Understanding honey bee forage requirements and the impacts of urban hives on wild bees

Sarah MacKell

A thesis submitted to the Faculty of Graduate Studies in partial fulfillment of the requirements
for the degree of Master of Science

Graduate program in Biology

YORK UNIVERSITY

TORONTO, ONTARIO

February 2021

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. There are also large knowledge gaps for the amount of floral resources honey bees require, which is needed for addressing whether landscapes have enough resources for all bees. I developed a model to calculate the number of flowers and area a honey bee hive requires in temperate regions using information compiled from published literature (Chapter 1), and I performed a field study to assess the impacts of urban beehives on wild bees (Chapter 2). My model's output is highly variable due to the limited amount of available peer-reviewed literature on needed parameters, but it serves as a starting point to assess how much floral resources honey bee hives require. My field study's main findings were that increasing honey bee abundance was associated with decreases in the abundance and body size of certain bee species, as well as reduced species richness and functional diversity. This research helps identify knowledge gaps in honey bee foraging and floral resource availability research (Ch. 1). It also adds to the growing body of literature aiming to assess whether honey bees are a stressor on wild bees in urban landscapes, which will be valuable for informing conservation management practices and future research (Ch. 2).

Acknowledgements

I would like to extend my deepest gratitude towards my colleague and friend, Hadil Elsayed, who helped me immensely with field work and identification. Hadil helped me most by encouraging me and listening to my complaints, but especially by listening to my general nonsense that I came up with when she was stuck with me for months in the field and lab. I would also like to thank my great supervisor Dr. Sheila Colla who let me really run with my interests and was always supportive and understanding whenever there were issues or missed deadlines. Also, thank you so much for providing me the opportunity to attend The Bee Course in Arizona, I can easily say that was one of the best experiences of my life. Similarly, I would like to thank my supervisory committee members Dr. Amro Zayed and Dr. Laurence Packer for your helpful and encouraging feedback. Dr. Laurence Packer, I would like to also thank you for extending your bee identification knowledge and helping me connect with experts in the field.

Thank you to my lab mates who helped me with methodology, statistics, identifying bees and even pinning bees. Specifically thank you to Amanda Liczner, Victoria MacPhail, Briann Dorin, Kennedy Shea, and the non-official lab member, Alex Filazzola. I would also like to thank my amazing field crew, Rebecca Gasman and Mila Gills. Thank you for eating lots of ice cream with me and getting excited about new bee species. Also, thank you to the many volunteers we had in the lab and in the field, without these lovely people helping sort, pin, and measure bees I am sure that I would not have been able to finish. In addition, thank you to Sheila Dumesh, Genevieve Rowe, Katherine Odanaka, and Evan Kelemen for identifying bee groups to species that were very difficult.

I would like to thank my friends and family for supporting me through this adventure. Specifically, my friends and fellow York MSc students, Malory Owen and Arshad Imrit. Malory, thank you for always being extremely cheerful and having full confidence in me, you are a gem. Arshad, thank you for being my dragon boat/bee researcher friend, you are very helpful and kind, but most importantly provide cake in times of need. Thank you to my partner Giang Le, who had to deal with many breakdowns over trying to finish my thesis and working full time during a pandemic. Finally, thank you to my parents for being loving and supportive no matter how stressed I was and never judging me for choosing to spend my time catching bees and then looking at dead bees for months on end.

Table of Contents

List of Tables

Chapter 1

Chapter 2

List of Figures

Chapter 1

Chapter 2

Introduction

About one third of food crops rely on or benefit from animal pollination to some degree (Klein et al. 2007), and bees are often the most effective pollinators of temperate flowering species (Fontaine et al. 2006; Winfree et al. 2008). However, some wild bee species are in decline (Potts et al. 2010a, 2016). There are several proposed reasons for pollinator loss, including pathogen spillover from managed bees to wild bees (Colla et al. 2006; Cameron et al. 2011; Alger et al. 2019), and floral resource competition between managed and wild bees (Mallinger et al. 2017). It is hypothesized that honey bees have the ability to compete with wild bees for floral resources for many reasons, including their large number of workers causing high pollen and nectar requirements (DeGrandi-Hoffman et al. 1989; Al-Ghamdi and Hoopingarner 2004). It is currently unclear if areas with introduced honey bees require additional floral resources, and if so the quantity of floral resources, to ensure landscapes have enough resources for all bees.

There is limited information about honey bee floral resource requirements, but it seems likely honey bees could be taking huge amounts of pollen and nectar resources from their surrounding environment, which may otherwise support wild bees (Cane and Tepedino 2017). Honey bee floral resource requirements should be studied further to estimate whether landscapes have enough resources for all bees. In addition, there is limited understanding of the conditions where introducing honey bees has a negative impact on wild bees. There have been mixed results from studies looking for associations between increasing honey bees and wild bee communities, however about 50% of them show negative impacts on wild bees and the other half had either mixed or non-significant impacts (Mallinger et al. 2017). Most studies on the impacts of honey bees on wild bees have been done in natural or agricultural areas, with only a few studies conducted in urban landscapes (Mallinger et al. 2017; Ropars et al. 2019; McCune et al. 2020). Further research is needed on honey bee resource floral resource requirements and urban beehives impacts on wild bees, so that we can have a better understanding of whether landscapes have adequate floral resources available for wild bees and urban beekeeping.

References

Al-Ghamdi A, Hoopingarner R (2004) Modeling of honey bee and Varroa mite population dynamics. Saudi J Biol Sci 11:21–36

Alger SA, Burnham PA, Boncristiani HF, Brody AK (2019) RNA virus spillover from managed honeybees (*Apis mellifera*) to wild bumblebees (*Bombus spp*.). PLoS One 14:e0217822. https://doi.org/10.1371/journal.pone.0217822

Cameron SA, Lozier JD, Strange JP, et al (2011) Patterns of widespread decline in North American bumble bees. Proc Natl Acad Sci U S A 108:662–667. https://doi.org/10.1073/pnas.1014743108

Cane JH, Tepedino VJ (2017) Gauging the effect of honey bee pollen collection on native bee communities. Conserv Lett 10:205–210. https://doi.org/10.1111/conl.12263

Colla SR, Otterstatter MC, Gegear RJ, Thomson JD (2006) Plight of the bumble bee: Pathogen spillover from commercial to wild populations. https://doi.org/10.1016/j.biocon.2005.11.013

DeGrandi-Hoffman G, Roth SA, Loper GL, Erickson EH (1989) BEEPOP: A honeybee population dynamics simulation model. Ecol Modell 45:133–150. https://doi.org/10.1016/0304-3800(89)90088-4

Fontaine C, Dajoz I, Meriguet J, Loreau M (2006) Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. PLoS Biol 4:e1. https://doi.org/10.1371/journal.pbio.0040001

Klein AM, Vaissière BE, Cane JH, et al (2007) Importance of pollinators in changing landscapes for world crops. Proc. R. Soc. B Biol. Sci. 274:303–313

Mallinger RE, Gaines-Day HR, Gratton C (2017) Do managed bees have negative effects on wild bees?: A systematic review of the literature. PLoS One 12:e0189268. https://doi.org/10.1371/journal.pone.0189268

McCune F, Normandin É, Mazerolle MJ, Fournier V (2020) Response of wild bee communities to beekeeping, urbanization, and flower availability. Urban Ecosyst 23:39–54. https://doi.org/10.1007/s11252-019-00909-y

Potts SG, Biesmeijer JC, Schweiger O, Kunin W (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts SG, Imperatriz-Fonseca V, Ngo HT, et al (2016) Safeguarding pollinators and their values to human well-being. Nature 540:220–229. https://doi.org/10.1038/nature20588

Ropars L, Dajoz I, Fontaine C, et al (2019) Wild pollinator activity negatively related to honey bee colony densities in urban context. PLoS One 14:e0222316. https://doi.org/10.1371/journal.pone.0222316

Winfree R, Williams NM, Gaines H, et al (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. J Appl Ecol 45:793–802. https://doi.org/10.1111/j.1365-2664.2007.01418.x

Chapter 1: Modelling the number of flowers and forage area needed for honey bee (*Apis mellifera*) hives using literature review data

Sarah E. MacKell, Sheila R. Colla

Author's Contributions:

SEM and SRC, conceived of the ideas. SEM conducted the literature review, processed all articles, extracted relevant data from articles retained for the review, constructed the model and summarized and analyzed the results. SEM led the writing of the manuscript. Both authors contributed to editing and gave final approval for inclusion into the dissertation and eventual publication to a peer-reviewed journal article.

We intend to submit this manuscript for publication in a peer-reviewed journal.

Introduction

Globally, many wild bee species are declining and there are regional declines in managed honey bee colony numbers (Neumann and Carreck 2010; Potts et al. 2010b, a, 2016). The European honey bee, *Apis mellifera* Linnaeus, is the most widely managed bee species in the world. It is used for pollination and honey production, and has been transported to every continent except Antarctica (Abrol 2012). Although, the global number of managed *Apis mellifera* hives is increasing, it may not be rising fast enough to deal with the "pollination deficit" caused by the increasing demand for animal pollinator-dependent crops (Aizen and Harder 2009). Thus, determining how to support both wild and managed bees is of upmost importance to ensure adequate pollination of our crops and wildflowers.

For honey bees, the most common reasons for hive losses are pesticide exposure (e.g. neonicotinoids) (Tsvetkov et al. 2017), pests (e.g. *Varroa destructor* Anderson and Trueman), pathogens (e.g. *Nosema* spp.) (Potts et al. 2010a; Goulson et al. 2015), and lack of proper nutrition (Naug 2009; Branchiccela et al. 2019). Colony losses have been found to be associated with areas that have a low ratio of open to developed land, which may indicate that lack of forage may be a stressor on honey bees (Naug 2009). If forage is increased for honey bees, beekeepers may save money and time by not having to supplement food (Honey Bee Health Coalition 2017). Honey bees are also more likely to be negatively affected by pests and diseases when they are lacking proper nutrition (Fries and Camazine 2001; Giacobino et al. 2014; Dolezal et al. 2019). Reduction in diet diversity has been shown to decrease honey bee baseline immunocompetence and social immunity (Fries and Camazine 2001). Correspondingly, high-quality pollen diets have been linked to decreased mortality from Israeli Acute Paralysis virus (Dolezal et al. 2019) and colonies that are fed pollen and nectar supplements were found to be less likely to have *Varroa destructor* over 3% load (Giacobino et al. 2014). The synergistic effect of pesticides and poor nutrition can greatly reduce honey bee survival and food consumption as well (Tosi et al. 2017).

Properly managing honey bees is also important for wild bee species' populations, specifically in areas where honey bees have been introduced. Various studies have found that increasing honey bee abundances had negative impacts on wild bees, such as decreases in body sizes (Goulson and Sparrow 2009a), fecundity (Badano and Vergara 2011), and floral visitation rates (Aizen and Feinsinger 1994). Floral resource competition is one of many proposed reasons for wild bee declines, and other stressors including climate change, pesticides, disease, and habitat loss, may pose greater risks (Potts et al. 2010a). Managed honey bee colonies can transmit pathogens to native bee populations as well (Singh et al. 2010). Pathogen spillover from managed bumble bees has been implicated in the declines of wild bumble bees (Colla et al. 2006; Cameron et al. 2011), but there is growing concern about pathogen spillover from managed honey bees as well (Colla and MacIvor 2017; Alger et al. 2019; Pritchard et al. 2021).

