* (2020) only investigated associations with honey bees for the eleven most common bee species that were caught, and Ropars *et al.* (2019) did not subsect the bee community further than separating out small and large solitary bees and bumble bees. In any case, our results may show that in cities with relatively moderate hive density, it is important to look for impacts on certain genera and/or species to see if their abundances differ with honey bee density, especially before increasing the density of hives.

Honey bees had a negative association with the abundance of two species, which have different values for all functional traits. Cleptoparasitic bees are often the first guild to respond to disturbance (Sheffield *et al.* 2013), which may explain the relationship between *Nomada bethunei* and abundance of honey bees. In contrast, *Lasioglossum hitchensi* is polylectic, active for the spring and summer, and social. They may be negatively impacted by honey bees because of competition for the same resources as generalists and having more interactions by being active

for many months. However, Prendergast et al. (2021) found that smaller bodied bees were least impacted by honey bees, which contradicts our findings that this small bodied *Lasioglossum* species is negatively associated with honey bees. However, we did not find any relationships between relative honey bee abundance and body size within our functional diversity models so it does not seem we found a clear relationship between body size and the likelihood of competition with honey bees within our study. More research is needed to see why these species may be more negatively associated with honey bees in urban areas than other species, including niche overlap investigations. Species richness has been found to be linked with abundance and may primarily show sites that have rare species (Lichtenberg et al. 2017). The presence of rare species is potentially linked to ecosystem resilience and functional redundancy (Mouillot et al. 2013). Species richness was found to be negatively associated with relative honey bee abundance, but richness at the genus level was not found to have a significant relationship with relative honey bee abundance. Studies that were conducted in agricultural and natural landscapes did not find any relationship between honey bee visitation and bee richness (Steffan-Dewenter and Tscharntke 2000; Torné-Noguera et al. 2016). Whereas we found that Shannon index at the species or generic level was not significantly associated with honey bees.

The negative relationship with honey bees on bee species richness was then translated to honey bees having a negative relationship with total functional diversity (i.e. all traits) as well. However, not all studies have found that species richness and functional diversity are linked (Cadotte et al. 2011). We did find a significantly negative association between honey bees and a few individual functional diversity traits (diet, tongue length, and seasonality). These three traits are generally related to floral resources. The negative relationship with diet and tongue length could imply that honey bees are decreasing the abundance of bees with certain diets and tongue

lengths due to floral resource competition. Similarly, honey bees may be decreasing abundance of wild bees that are out at certain times in the season, likely when there are scarce resources and competition for floral resources would be the most intense. Further research is needed to find causations for these relationships between honey bees and diversity of these wild bee traits in urban landscapes. Many researchers have stated the need to look at impacts on communities through functional diversity in addition to traditional diversity indices (i.e. Shannon index, richness, etc.) (Díaz and Cabido 2001; Cadotte et al. 2011; Sheffield et al. 2013; Buchholz and Egerer 2020). Functional diversity is very important because it reflects the diversity in functional roles in a community (Laliberte and Legendre 2010) and reduced functional diversity may impact overall ecosystem functioning and sustainability (Loreau 1998; Díaz and Cabido 2001). High bee community functional diversity has been associated with increased crop yield (Hoehn et al. 2008) and crop seed set (Martins et al. 2015), which indicates that pollination services are enhanced with increased functional diversity. There are only a few studies that have investigated urban stressors' impacts on bee functional diversity (Eggenberger et al. 2019; Buchholz and Egerer 2020) and this is the first study to investigate honey bee abundance impacts on functional diversity. Future studies should consider the socio-economic impacts of reduced ecosystem functioning in cities.

The results of the body size analyses also show mixed associations with honey bees. *Augochlorella aurata* was the only species that had a negative association with relative honey bee abundance, and *Bombus rufocinctus* had a positive relationship with honey bee abundance. Body size is correlated to the amount of food consumed at the larval stage (Ribeiro 1994; Bosch and Vicens 2002). Therefore, body size can be a proxy for forage availability for the time period of when forage was collected for the larval stage (Goulson and Sparrow 2009b); this time period

refers to when mass provisions were made for solitary and social bees or when forage was collected for *Bombus spp.* and *Apis mellifera* larvae throughout their larval stage. Evans *et al.* (2018) did find that honey bees and wild bees can benefit from similar habitats within an agricultural setting, so positive relationships between honey bees and body size may be due to them preferring similar forage and sites having enough floral resources to sustain both groups. However, the only other study on the impacts of honey bees on wild bee body sizes found a negative relationship between honey bees and bumble bee body size (Goulson and Sparrow 2009b). The negative associations between honey bees and *Augochlorella aurata* body size, but not abundance, may be a sign that there is floral resource competition that has not led to a population decline. Beekeeping impacts on wild bee body sizes should be further investigated to find additional trends across landscapes as well as temporally throughout the growing season.