Floral resource competition also may have negative implications for honey bees as well as wild bees. Henry and Rodet (2018) found that high hive densities (over 14 colonies/km^2) had a negative relationship with nectar (-44%) and pollen (-36%) harvesting by honey bees. Lower hive density has also been associated with a reduced prevalence of diseases and parasites, and higher honey production and overwintering colony survival (Brosi et al. 2017; Dynes et al. 2019). It is becoming increasingly important to ensure that there are enough floral resources available for all bees in the landscape because many wild bee populations are declining, and substantial management concerns for honey bees (Potts et al. 2010a).

Multiple studies have investigated honey bee nutritional needs and optimal hive density of their colonies, which is an important aspect of understanding if landscapes have enough resources for both honey bees and wild bees. Rodney and Purdy (2020) describe the current body of literature on nectar and pollen requirements of honey bees, however most of the articles that state the overall amount of nectar, honey, or pollen that is required by a hive do not cite supporting data or sources. This shows the need for modelling these nutritional needs to provide empirical evidence to these claims. Al-Ghamdi et al. (2016) conducted a field study to calculate an optimum honey bee hive density in selected fields in the Kingdom of Saudi Arabia dominated by flowering trees (fields dominated by *Ziziphus spina-christi* or *Acacia tortilis*). Another study, also in Saudia Arabia, used a GIS approach to determine optimum honey bee hive density within fields of Talh trees (*Acacia gerrardii*) using the number of colonies/tree as their metric (Alqarni 2015). Esteves et al. (2010) developed a model to provide optimal distribution of bee colonies with no specific locality, however this model did not incorporate the amount of resources plants provide to bees in a certain area, instead they assume that the user knows the “carrying capacity” of the plants, which is the number of bees that the plants can provide resources for. Given that there is little empirical evidence for floral requirements of honey bee colonies and there has been only one proposed model for optimizing honey bee colony density that could be used in temperate areas, it is crucial to continue investigating methods that could estimate optimum honey bee densities for land managers for multiple landscape types and contexts.

Hive density impacts all forms of honey bee management, including disease and diet management (Brosi et al. 2017; Dynes et al. 2019). From a policy and monitoring perspective, hive density is much easier to manage than disease and diet, as it is less labour intensive. Optimal hive densities are recommended values for hives per unit area, but they do not necessarily take into consideration the distribution across the area. Estimates of ideal hive densities for honey bees have considerable uncertainty because of dynamic floral resource phenology and honey bee management protocols. It would be difficult to create varying hive density policies across regions because this would require many local-scale studies. Modeling optimal hive density is a starting point for gaining empirical evidence to back up policy discussions for improving honey bee and wild bee health. The objectives of this study were to: 1) identify honey bee floral requirements and 2) model the number of flowers and forage area a managed honey bee colony requires per year in agricultural and urban landscapes for adequate honey harvesting in temperate climates, based on data from existing literature.

Methods

Literature Search

Before our literature search was conducted, we discussed the appropriate parameters needed to model the number of flowers and foraging area for a honey bee colony per year with multiple honey bee experts. A systematic literature search was then done using Web of Science Core Collection for articles published up to, but not including, 2019 to extract information on honey bee pollen and nectar requirements. Due to the nature of the question being asked in this review, a systematic review was needed to collect information on multiple parameters. The search was conducted with the following search terms: ((habitat OR “floral requirement*” OR “pollen collection” OR “nectar collection” OR “honey requirement*” OR “sugar content*” OR “area needed” OR “honey production”) AND (honey bee OR “honey bee” OR “Apis mellifera”)). Nectar and honey sugar content data were searched for within the same search as terms relating to honey bees because we were hoping to capture sugar content from flowers that honey bees are associated with and are known to forage from. There were 1035 search results with these terms, and each article had its abstract read (some required that the whole article be skimmed to see if it had the data needed for the following model parameterization). From of the original 1035 articles, 893 were excluded for further inspection due to their content not being relevant to the research question or not having required information for the calculations. The remaining 142 articles were read thoroughly, including supplementary material. The following data were extracted from the articles: average amount of honey per colony per year, mass of nectar in one foraging trip, sugar content of nectar (%), sugar content of honey (%), pollen collection per colony per year, mass of pollen collected per foraging trip, and number of flowers visited per foraging trip for pollen and nectar foraging, separately. Papers were kept if they had at least one estimate for at least one of the essential parameters; this resulted in the exclusion of 121 papers. The remaining 21 papers were then used for calculations outlined below. Note, we only extracted information on managed honey bee colonies, not feral colonies.

We also performed a separate literature search to determine estimates of pollen and nectar collection not found during the systematic search; eight articles were used from this separate search. This separate search was done by going through references of papers found within the initial systematic search. The following parameters had data added from this separate search: mass of nectar in one load, pollen collection per colony per year, mass of pollen collected per foraging trip, and number of flowers visited per foraging trip for pollen and nectar, separately.

Separate literature searches were performed for finding data for urban and agricultural floral densities since these terms did not relate well to the original systematic search; the search terms used were: (("number of inflorescence*" OR "number of flower*" OR "floral unit*" OR "floral densit*") AND ("urban" OR "agricultur*" OR “city”)). This search was also done in Web of Science and yielded 583 results. After filtering (as above) twelve articles for urban floral density and nine articles for agricultural floral density were retained. Articles were not used if they did not have units that could be converted to the units selected for our calculations. This resulted in one article for urban floral density (Scriven et al. 2013), and one for agricultural floral density (Haenke et al. 2009). Floral density is defined as the number of flowers (counting a capitulum as one flower) within a unit of area.

However, not all model input was from systematic literature searches as described above (refer to Fig. 1). Data for modeling wax production, worker honey consumption, the number of times a bee can visit a flower for pollen, and the number of times a bee can visit a flower for nectar were compiled from the literature after the systematic searches; these parameters were suggested by honey bee experts after we had conducted our literature searches. The studies used for these equations are within the description below the respective equation.

Measures of centrality for each parameter were extracted from the articles, using the mean or median depending on the variable’s distribution. Specifically, the mean of the parameter was calculated across articles if the data had a normal distribution, or median if it had a skewed distribution. The absolute maximum and minimum value of each parameter was also extracted from either the study level average with the lowest/highest value when multiple study estimates were available or from the lowest/highest value within one study when only one study was available for the parameter. However, lowest/highest within a study were not noted if they were not available or were not reasonable for calculations (e.g. values of 0). These maximum and minimum values were then later used to model the maximum and minimum model outputs, which are described within the model development methods. For studies that did not state measures of centrality for the parameter being investigated, median or mean values were extracted from the related figures using WebPlotDigitizer©, depending on the distribution, as explained above. Ideally, study level variance estimates and study quality (e.g. methodological and data quality) would be weighted in the model, however due to lack of data, the mean or median were the most consistently available data to extract.

Model Development

Data collected from the studies identified from the literature review process were used to build our model (illustrated in Fig. 1) for the number of flowers and forage area requirements for a managed honey bee hive per year, for adequate honey harvesting. Adequate honey harvesting (or honey collected from a colony) is defined as the median of the honey production per colony per year values found from our literature search; this value represents the amount of honey that is taken by the beekeeper and not consumed by the hive. The first step was to calculate the number of flowers needed for nectar and pollen collection per hive per year, then the total number of flowers needed was converted to area needed for a hive using floral density values obtained. The number of flowers needed per colony per year was assumed as the same for both agricultural and urban landscapes. For future models, the number of flowers needed per colony per year should be separated for agricultural and urban landscapes if there is enough information on the required parameters to conclude that this is appropriate. However, the amount of forage area needed per colony per year was calculated for urban and agricultural landscapes separately due to the potential differences in floral densities across these habitats. The number of flowers and amount of forage area for a honey bee hive was calculated three different ways: average, minimum and maximum. Minimum and maximum model outputs were calculated by testing every model input to identify whether the absolute maximum or minimum value in their known range from literature would lead to the absolute minimum or maximum model output (i.e. number of flowers and foraging area). As described previously, the absolute maximum or minimum value of each parameter was either taken from study level averages when there was more than one study available, or from the extreme values within one study when only one study was available. The minimum and maximum calculations represent the variability within our data, not implying biological implications of the maximum or minimum a colony needs for honey production. The driving equations of our model are as follows:

The amount of nectar collected per colony per year is given by:

$$\begin{aligned}
\mathbf{NC} = {} & \frac{\mathbf{HP}}{\left(\frac{\mathbf{NSC}}{\mathbf{HSC}}\right)} + \left(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1 + (DMxW)_2 + \cdots (DMxW)_6]\right) + \\
& \left(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1 + (DMxW)_2 + \cdots (DMxW)_7]\right)\ x\ 0.60) + ([(ASH\ x\ 2) + \\
& (RSH\ x\ 22)]\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1 + (DMxW)_2 + \cdots (DMxW)_7])\ x\ 0.40) + \\
& (\left(\frac{A\ x\ D\ x\ NB\ x\ NF\ x\ NSF}{WC}\right)\ x\ WH) \qquad \mathbf{(1)}
\end{aligned}$$

where, NC is nectar collected per colony per year, HP is honey production per colony per year, NSC is nectar sugar content, HSC is honey sugar content, RS is sugar required per day while resting, RSH is sugar required per hour while resting, DM is days per month, W is number of workers per month, ASH is sugar required per hour while active, A is area of a frame, D is density of comb cells, NB is number of deep boxes per colony, NF is number of frames per box, NSF is number of sides per frame, WH is the conversion factor of wax to honey, and WC is the conversion factor of wax to comb cells.

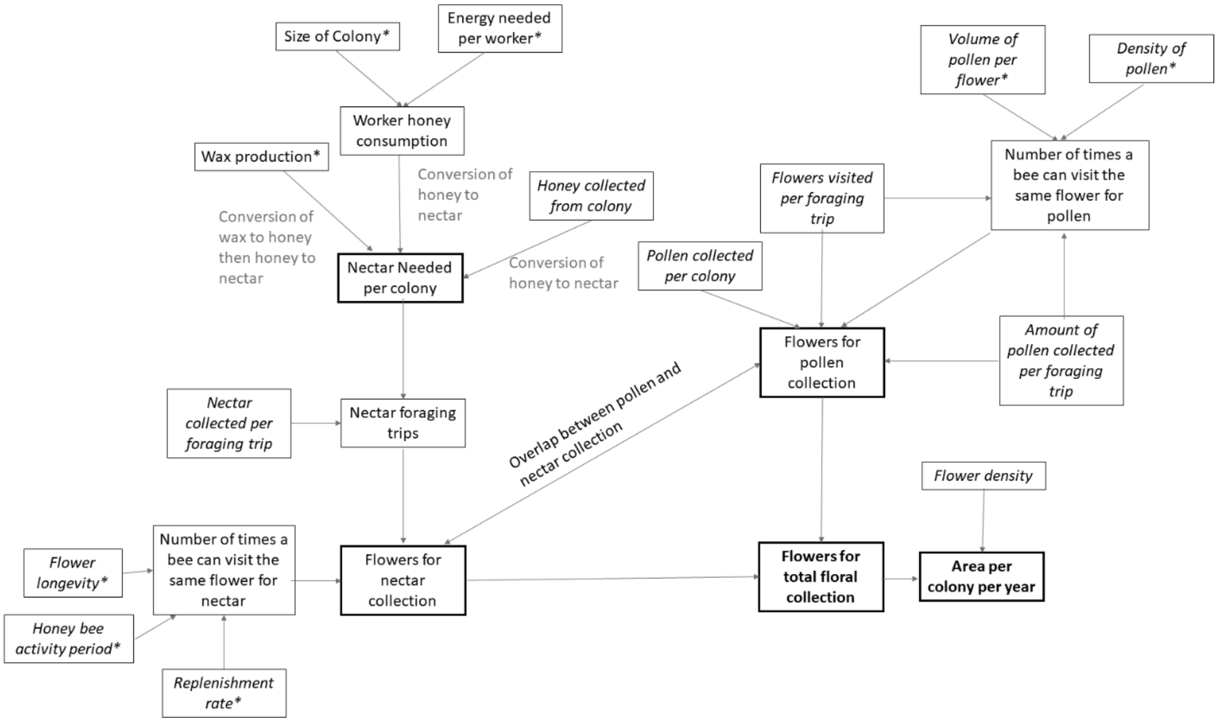


Figure 1. Schematic of the basic elements of our model of honey bee floral and forage area requirements. Italicized text indicates that these values were taken from literature and all other values were calculated using literature data. Bolded text indicates that these are the model outputs that are focused on in this paper. The only values taken from literature that are not included in this diagram are for wax production and worker honey consumption (refer to equation 1 for all parameters used in the wax and honey calculations). Honey collected from colony is equivalent to the "mass of honey collected from a colony per year" and "honey production per colony per year". *These values were found from literature after the systematic literature searches were conducted.

Our equation for nectar collected per colony per year accounts for honey harvested, colony honey consumption, and wax production. Honey bee worker number within a colony varies significantly throughout the year in temperate climates and varies largely depending on climate and management, which makes calculating the amount of honey needed per year per colony difficult. It is often cited that honey bee colony numbers can fluctuate between approximately 15,000 to 60,000 workers (Farrar 1934; DeGrandi-Hoffman et al. 1989; Al-Ghamdi and Hoopingarner 2004; Schmickl and Crailsheim 2004). Depending on the climate and management honey bee colony sizes are known to reach their maximum (approximately 60,000 workers) sometime between June and August for about a month (DeGrandi-Hoffman et al. 1989; Harris 2008) and hit their minimum from about November to March (approximately 15,000 workers) (as per Russell et al. 2013). To estimate the amount of additional nectar a honey bee colony needs to produce for honey consumption, the amount of sugar needed to sustain a worker was accounted for. It is known that honey bee workers need more sugar if they are active (7.5 mg sugar/hr) relative to if they are resting and/or performing lower energy consuming tasks (0.075 mg sugar/hr) (Moffat 2000; Schmolz et al. 2002; Rodney and Purdy 2020). We assumed the following: (1) bees within the hive are resting and bees outside the hive are flying/hovering, (2) about 40% of workers are foragers during active months (leaving 60% as resting) (as per Rueppell et al. 2007), (3) foragers spend about 2 hours outside of the hive in a day (based on Rodney and Purdy 2020), (4) honey is approximately 75% sugar, (5) foragers are active from April to September, and (6) the colony population dynamics is as in Appendix A. The amount of honey needed per colony for wax production was calculated based on a hive having two ten-frame, wooden Langstroth deep boxes (same as Meikle et al. 2016). The dimensions of these boxes and density of comb cells measured in Meikle et al. (2016) was used as well. We assumed that: 1) it takes about 8.4 kg of honey to produce 1 kg of wax (based on Black 2006), 2) 1 kg of wax produces about 77,000 comb cells (as per Dadant 1992), and 3) a hive has about 141,545 comb cells (as per Meikle et al. 2016).

The number of nectar foraging trips per colony per year was calculated using the following equation:

$$\mathbf{FTN} = \frac{\mathbf{NC}}{\mathbf{NCFT}} \qquad \mathbf{(2)}$$

where, FTN is number of foraging trips per colony per year for nectar collection, NC is nectar collected per colony per year, and NCFT is nectar collected per foraging trip.

The total number of flowers for nectar collection was calculated using the following equation:

$$\mathbf{FN} = (\mathbf{FTN\ x\ FVN})\boldsymbol{x}\,\left(\frac{\mathbf{1}}{\boldsymbol{NRR\ x\ FL\ x\ HBA}}\right) \qquad \mathbf{(3)}$$

where FN is the number of flowers for nectar collection, FTN is number of foraging trips per colony per year for nectar collection, FVN is number of flowers visited per nectar foraging trip, NRR is nectar replenishment rate, FL is flower longevity, HBA is honey bee activity period. The number of flowers needed for colony nectar requirements is greatly reduced from the assumption that bees can visit the same flower more than once for nectar. This assumption was made based off: 1) honey bees are known to visit multiple flowers within a minute (Couvillon et al. 2015b), 2) honey bees are active for at least eight hours a day (Abou-Shaara 2014), 3) many flowers can replenish very quickly (i.e. within a minute) (based from Luo et al. 2014) , and 4) flowers can have an average flower longevity of a few days (Hicks et al. 2016). The extensive study performed by Hicks et al. (2016) was used for flower longevity values and was assumed to be a representative for most insect visited flowers in temperate areas since they measured flower longevity for 37 different species used within pollinator flower mixes and sampled over two million flowers.

The total number of flowers needed for pollen collection was calculated as follows:

$$\mathbf{FP} = \left(\frac{\mathbf{PC}}{\mathbf{PF}} \times \boldsymbol{FTP}\right) \boldsymbol{x}\ \frac{\mathbf{1}}{\left(\frac{\boldsymbol{PPF}}{\left(\frac{\boldsymbol{PF}}{\boldsymbol{FTP}}\right)}\right)} \tag{4}$$

where, FP is number of flowers for pollen collection, PC is pollen collected per colony per year, PF is pollen collected per foraging trip (mg), FTP is number of flowers visited per pollen foraging trip, and PPF is pollen production per flower (mg). The number of flowers needed for pollen collection takes into consideration that bees are likely able to visit the same flower more than once for pollen collection, based off our calculations that flowers produce more pollen in their lifetime than what they collect in a single pollen trip to a flower. For pollen requirement calculations we therefore took into consideration: 1) pollen produced per flower during their whole flowering period (from Hicks et al. 2016) and 2) pollen collected by honey bees per flower visit (pollen load weight divided by flowers visited per foraging trip). Pollen produced per flower (mg) was calculated using the volume of pollen produced from the flowers in Hicks et al. (2016), and the pollen densities from Sosnoskie et al. (2009) and Harrington and Metzger (1963).

The fifth equation calculates the total number of flowers needed per colony per year and was calculated with different values of "overlap use". The following equation is the last equation for all of three calculations, minimum, average, and maximum:

$$\boldsymbol{TF} = \left(\mathbf{FN} - (\mathbf{FN\ x\ OP})\right) + \left(\mathbf{FP} - (\mathbf{FN\ x\ OP})\right) + (\mathbf{FN\ x\ OP}) \qquad \mathbf{(5)}$$

where, TF is number of flowers for total floral collection per colony per year, FN is number of flowers needed for nectar collection, FP is number of flowers needed for pollen collection, and OP is overlap percentage of nectar and pollen collection. Bees can collect pollen and nectar from the same flower, but some flower species are only used for pollen or nectar collection (Gonzalez et al. 1995). Measurements of overlap between nectar and pollen collections range from 17-50% (Parker 1926; Free 1963; Renner et al. 2021). Therefore, for modelling the number of flowers and forage area, the number of flowers for total floral collection (number of flowers for pollen and nectar collection added) had three percentages (20% for maximum, 35% for average and 50% for minimum) of estimated collection overlap. The number of flowers needed for nectar collection was smaller than the number needed for pollen collection for the minimum, average, and maximum calculations. Therefore, when calculating the "overlap flowers", the equation was based on the number for nectar collection (FN) since these flowers would be the max number of flowers available for simultaneous nectar and pollen collection.

The final equation calculated the total amount of forage area a honey bee colony needs per year as follows:

$$\mathbf{AC} = \frac{\mathbf{TF}}{\mathbf{FD}} \qquad \mathbf{(6)}$$

where, AC is forage area per colony per year (km^2), TF is number of flowers for total floral collection per colony per year, and FD is flower density. Only articles that were representative of the whole landscape (e.g. consider water features and non-flowering crop area) were used for model input. The full model can be found in the Appendix B.

Parameter Sweeps

Parameter sweeps were conducted for the major sources of variation in results. Major sources of variation were found by graphing differences between the minimum, average and maximum results. Parameter sweeps were conducted by keeping every value at the average or median value (based on distribution as described above), except one parameter at a time that was changed to a value found from the literature search, that would result in the lowest or largest possible model output.

Results

The parameter values from published literature used to calculate the number of flowers and forage area needed for a honey bee colony per year can be found in Table 1. The calculated honey and nectar needed per colony per year, both include the 80.1kg of honey needed for consumption and the 15.4kg of honey needed for wax production for all results (minimum, average, and maximum). The calculated minimum, average, and maximum mass of honey needed per colony per year are: 118.3kg, 143.7kg, 195.1kg, respectively. The calculated minimum, average, and maximum mass of nectar needed per colony per year are: 148.4kg, 271.5kg, 522.6kg, respectively. The increased variation in honey requirements compared to nectar requirements is due to nectar sugar contents being different for minimum, average and maximum. The calculated minimum, average, and maximum number of flowers needed for a honey bee colony to have adequate honey production in either landscape (i.e. agricultural and urban landscapes were not calculated separately) are: 0.9 million, 72.7 million, and 54,842.4 million flowers, respectively (Fig. 2). The minimum, average, and maximum calculated forage area needed for a honey bee colony in urban landscapes are: 0.76 km^2, 59.77 km^2, 45,085.27 km^2, respectively. Lastly, the minimum, average, and maximum calculated forage area needed for a honey bee colony in agricultural landscapes are: 0.34 km^2, 26.99 km^2, 20,360.06 km^2, respectively. The major source of variation between the minimum, average, and maximum calculations was clearly from the number of flowers needed for pollen collection (refer to Fig. 2). All parameters that were associated with modeling the number of flowers needed for pollen collection were used for the parameter sweeps. Refer to Appendix A for parameter sweep results.