Floral resource and impervious surface impacts

Available floral resources and amount of impervious surface had varied associations with bee communities. For abundance, flower richness had largely negative relationships, whereas for body size, flower density and richness had mixed associations. For individual functional trait diversity, flower density had had a positive relationship with seasonality and type of nesting, but richness had a negative association with seasonality. It is common for floral resources to have positive impacts on bee communities (Ebeling *et al.* 2008; Frankie *et al.* 2009a; Grundel *et al.* 2010); however, Geslin *et al.* (2016) did not find that floral resources had an impact on bee assemblage in an urban landscape. A possible reason for not finding positive impacts of floral resources is that in areas with abundant resources, pan traps become less attractive to bees (Wilson *et al.* 2008; Plascencia and Philpott 2017); this could explain some of the variation,

especially for species and generic abundance results. Another reason may be that our floral resource measurements were concentrated around the pan traps, which may not be at a large enough scale, since floral resources have been found to be more correlated to netting (Westphal et al. 2003; Popic et al. 2013). Regarding bee abundance associations with impervious surface, at 500m there were only negative associations, and this was the most common variable to have a significant relationship with species and genus abundance (mainly *Lasioglossum* spp. and *Osmia* spp). Whereas at 1km there were mixed associations. For body size, impervious surface at 500m had mixed relationships and impervious surface at 1km had positive relationships for the few models that were found to be significant. However, impervious surface at 1km had negative relationships with diet and seasonality functional diversity. Urbanization can lead to habitat loss for wild bees (Goddard et al. 2010) and may also shift community composition through changing the type of habitats available (Shochat et al. 2010). Other studies also found that increasing impervious surface at 500m had a negative impact on bee abundance (Zanette et al. 2005; Geslin et al. 2016). Whereas research that has also used proportion of impervious surface as a proxy for urbanization, have found mixed effects of urbanization on bee functional diversity. Buchholz et al. (2020) did not find any relationship between urbanization and functional diversity, but Eggenberger et al. (2019) found a positive relationship between urbanization and functional diversity for bumble bees. Our findings, and those of others, warrant further study to understand the relationships between floral resource availability, proportion of impervious surfaces, and urban bee community health and functional diversity, especially with a focus with impervious surface at 500m as this was shown to have a negative association with several species and genera abundances.

Caveats and shortcomings

Our results contribute to a better understanding of how bee communities may respond to varying levels of honey bee abundance in an urban landscape. However, causal mechanisms were not explored, therefore our results show correlation, not necessarily causation. In addition, our sampling effort was very high to accurately estimate abundance; however, this only allowed us to sample at ten sites and we also sampled for one season only. Ideally, this study should be redone over multiple seasons and at more sites to see if the relationships we found change over time and whether the sites chosen were representative of the GTA as a whole. The need for more sites is shown through the near significant negative correlation between relative abundance of honey bees and flower richness; this correlation may not be representative of sites with hives in general and should be investigated further. Prendergast et al. (2021) found that associations between honey bees and wild bees can change depending on year (with some years showing negative relationships and others showing positive) and floral interactions within that year (e.g. niche overlap) as well, which further highlights the need for longer term studies. In addition, our study was not able to address the possible mechanism for negative impacts on wild bee communities, as negative associations with increasing honey bees could be from floral resource competition and/or pathogen spillover (Mallinger et al. 2017; Alger et al. 2019). Investigation of resource overlap for individual species and genera would have strengthened our study as well by providing further explanation for any negative associations between wild bee and honey bees. However, we did collect pollen from a portion of bees caught in this study to assess resource overlap, but due to time limitations this information is not yet published and will be a separate manuscript. In addition, our study focused only on possible competition between honey bees and wild bees for floral resources we did not address the possibility of competition between wild

bees existing which should be further explored. Future studies are needed to explore urban beekeeping impacts on wild bee communities that include investigating the causal link for these trends and less localized sampling of floral resources.

Conclusion

Cities can sustain high levels of bee diversity (Baldock et al. 2015a; Sirohi et al. 2015), but increasing beekeeping may be putting pressure on their populations. Urban landscapes provide a unique opportunity for decreasing beekeeping as to our knowledge, there is no current evidence for a pollination deficit, unlike in agricultural landscapes (Aizen and Harder 2009). Our study shows that increasing honey bee abundance may lead to decreases in: abundance and body size of certain groups of bees, species richness, and functional diversity. This highlights the need to focus research into the causations of these relationships and conservation efforts in urban landscapes on wild bees and further investigate stressors, including beekeeping. Our results also indicate that can be diverse and context-dependent responses at the species and genus levels, which may be lost if comparing honey bee to wild bees as a single group.

There are numerous benefits to maintaining diverse and abundant wild bee communities and the pollination services they provide in urban settings. Urban farming and gardening are known to increase food security and mental health (Kortright and Wakefield 2011; Barthel and Isendahl 2013). In addition, wild bees are also a great way to introduce the public to conservation initiatives since the public is very concerned about their populations and understands their ecological importance (Schönfelder and Bogner 2017; Vierssen Trip et al. 2020). Maintaining high abundance and biodiversity of bees in cities will ensure pollination of gardens and wildflowers that are crucial for connecting human populations with nature and tackling food insecurity.

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