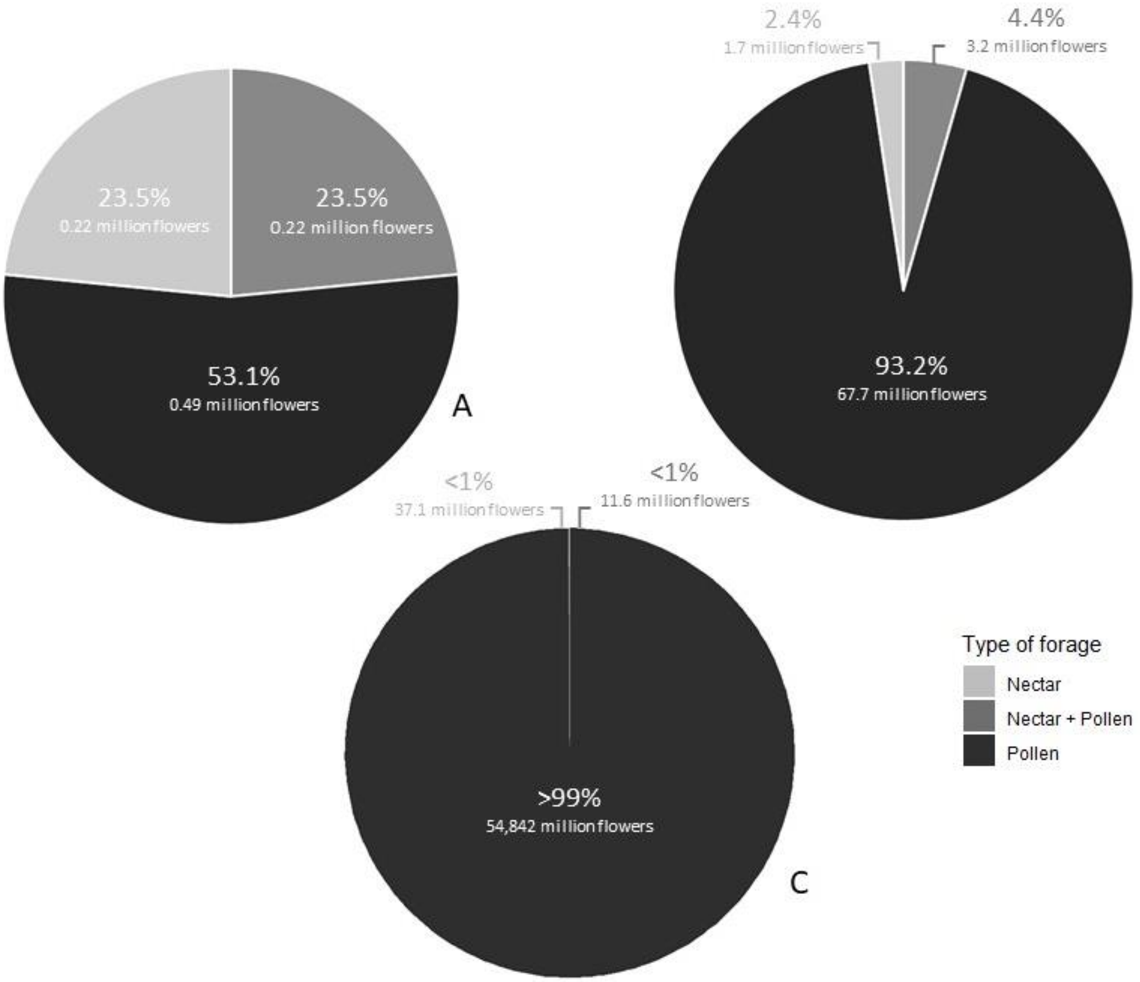


Figure 2. Proportions and numbers of flowers needed for pollen, nectar, and overlapping collection for minimum (A), average (B), and maximum (C) outputs for both agricultural and urban landscapes.

Table 1. Data from the literature reviews used to calculate the number of flowers and forage area a honey bee colony needs per year. SD stands for standard deviation.

Parameter	**Mean^a or Median^b ± SD**	**Minimum calculation value**	**Maximum calculation value**	**References**
Mass of honey collected from a colony per year (kg)^b	49.0 ± 23.7	22.9	97.2	(Seeley 1985; Nelson et al. 1993; Gatien and Currie 2003; Underwood et al. 2004; Currie and Gatien 2006; Mattila and Otis 2006; Cutler et al. 2014; Emsen et al. 2014; Smart et al. 2016; Langowska et al. 2017; Ovinge and Hoover 2018)
Mass of nectar per foraging trip (mg)^a	29.7 ± 14.6	40	19.3	(Park 1922; Ovinge and Hoover 2018)
Number of flowers visited per nectar forage bout	822.5			(Ribbands 1949)
Sugar content of nectar (%)^a	39.7 ± 14.9	59.8	28.0	(Kumar and Gupta 1993; Kreitlow and Tarpy 2006; Nagy-Déri et al. 2013; Fowler et al. 2016; Bandeira et al. 2018)
Sugar content of honey (%)	75.8			(Bandeira et al. 2018)
Mass of pollen collected per colony per year (kg)^a	18.2 ± 4.7	13.8	24.0	(Southwick and Pimentel 1981; O'Neal and Waller 1984; Seeley 1995; Mauriello et al. 2017)
Mass of pollen per foraging trip (mg)^a	12.2 ± 4.3	20.0	7.0	(Park 1922; Parker 1926; Vaissière and Vinson 1994; Fewell and Winston 1996; Kreitlow and Tarpy 2006; Leonhardt and Blüthgen 2012; Ovinge and Hoover 2018)
Number of flowers visited per pollen forage bout^a	202.7 ± 205	32.3	494	(Vansell 1942; Ribbands 1949; Percival 1950; Weaver et al. 1953)
***Urban floral density* (flowers per m^2)**	1.2			(Scriven et al. 2013)
***Agricultural floral density* (flowers per m^2)**	2.7			(Haenke et al. 2009)

Discussion

Understanding optimum hive densities that would ensure enough floral resources for managed honey bees and wild bee communities is needed for best management practices. This is the first model estimating the number of flowers and amount of forage area a honey bee hive requires for adequate honey harvesting for a full year within a temperate region. Future models of this nature may be a good starting point for policy decisions on hive densities, combined with field studies on bee competition, and local studies of floral resource availability. However, these estimates come with large amounts of uncertainty due to dynamic honey bee biology, floral resource phenology, and lack of multiple published data sources for many useful parameters.

Output Variability and Input Accuracy

The high amount of variation in model output is shown from the difference between the minimum and maximum estimates for both the number of flowers (a difference of 54,842 million flowers) and forage area needed (a difference of 20,360-45,085 km^2). The estimates for the average and minimum requirements are relatively close to each other comparatively, with a difference of 71.8 million flowers, and 26.6 km^2-59.0 km^2. This variation between average and maximum calculations mainly comes from the number of flowers required for pollen collection (Fig. 2). The number of flowers needed for pollen collection is about 800x larger for the maximum calculations than the average calculations. The parameter that had the largest impact on the number of flowers needed for pollen collection, and subsequentially the amount of forage area, was volume of pollen per flower (refer to Appendix A). If volume of pollen per flower was increased to the maximum value (while keeping all other values at the average) from Hicks et al.

(2016), then the flowers needed for pollen collection decreased by 99% (-6.71 million flowers), and the area needed for agricultural and urban areas both decreased by 92% (approximately -55km^2 for urban and -25km^2 for agricultural). If pollen volume per flower was decreased to the minimum value from Hicks et al. (2016) then the flowers needed for pollen collection increased by 60,518% (+40,900 million flowers) and the area needed for agricultural and urban areas both increased by 56,349% (approximately +33,619km^2 for urban and +15,182km^2 for agricultural). The differences in volume of pollen per flower from Hicks et al. (2016) corresponds to differences in the pollen volume across flower species, with the lowest volume from *Myosotis arvensis* (less than 0.01 μL) and the highest from *Leucanthemum vulgare* (15.92 μL). The only other parameter change that altered area output by 10% or more was pollen collected per colony per year, with the lowest input value decreasing area output by 23.5%, and the highest input value increasing area output by 30.8%. However, considering the relative agreement between the minimum (0.67 hives km^{-2} in urban and 0.30 hives km^{-2} in agricultural landscapes) and average (59.2 hives km^{-2} in urban and 26.7 hives km^{-2} in agricultural landscapes) calculations these estimates are likely to be more reliable. As such, we will primarily focus on the minimum and average calculations for the rest of the discussion.

We are unable to compare many of our parameters to other datasets that include unpublished literature; however, honey production is easily comparable. For example, the USDA and Statistics Canada provide values for honey production in terms that are either honey production per colony, or easily can be converted to honey production per colony, respectively. From 2016-2019, US colonies produced about 25.4 kg of honey on average (USDA 2019) and Canadian hives produced about 53.7 kg per colony (Statistics Canada 2020). However, most Canadian hives are within prairie provinces, which have higher honey yields than other provinces. Almost half of the studies used were also from the Canadian prairies (Nelson et al. 1993; Gatien and Currie 2003; Underwood et al. 2004; Currie and Gatien 2006; Ovinge and Hoover 2018), therefore our results of 49 kg for average honey harvest per colony may be representative of these specific provinces in Canada. However, this input could easily be changed according to honey production per colony values within the region of interest.

Output Implications

Although our results may not be uniformly representative due to the high variability of model output and lack of literature, some model output values are comparable to those from studies that have calculated foraging ranges of honey bees in agricultural and urban environments. Honey bees often stay within 1 km of their hive unless resources become very scarce (i.e. summer), which equates to about a 3.14 km^2 foraging area (Couvillon et al. 2014, 2015a; Garbuzov et al. 2015a, b); both of our minimum calculations are within a 1 km radius from the hive (0.34km^2 in urban landscapes and 0.76km^2 in agricultural landscapes). However, it has also been shown that honey bees may travel up to 3 km, especially during periods of dearth, which equates to about 28.3 km^2 (Couvillon et al. 2014, 2015a; Garbuzov et al. 2015b). Our average calculation for agricultural landscapes (27 km^2), might be more representative for honey bee colonies during periods with scarce floral resources.

Our findings also highlight that honey bees may need a much larger number of flowers for pollen collection relative to nectar, with about 53% to >99% of flowers being specifically for pollen collection (for the minimum and average estimates), and the other <1% to 47% for nectar collection and combined nectar and pollen collection. Although hives need more nectar than pollen per year, this large difference between the number of flowers needed comes from our model calculating that nectar flowers can be visited more times during their bloom period relative to pollen flowers, mainly due to high nectar replenishment rates (Luo et al. 2014). Additionally, in temperate habitats, 10%-37% of total solitary bee species are oligolectic (i.e. they specialize in pollen collection from certain genera or species) (Moldenke 1979; Frankie et al. 2009b; Danforth et al. 2019); this may cause them to be particularly vulnerable to depleted pollen resources, especially for plant species that are commonly used by honey bees. This emphasizes potential importance of providing pollen producing plants to support more bees in a given area.

Knowledge Gaps, Suggestions for Future Research, and Conclusions

There are many input values for this model that should be interpreted with caution, due to limitations of the available published literature. Multiple parameters only had a single study associated with them and require further replication (Table 1). For example, only one study measured how many flowers a bee had to visit to gather one load of nectar (Ribbands 1949). This study only measured this parameter for two genera of flowers, *Limnanthes* and *Nemophila*, and for four out of the six measurements the bees gathered both pollen and nectar. While clearly limited, we included the numbers from pollen and nectar foraging trips within our estimates because they make for a more conservative estimate of the number of flowers needed for nectar foraging (since on average the number of flowers for nectar foraging was about double the number for nectar and pollen foraging; Ribbands 1949). Pollen volume per flower is another parameter that should be investigated further considering the huge impact that it had on the model output (as mentioned previously). More local studies are needed to understand pollen availability across different habitats. Hicks et al. (2016) include a variety of plant species, but data for the most common species in areas of interest are needed to more accurately model honey bee requirements.

Another important knowledge gap is floral density values for both urban and agricultural landscapes. Our literature search only produced one study for both landscape types, and these values are very likely not representative of all urban areas or agricultural landscapes on a larger scale, and likely better represent the specific system they were measured in. Scriven et al. (2013) conducted their study on land surrounding an aluminium smelter in the UK, which mainly consisted of intensively managed grassland, that would likely have a very different floral density compared to a dense, urban center. Haenke et al. (2009) conducted their study in North Germany in an area that was dominated by agricultural use, with the main crop being wheat, and with sites having a range of 30-100% arable land. Their measured floral density may not be representative of areas that are more or less intensively dominated by agriculture, and the different crops in the area would have a large impact on how many flowers are available and accessible for honey bee foraging. Most current studies do not measure flower density at a large enough scale for these estimates and only include areas that are likely to have flowers, for example gardens and sown flower strips (Sutherland et al. 2001; Egerer et al. 2018). Honey bees have also been found to mainly collect pollen from trees in temperate urban and agricultural landscapes (Richardson et al. 2015; Lau et al. 2019) and ensuring we include accurate estimates of flowering trees is very important for increasing our understanding of honey bee forage area requirements. Further studies should be done to capture floral density values to ensure we understand how many resources bees have in landscapes for modelling honey bee area requirements.

Other than parameter values, our current model also lacks an understanding of many processes that should be taken into consideration. Flowers for nectar collection were not the main driver of model output variability, but future models should include more information on nectar replenishment and flower longevity. Luo et al. (2014) is currently the best study on nectar replenishment rates since previous experiments measured replenishment every few hours instead of minutes (e.g. Castellanos et al. (2002)), however more research is needed to confirm how common rapid nectar replenishment is among bee-visited plants. Our model assumed that a flower could refill with nectar every minute, which is potentially an overestimate of replenishment rates. Williams (1998) found that 50% of honey bees will visit a flower that was recently visited by a honey bee if the nectar is replenished and Stout and Goulson (2001) found that honey bees rejected flowers (*Melilotus officinalis*) 50% of the time, even if they were never visited by any bees previously. Despite these differences, calculations of the number of flowers needed for nectar collection in this paper are still likely to be conservative based on the assumptions of honey bee visitation and nectar replenishment rates. Other processes that should be taken into consideration in future models are: honey bee management differences (i.e. initial colony sizes, disease management, etc.), foraging effort of honey bees (which impacts resource requirements of foragers), turn over of plants (since the current model assumes that plants take up a certain area for the whole growing season), and variation in honey bee energy consumption throughout the year (e.g. summer vs winter as well, not just forager vs worker in the nest). This current model does not include these processes because of a lack of information in the published literature. In addition, future models should take into consideration the nutritional quality of pollen (e.g. protein content), as this may impact the quantity of resources needed by a hive and the health of the hive (Di Pasquale et al. 2013; Ghosh et al. 2020). Therefore, the current output from this model should be taken as a starting point as more research is needed to better understand honey bee forage requirements.

Honey bees and wild bees have both been shown to be negatively affected by high honey bee hive density (Goulson and Sparrow 2009a; Badano and Vergara 2011; Henry and Rodet 2018). Our results provide a foundation for modelling optimal hive densities for honey bee health, and may be informative for future wild bee population conservation research and management. Local-scale studies on many parameters are needed to model forage area requirements accurately for policy decisions, for example flower phenology and density, honey bee overwintering energy requirements, and impacts of hive management. Both managed honey bees and diverse wild bee communities are necessary to fulfill the pollination requirements for several crops and natural ecosystems (Button and Elle 2014; Klein et al. 2018), and bee competition is one of many anthropogenically-induced stressors on both managed honey bees (Henry and Rodet 2018) and wild pollinators (Potts et al. 2010a), but we need to start developing best management practices to prevent further losses of native pollinators and the ecosystem services they provide.

References

Abou-Shaara HF (2014) The foraging behaviour of honey bees, *Apis mellifera*: a review. Vet Med (Praha) 59:1–10. https://doi.org/10.17221/7240-VETMED

Abrol DP (2012) Consequences of introduced honeybees upon native bee communities. In: Pollination Biology: Biodiversity Conservation and Agricultural Production. Springer Netherlands, Dordrecht, pp 635–667

Aizen MA, Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano." Ecol Appl 4:378–392. https://doi.org/10.2307/1941941

Aizen MA, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr Biol 19:915–918. https://doi.org/10.1016/J.CUB.2009.03.071

Al-Ghamdi A, Adgaba N, Getachew A, Tadesse Y (2016) New approach for determination of an optimum honeybee colony's carrying capacity based on productivity and nectar secretion potential of bee forage species. Saudi J Biol Sci 23:92–100. https://doi.org/10.1016/j.sjbs.2014.09.020

Al-Ghamdi A, Hoopingarner R (2004) Modeling of honey bee and Varroa mite population dynamics. Saudi J Biol Sci 11:21–36

Alger SA, Burnham PA, Boncristiani HF, Brody AK (2019) RNA virus spillover from managed honeybees (*Apis mellifera*) to wild bumblebees (*Bombus spp*.). PLoS One 14:e0217822. https://doi.org/10.1371/journal.pone.0217822

Alqarni AS (2015) Honeybee foraging, nectar secretion, and honey potential of wild jujube trees, *Ziziphus nummularia*. Neotrop Entomol 44:232–241. https://doi.org/10.1007/s13744-015-0279-4

Badano EI, Vergara CH (2011) Potential negative effects of exotic honey bees on the diversity of native pollinators and yield of highland coffee plantations. Agric For Entomol 13:365–372. https://doi.org/10.1111/j.1461-9563.2011.00527.x

Bandeira AMP, Gomes VV, Vasconcelos AA, et al (2018) Antioxidant activity and physicochemical characteristics of honeys from the eastern Amazon region, Brazil. Acta Amaz 48:158–167. https://doi.org/10.1590/1809-4392201702721

Black J (2006) Honeybee Nutrition: Review of re-search and practices. Barton, Australia

Branchiccela B, Castelli L, Corona M, et al (2019) Impact of nutritional stress on the honeybee colony health. Sci Rep 9:1–11. https://doi.org/10.1038/s41598-019-46453-9

Brosi BJ, Delaplane KS, Boots M, De Roode JC (2017) Ecological and evolutionary approaches to managing honey bee disease. Nat Ecol Evol 1:1250–1262. https://doi.org/10.1038/s41559-017-0246-z

Button L, Elle E (2014) Wild bumble bees reduce pollination deficits in a crop mostly visited by managed honey bees. Agric Ecosyst Environ 197:255–263. https://doi.org/10.1016/j.agee.2014.08.004

Cameron SA, Lozier JD, Strange JP, et al (2011) Patterns of widespread decline in North American bumble bees. Proc Natl Acad Sci U S A 108:662–667. https://doi.org/10.1073/pnas.1014743108

Castellanos MC, Wilson P, Thomson JD (2002) Dynamic nectar replenishment in flowers of *Penstemon* (Scrophulariaceae). Am J Bot 89:111–118. https://doi.org/10.3732/ajb.89.1.111

Colla SR, MacIvor JS (2017) Questioning public perception, conservation policy, and recovery actions for honeybees in North America. Conserv Biol 31:1202–1204. https://doi.org/10.1111/cobi.12839

Colla SR, Otterstatter MC, Gegear RJ, Thomson JD (2006) Plight of the bumble bee: Pathogen spillover from commercial to wild populations.

https://doi.org/10.1016/j.biocon.2005.11.013

Couvillon MJ, Riddell Pearce FC, Accleton C, et al (2015a) Honey bee foraging distance depends on month and forage type. Apidologie 46:61–70. https://doi.org/10.1007/s13592-014-0302-5

Couvillon MJ, Schü Rch R, Ratnieks FLW (2014) Waggle dance distances as integrative indicators of seasonal foraging challenges. PLoS One 9:93495. https://doi.org/10.1371/journal.pone.0093495

Couvillon MJ, Walter CM, Blows EM, et al (2015b) Busy bees: variation in insect flower-visiting rates across multiple plant species. Psyche. https://doi.org/10.1155/2015/134630

Currie R., Gatien P (2006) Timing acaricide treatments to prevent *Varroa destructor* (Acari: Varroidae) from causing economic damage to honey bee colonies - ProQuest. Can Entomol 138:238–252

Cutler GC, Scott-Dupree CD, Sultan M, et al (2014) A large-scale field study examining effects of exposure to clothianidin seed-treated canola on honey bee colony health, development, and overwintering success. PeerJ. https://doi.org/10.7717/peerj.652

Dadant C (1992) The hive and the honey bee. Dadant & Sons Inc., Hamilton, USA

Danforth BN, Minckley RL, Neff JL (2019) The solitary bees: biology, evolution, conservation. Princeton University Press, Princeton, NJ

DeGrandi-Hoffman G, Roth SA, Loper GL, Erickson EH (1989) BEEPOP: A honeybee population dynamics simulation model. Ecol Modell 45:133–150. https://doi.org/10.1016/0304-3800(89)90088-4

Di Pasquale G, Salignon M, Le Conte Y, et al (2013) Influence of pollen nutrition on honey bee health: do pollen quality and diversity matter? PLoS One 8:e72016. https://doi.org/10.1371/journal.pone.0072016

Dolezal A, Carrillo-Tripp J, Judd T, et al (2019) Interacting stressors matter: diet quality and virus infection in honeybee health. R Soc Open Sci 6:. https://doi.org/http://dx.doi.org/10.1098/rsos.181803

Dynes TL, Berry JA, Delaplane KS, et al (2019) Reduced density and visually complex apiaries reduce parasite load and promote honey production and overwintering survival in honey bees. PLoS One 14:. https://doi.org/10.1371/journal.pone.0216286

Egerer MH, Liere H, Lin BB, et al (2018) Herbivore regulation in urban agroecosystems: Direct and indirect effects. Basic Appl Ecol 29:44–54. https://doi.org/10.1016/j.baae.2018.02.006

Emsen B, Guzman-Novoa E, Kelly PG (2014) Honey production of honey bee (Hymenoptera: Apidae) colonies with high and low Varroa destructor (Acari: Varroidae) infestation rates in eastern Canada. Can Entomol 146:236–240. https://doi.org/10.4039/tce.2013.68

Farrar C (1934) Bees must have pollen. Bee Cult 62:276–278

Fewell JH, Winston ML (1996) Regulation of nectar collection in relation to honey storage levels by honey bees, *Apis mellifera*. Behav Ecol 7:286–291

Fowler RE, Rotheray EL, Goulson D (2016) Floral abundance and resource quality influence pollinator choice. Insect Conserv Divers 9:481–494. https://doi.org/10.1111/icad.12197

Frankie GW, Thorp RW, Pawelelk J, et al (2009) Urban bee diversity in a small residential garden in Northern California. J Hymenopt Res 18:368–379

Free J (1963) The flower constancy of honeybees. J Anim Ecol 32:119–131

Fries I, Camazine S (2001) Implications of horizontal and vertical pathogen transmission for honey bee epidemiology. Apidologie 32:199–214

Garbuzov M, Couvillon MJ, Schürch R, Ratnieks FLW (2015a) Honey bee dance decoding and pollen-load analysis show limited foraging on spring-flowering oilseed rape, a potential source of neonicotinoid contamination. Agric Ecosyst Environ 203:62–68. https://doi.org/10.1016/j.agee.2014.12.009

Garbuzov M, Schürch R, Ratnieks FLW (2015b) Eating locally: dance decoding demonstrates that urban honey bees in Brighton, UK, forage mainly in the surrounding urban area. Urban Ecosyst 18:411–418. https://doi.org/10.1007/s11252-014-0403-y

Gatien P, Currie R (2003) Timing of acaracide treatments for control of low-level populations. Can Entomol 135:749–763

Ghosh S, Jeon H, Jung C (2020) Foraging behaviour and preference of pollen sources by honey bee (Apis mellifera) relative to protein contents. J Ecol Environ 44:1–7. https://doi.org/10.1186/s41610-020-0149-9

Giacobino A, Cagnolo NB, Merke J, et al (2014) Risk factors associated with the presence of Varroa destructor in honey bee colonies from east-central Argentina. Prev Vet Med 115:280–287. https://doi.org/10.1016/j.prevetmed.2014.04.002

Gonzalez A, Rowe C, Weeks R, Whittle Gilbert CJ Barnard DF (1995) Flower choice by honey bees (Apis mellifera L.): sex-phase of flowers and preferences among nectar and pollen foragers. Oecologia 101:258–264

Goulson D, Nicholls E, Botías C, Rotheray EL (2015) Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science 34. https://doi.org/10.1126/science.1255957

Goulson D, Sparrow KR (2009) Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. J Insect Conserv 13:177–181. https://doi.org/10.1007/s10841-008-9140-y

Haenke S, Scheid B, Schaefer M, et al (2009) Increasing syrphid fly diversity and density in sown flower strips within simple vs. complex landscapes. J Appl Ecol 46:1106–1114. https://doi.org/10.1111/j.1365-2664.2009.01685.x

Harrington JB, Metzger K (1963) Ragweed pollen density. Am J Bot 50:532–539. https://doi.org/10.1002/j.1537-2197.1963.tb07226.x

Harris J (2008) Effect of brood type on Varroa sensitive hygiene by worker honey bees (Hymenoptera: *Apidae*). Entomol Soc Am 101:1137–1144

Henry M, Rodet G (2018) Controlling the impact of the managed honeybee on wild bees in protected areas. Sci Rep 8:. https://doi.org/10.1038/s41598-018-27591-y

Hicks DM, Ouvrard P, Baldock KCR, et al (2016) Food for pollinators: quantifying the nectar and pollen resources of urban flower meadows. PLoS One 11:e0158117. https://doi.org/10.1371/journal.pone.0158117

Honey Bee Health Coalition (2017) Beekeeper insights on honey bee nutrition supplements. Keystone Policy Center

Joseph Esteves RP, Villadelrey MC, Rabajante JF (2010) Determining the optimal distribution of bee colony locations to avoid overpopulation using mixed integer programming. J Nat Stud 9:79–82

Klein AM, Boreux V, Fornoff F, et al (2018) Relevance of wild and managed bees for human well-being. Curr. Opin. Insect Sci. 26:82–88

Kreitlow KL, Tarpy DR (2006) Environmental and genotypic effects on Russian-hybrid and Italian honey bee (*Apis mellifera*) (Hymenoptera: Apidae) Foraging Behavior. Environ Entomol 35:1610–1616

Kumar J, Gupta J. (1993) Nectar sugar production and honeybee foraging activity in 3 species of onion (*Allium* species). Apidologie 24:391–396

Langowska A, Zawilak M, Sparks TH, et al (2017) Long-term effect of temperature on honey yield and honeybee phenology. Int J Biometeorol 61:1125–1132. https://doi.org/10.1007/s00484-016-1293-x

Lau P, Bryant V, Ellis JD, et al (2019) Seasonal variation of pollen collected by honey bees (*Apis mellifera*) in developed areas across four regions in the United States. PLoS One 14:. https://doi.org/10.1371/journal.pone.0217294

Leonhardt SD, Blüthgen N (2012) The same, but different: pollen foraging in honeybee and bumblebee colonies. Apidologie 43:449–464. https://doi.org/10.1007/s13592-011-0112-y

Luo EY, Ogilvie JE, Thomson JD (2014) Stimulation of flower nectar replenishment by removal: A survey of eleven animal-pollinated plant species. J Pollinat Ecol 12:52–62

Mattila HR, Otis GW (2006) Influence of pollen diet in spring on development of honey bee (Hymenoptera: *Apidae*) colonies. J Econ Entomol 99:604–613.

https://doi.org/10.1093/jee/99.3.604

Mauriello G, De Prisco A, Di Prisco G, et al (2017) Microbial characterization of bee pollen from the Vesuvius area collected by using three different traps. PLoS One 12:e0183208. https://doi.org/10.1371/journal.pone.0183208

Meikle WG, Weiss M, Stilwell AR (2016) Monitoring colony phenology using within-day variability in continuous weight and temperature of honey bee hives. Apidologie 47:1–14. https://doi.org/10.1007/s13592-015-0370-1

Moffat L (2000) Changes in the metabolic rate of the foraging honeybee: effect of the carried weight or of the reward rate? J Comp Physiol A 186:299–306

Moldenke A (1979) Host-plant coevolution and the diversity of bees in relation to the flora of North America. Phytologia 43:357–419

Nagy-Déri H, Orosz-Kovács Z, Farkas Á (2013) Comparative studies on nectar from two self-fertile and two self-sterile cultivars of quince (*Cydonia oblonga* Mill.) and their attractiveness to honeybees. J Hortic Sci Biotechnol 88:776–782. https://doi.org/10.1080/14620316.2013.11513038

Naug D (2009) Nutritional stress due to habitat loss may explain recent honeybee colony collapses. Biol Conserv 142:2369–2372. https://doi.org/10.1016/J.BIOCON.2009.04.007

Nelson D, Sporns P, Kristiansen P, et al (1993) Effectiveness and residue levels of 3 methods of menthol application to honey bee colonies for the control of tracheal mites. Apidologie 24:549–556

Neumann P, Carreck NL (2010) Honey bee colony losses. J Apic Res 49:1–6.

https://doi.org/10.3896/IBRA.1.49.1.01

O'Neal RJ, Waller GD (1984) On the pollen harvest by the honey bee (*Apis mellifera* L.) near Tucson, Arizona (1976-1981). Desert Plants 6:81–109

Ovinge LP, Hoover SE (2018) Comparison of honey bee (Hymenoptera: Apidae) colony units of different sizes as pollinators of hybrid seed canola. J Econ Entomol 111:1535–1541. https://doi.org/10.1093/jee/toy155

Park W (1922) Time and labor factors involved in gathering pollen and nectar. J Econ Entomol 15:129–134

Parker R (1926) The collection and utilization of pollen by the honey bee. Cornell Univ Agric Exp Stn 98.

Percival M (1950) Pollen Presentation and Pollen Collection. New Phytol 46.

Potts SG, Biesmeijer JC, Schweiger O, Kunin W (2010a) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353. https://doi.org/10.1016/j.tree.2010.01.007

Potts SG, Imperatriz-Fonseca V, Ngo HT, et al (2016) Safeguarding pollinators and their values to human well-being. Nature 540:220–229. https://doi.org/10.1038/nature20588

Potts SG, Roberts SPM, Dean R, et al (2010b) Declines of managed honey bees and beekeepers in Europe. J Apic Res 49:15–22. https://doi.org/10.3896/IBRA.1.49.1.02

Pritchard ZA, Hendriksma HP, St Clair AL, et al (2021) Do viruses from managed honey bees (Hymenoptera: *Apidae*) endanger wild bees in native prairies? Environ Entomol. https://doi.org/10.1093/ee/nvaa181

Renner SS, Graf MS, Hentschel Z, et al (2021) High honeybee abundances reduce wild bee abundances on flowers in the city of Munich. Oecologia 1:3. https://doi.org/10.1007/s00442-021-04862-6

Ribbands CR (1949) The foraging method of individual honey-bees. J Anim Ecol 18:47–66

Richardson RT, Lin C-H, Sponsler DB, et al (2015) Application of ITS2 metabarcoding to determine the provenance of pollen collected by honey bees in an agroecosystem. Appl Plant Sci 3:1400066. https://doi.org/10.3732/apps.1400066

Rodney S, Purdy J (2020) Dietary requirements of individual nectar foragers, and colony-level pollen and nectar consumption: a review to support pesticide exposure assessment for honey bees. Apidologie 51:163–179. https://doi.org/10.1007/s13592-019-00694-9

Rueppell O, Bachelier C, Fondrk MK, Page RE (2007) Regulation of life history determines lifespan of worker honey bees (*Apis mellifera* L.). Exp Gerontol 42:1020–1032. https://doi.org/10.1016/j.exger.2007.06.002

Russell S, Barron AB, Harris D (2013) Dynamic modelling of honey bee (*Apis mellifera*) colony growth and failure. Ecol Modell 265:158–169. https://doi.org/10.1016/j.ecolmodel.2013.06.005

Schmickl T, Crailsheim K (2004) Inner nest homeostasis in a changing environment with special emphasis on honey bee brood nursing and pollen supply. Apidologie 35:249–263. https://doi.org/10.1051/apido:2004019

Schmolz E, Hoffmeister D, Lamprecht I (2002) Calorimetric investigations on metabolic rates and thermoregulation of sleeping honeybees (*Apis mellifera carnica*). Thermochim Acta

382:221–227

Scriven LA, Sweet MJ, Port GR (2013) Flower density is more important than habitat type for increasing flower visiting insect diversity. Int J Ecol 2013:. https://doi.org/10.1155/2013/237457

Seeley TD (1985) Honeybee ecology: A study of adaptation in social life. Princeton University Press, Princeton, NJ

Seeley TD (1995) The Wisdom of the Hive. Harvard University Press, Cambridge, MA

Singh R, Levitt AL, Rajotte EG, et al (2010) RNA viruses in Hymenopteran pollinators: evidence of inter-taxa virus transmission via pollen and potential impact on non-*Apis* Hymenopteran species. PLoS One 5:e14357. https://doi.org/10.1371/journal.pone.0014357

Smart MD, Pettis JS, Euliss N, Spivak MS (2016) Land use in the Northern Great Plains region of the U.S. influences the survival and productivity of honey bee colonies. Agric Ecosyst Environ 230:139–149. https://doi.org/10.1016/j.agee.2016.05.030

Sosnoskie LM, Webster TM, Dales D, et al (2009) Pollen grain size, density, and settling velocity for Palmer Amaranth (*Amaranthus palmeri*). Weed Sci 57:404–409. https://doi.org/10.1614/WS-08-157

Southwick EE, Pimentel D (1981) Energy efficiency of honey production by bees. Bioscience 31:730–732. https://doi.org/10.2307/1308779

Statistics Canada (2020) Production and value of honey. In: 2020. https://www150.statcan.gc.ca/t1/tbl1/en/tv.action?pid=3210035301. Accessed 20 Sep 2020

Stout J, Goulson D (2001) The use of conspecific and interspecific scent marks by foraging bumblebees and honeybees. Anim Behav 62:183–189. https://doi.org/https://doi.org/10.1006/anbe.2001.1729

Sutherland JP, Sullivan MS, Poppy GM (2001) Distribution and abundance of aphidophagous hoverflies (Diptera: *Syrphidae*) in wildflower patches and field margin habitats. Agric For Entomol 3:57–64. https://doi.org/10.1046/j.1461-9563.2001.00090.x

Tosi S, Nieh JC, Sgolastra F, et al (2017) Neonicotinoid pesticides and nutritional stress synergistically reduce survival in honey bees. Proc R Soc B 284:20171711. https://doi.org/10.1098/rspb.2017.1711

Tsvetkov N, Samson-Robert O, Sood K, et al (2017) Chronic exposure to neonicotinoids reduces honey bee health near corn crops. Science 356:1395–1397. https://doi.org/10.1126/science.aam7470

Underwood RM, Lewis MJ, Hare JF (2004) Reduced worker relatedness does not affect cooperation in honey bee colonies. Can J Zool 82:1542–1545. https://doi.org/10.1139/Z04-138

USDA (2019) Honey. In: Stat. Mark. Inf. Syst. https://usda.library.cornell.edu/concern/publications/hd76s004z?locale=en. Accessed 30 Jan 2021

Vaissière BE, Vinson SB (1994) Pollen morphology and its effect on pollenl collection by honey bees, Apis Mellifera L. (Hymenoptera: Apidae), with special Reference to Upland Cotton, Gossypium Hirsutum L. (Malvaceae). Grana 33:128–138. https://doi.org/10.1080/00173139409428989

Vansell G (1942) Factors affecting the usefulness of honey-bees in pollination. US Dep Agric 650:31

Weaver N, Alex A, Thomas F (1953) Pollination of Hubam clover by honeybees. Prog Reports Texas Agric Exp Stn 1559:1–3

Williams CS (1998) The identity of the previous visitor influences flower rejection by nectar-collecting bees. Anim Behav 56:673–681

Chapter 2: Assessing the impacts of urban beehives on wild bees using individual, population-level, and community level metrics

Sarah E. MacKell, Hadil L. Elsayed, and Sheila R. Colla

Author's Contributions:

SEM and SRC, conceived of the ideas. SEM led the development of the field methodology. SEM and HLE contributed equally to the collection of data in the field and processing of samples (i.e. identifying and measuring). SEM led the data analysis, but HLE conducted the trait composition analysis. SEM led the writing of the manuscript. All authors contributed to editing and gave final approval for inclusion into the dissertation and eventual publication to a peer-reviewed journal article.

We intend to submit this manuscript for publication in a peer-reviewed journal.

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). Alarmingly, 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, 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 and can deplete resources quickly in areas with abundant floral resources (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. 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 (Mallinger et al. 2017). Only two studies have investigated honey bee and native bee competition within urban landscapes and one found that there was evidence of competition with relatively high hive density (6.5 hives/km^2) (Ropars et al. 2019) and the other found no signs of competition with relatively low hive density (0.32 – 0.48 hives/km^2) (McCune et al. 2020). 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 (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/km^2 for 2019 and 0.93 hives/km^2 for 2018 (OMAFRA 2021, personal communication). We assess 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).

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.

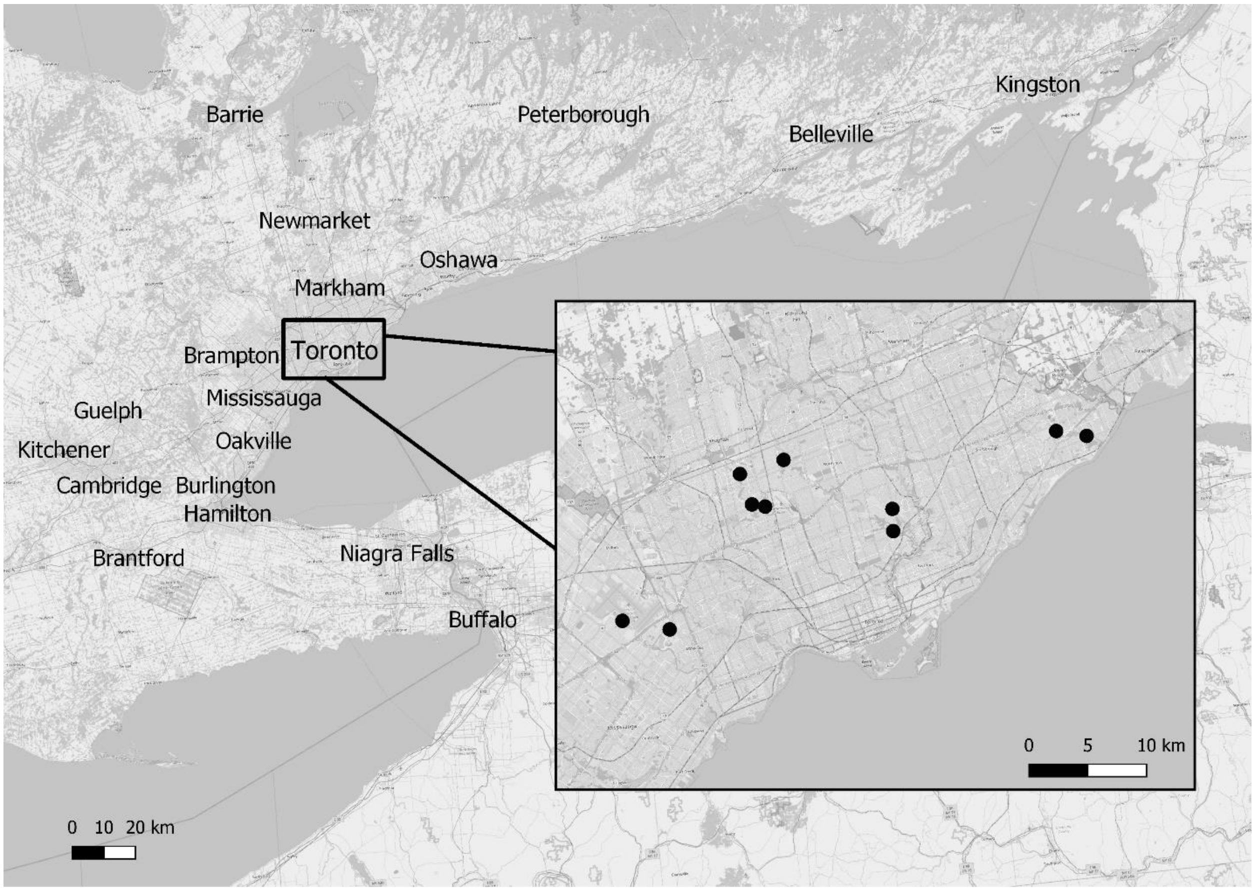


Figure 1. Map of the ten study sites across the GTA.

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 stored at York University, except *Triepeolus* specimens that are stored at the Canadian Museum of Nature. Refer to Appendix C 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 had their heads and thoraxes measured. 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). 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.

Floral resource assessment

Floral density (number of flowers per m^2) 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 $0.58m^2$ 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.

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 Δ $AIC_c < 2$ (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, an 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. 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 unweighted functional dispersion (FDis), was calculated from our trait database and presence-absence data of all species at our 10 sites. 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. FDis was chosen because this parameter is independent of species richness and represents the mean distance of each species to the centroid of all other species within trait space (Laliberte and Legendre 2010). 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 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.

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 Eusocial 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 Fall 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)

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 Appendix D. 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	-0.19		0.78**	0.2	0.3
Impervious surface at 1km	-0.36	0.78**		0.37	0.48
Flower Density	-0.33	0.2	0.37		0.69*
Flower Richness	-0.63^{N}	0.3	0.48	0.69*	

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

Abundance

Two species were found to be negatively associated with relative honey bee abundance (*Lasioglossum mitchelli* Gibbs and *Nomada bethunei* Grote and Robinson) (Figure 2A and 2B, respectively) and none of the genera or species were positively associated with relative honey bee abundance. However, 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. The genera that were identified for further investigation from the RDA were: *Agapostemon, Andrena, Anthidium, Calliopsis, Coelioxys, Colletes, Halictus, Lasioglossum, Nomada, Osmia, Sphecodes, Stelis, Triepeolus,* and *Xylocopa*. Therefore, 14 out of the total 31 genera of wild bee species were further investigated for trends with relative honey bee abundance. Refer to Appendix E 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. mitchelli, L. paradmirandum* Knerer and Atwood, *L. weemsi* Mitchell, and *Osmia conjuncta* Cresson) had negative relationships with impervious surface at 500m. However, *Nomada bethunei* 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 mitchelli,* and *L. paradmirandum*) had a positive relationship with impervious surface at 1km. One genera (*Osmia)* and three species (*Lasioglossum mitchelli, L. paradmirandum,* and *L. weemsi*) had a significantly negative relationship with flower richness, but two species (*Halictus ligatus* Say and *Colletes inaequalis* Say) 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 trait composition (i.e. FDis with all traits) was found to have a significantly negative association with relative abundance of honey bees (Gaussian GLM, $\chi^2(7) = 0.005$, t = -2.64, p = 0.028; refer to Figure 2D) and only relative abundance of honey bees and impervious surface at 1km were included in the final model after model selection. None of the individual trait FDis models had a significantly negative relationship with relative abundance of honey bees, but diet had a near significant negative relationship with relative abundance of honey bees (Gaussian GLM, $\chi^2(8) = 0.045$, t = -1.939, p = 0.052). Sociality FDis had a significantly negative relationship with flower density, but pollen strategy had a significantly positive relationship with flower density. Seasonality FDis had a significantly positive relationship with flower richness and sociality had a significantly negative relationship with impervious surface at 500m. Refer to Appendix F 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

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

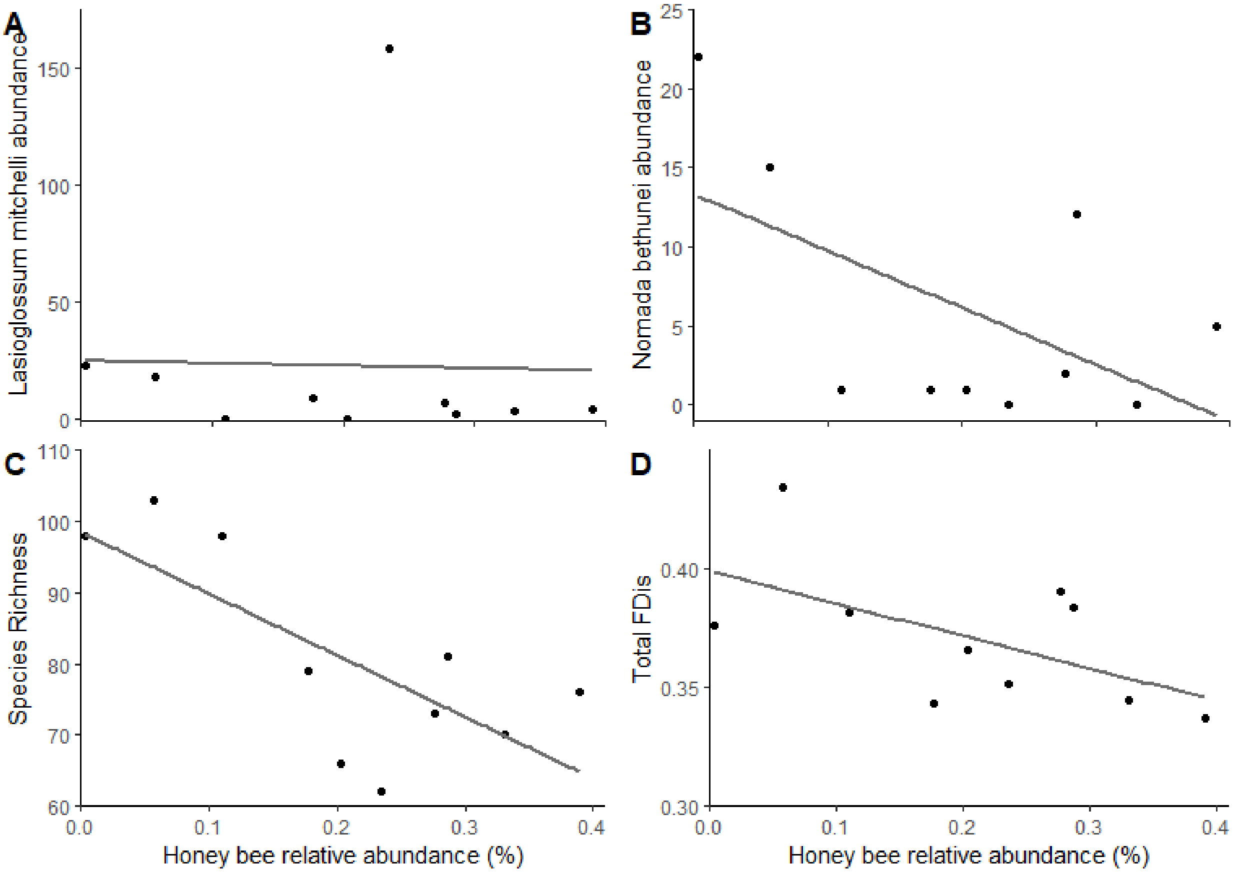


Figure 2. A: *Lasioglossum mitchelli* was negatively associated with relative honey bee abundance (Poisson GLM, $\chi^2(7) = 439.02$, $z = -6.577$, $p<0.001$). When the outlier was taken out the relationship between relative honey bee abundance and *L. mitchelli* became further negative and the p-value 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 ($p = 0.028$). 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.

			Flower Density			***Flower Diversity***			***Relative Apis***			***Imp.Surface.1000***			***Imp.Surface.500***		
Species	**F/M**	**T/H**	**Res. Dev**	**t**	**Est.**	**Res. Dev**	**t**	**Est.**	**Res. Dev**	**t**	**Est.**	**Res. Dev**	**t**	**Est.**	**Res. Dev**	**t**	**Est.**
Augochlorella aurata	F	T	2.692	0.651	0.001				2.576	0.430	0.205^{N}	2.539	2.639	0.900	2.442	-2.265	-0.671^{N}
Augochlorella aurata	F	H	1.016	-4.340	-0.001				0.896	-5.246	-0.780***	0.837	3.026	0.387*			
Bombus griseocollis	M	T				9.796	1.803	0.059	8.964	2.567	1.669^{N}						
Bombus impatiens	F	H	70.499	1.811	0.001	62.477	-2.481	-0.076***	61.937	1.663	0.251^{N}				61.261	-2.432	-0.313^{N}
Bombus rufocinctus	F	H	23.212	1.625	0.000				22.866	2.305	0.325^{N}						
Bombus rufocinctus	M	T							28.694	3.599	1.879**	28.495	2.081	2.751	27.907	-1.909	-1.580
Bombus rufocinctus	M	H							7.116	2.271	0.594^{N}	7.036	1.171	0.775	7.001	-0.928	-0.384
Colletes inaequalis	F	H	14572.500	-3.760	-0.189	8894.700	8.398	27.042***	7570.600	3.945	74.641**						
Nomada bethunei	F	T	7.146	1.763	0.004	7.026	-2.157	-0.452	6.376	-2.125	-0.917^{N}	2.317	2.167	5.779^{N}			

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

Discussion

Impact of honey bees on wild bees

We found that increasing abundance of honey bees was negatively associated with total wild bee functional diversity, species richness, and certain species' abundance (*Lasioglossum mitchelli* and *Nomada bethunei*) and body size (*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/km^2) and the relatively high hive density of Ropars *et al.* (2019) (6.5 hives/km^2), which are the only other studies that have investigated 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/km^2 (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 mitchelli* 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. More research is needed to see why these species may be more negatively associated with honey bees in urban areas than other species.

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 generic richness 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 dispersion (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 not find a significantly negative association between honey bees and any individual trait functional dispersion, however diet functional dispersion was very close to significantly negative. This could indicate that floral resource competition between wild bees and honey bees may be leading to restricted diet diversity of wild bees. 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 dispersion 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* and *Colletes inaequalis* had positive relationships 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 (i.e. when mass provisions were made for solitary bees or when forage was collected by social bees throughout the larval stage) (Goulson and Sparrow 2009b). 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. Similarity, for individual functional trait diversity, flower density had mixed associations, but flower richness had a positive 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, 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 500m had a negative association with functional dispersion for sociality. 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.

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, our study has methodological shortcomings and causal mechanisms were not explored. 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. 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). 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 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.

References

Ahrné K, Bengtsson J, Elmqvist T (2009) Bumble bees (*Bombus spp*) along a gradient of increasing urbanization. PLoS One 4:e5574. https://doi.org/10.1371/journal.pone.0005574

Aizen MA, Feinsinger P (1994) Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serrano." Ecol Appl 4:378–392. https://doi.org/10.2307/1941941

Aizen MA, Harder LD (2009) The global stock of domesticated honey bees is growing slower than agricultural demand for pollination. Curr Biol 19:915–918. https://doi.org/10.1016/J.CUB.2009.03.071

Al-Ghamdi A, Hoopingarner R (2004) Modeling of honey bee and Varroa mite population dynamics. Saudi J Biol Sci 11:21–36

Alger SA, Burnham PA, Boncristiani HF, Brody AK (2019) RNA virus spillover from managed honeybees (*Apis mellifera*) to wild bumblebees (*Bombus spp*.). PLoS One 14:e0217822. https://doi.org/10.1371/journal.pone.0217822

Badano EI, Vergara CH (2011) Potential negative effects of exotic honey bees on the diversity of native pollinators and yield of highland coffee plantations. Agric For Entomol 13:365–372. https://doi.org/10.1111/j.1461-9563.2011.00527.x

Baldock KCR, Goddard MA, Hicks DM, et al (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. Proc R Soc B Biol Sci 282:. https://doi.org/10.1098/rspb.2014.2849

Barthel S, Isendahl C (2013) Urban gardens, Agriculture, And water management: Sources of resilience for long-term food security in cities. Ecol Econ 86:224–234.

https://doi.org/10.1016/j.ecolecon.2012.06.018

Batra SWT (1984) Solitary Bees. 250:120–127. https://doi.org/10.2307/24969305

Beekman M, Ratnieks FLW (2000) Long-range foraging by the honey-bee, *Apis mellifera* L. Funct Ecol 14:490–496. https://doi.org/10.1046/j.1365-2435.2000.00443.x

Biesmeijer JC, Roberts SPM, Reemer M, et al (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. Science 313:351–354. https://doi.org/10.1126/science.1127863

Bosch J, Vicens N (2002) Body size as an estimator of production costs in a solitary bee. Ecol Entomol 27:129–137. https://doi.org/10.1046/j.1365-2311.2002.00406.x

Buchholz S, Egerer MH (2020) Functional ecology of wild bees in cities: towards a better understanding of trait-urbanization relationships. Biodivers. Conserv. 29:2779–2801

Buchholz S, Gathof AK, Grossmann AJ, et al (2020) Wild bees in urban grasslands: Urbanisation, functional diversity and species traits. Landsc Urban Plan 196:103731. https://doi.org/10.1016/j.landurbplan.2019.103731

Burdine JD, McCluney KE (2019) Interactive effects of urbanization and local habitat characteristics influence bee communities and flower visitation rates. Oecologia 190:715–723. https://doi.org/10.1007/s00442-019-04416-x

Burnham KP, Anderson DR (2002) Model selection and multimodel inference, 2nd edn. Springer New York

Cadotte MW, Carscadden K, Mirotchnick N (2011) Beyond species: Functional diversity and the maintenance of ecological processes and services. J. Appl. Ecol. 48:1079–1087

Cameron SA, Lozier JD, Strange JP, et al (2011) Patterns of widespread decline in North American bumble bees. Proc Natl Acad Sci U S A 108:662–667. https://doi.org/10.1073/pnas.1014743108

Cane JH (1987) Estimation of Bee Size Using Intertegular Span (Apoidea). J Kansas Entomol Soc 60:145–147

Cane JH, Tepedino VJ (2017) Gauging the effect of honey bee pollen collection on native bee communities. Conserv Lett 10:205–210. https://doi.org/10.1111/conl.12263

Cariveau DP, Nayak GK, Bartomeus I, et al (2016) The allometry of bee proboscis length and its uses in ecology. PLoS One 11:e0151482. https://doi.org/10.1371/journal.pone.0151482

Carneiro LT, Martins CF (2012) Africanized honey bees pollinate and preempt the pollen of *Spondias mombin* (Anacardiaceae) flowers. Apidologie 43:474–486. https://doi.org/10.1007/s13592-011-0116-7

City of Toronto (2016) Bees of Toronto: a guide to their remarkable world: City of Toronto biodiversity series. City of Toronto, Toronto, Canada

Colla SR, MacIvor JS (2017) Questioning public perception, conservation policy, and recovery actions for honeybees in North America. Conserv Biol 31:1202–1204. https://doi.org/10.1111/cobi.12839

Colla SR, Otterstatter MC, Gegear RJ, Thomson JD (2006) Plight of the bumble bee: Pathogen spillover from commercial to wild populations. Biol Conserv 129:461–467. https://doi.org/10.1016/j.biocon.2005.11.013

Colla SR, Packer L (2008) Evidence for decline in eastern North American bumblebees

(Hymenoptera: *Apidae*), with special focus on *Bombus affinis* Cresson. Biodivers Conserv 17:1379–1391. https://doi.org/10.1007/s10531-008-9340-5

Davison PJ, Field J (2017) Season length, body size, and social polymorphism: size clines but not saw tooth clines in sweat bees. Ecol Entomol 42:768–776. https://doi.org/10.1111/een.12448

DeGrandi-Hoffman G, Roth SA, Loper GL, Erickson EH (1989) BEEPOP: A honeybee population dynamics simulation model. Ecol Modell 45:133–150. https://doi.org/10.1016/0304-3800(89)90088-4

Díaz S, Cabido M (2001) Vive la différence: Plant functional diversity matters to ecosystem processes. Trends Ecol. Evol. 16:646–655

Droege S (2015) The very handy manual: How to catch and identify bees and manage a collection. Maryland, USA.

Dupont YL, Hansen DM, Valido A, Olesen JM (2004) Impact of introduced honey bees on native pollination interactions of the endemic *Echium wildpretii* (Boraginaceae) on Tenerife, Canary Islands. Biol Conserv 118:301–311. https://doi.org/10.1016/j.biocon.2003.09.010

Ebeling A, Klein AM, Schumacher J, et al (2008) How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos 117:1808–1815. https://doi.org/10.1111/j.1600-0706.2008.16819.x

Eggenberger H, Frey D, Pellissier L, et al (2019) Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. J Anim Ecol 88:1522–1533.

https://doi.org/10.1111/1365-2656.13051

Elbgami T, Kunin WE, Hughes WOH, Biesmeijer JC (2014) The effect of proximity to a honeybee apiary on bumblebee colony fitness, development, and performance. Apidologie 45:504–513. https://doi.org/10.1007/s13592-013-0265-y

Evans E, Smart M, Cariveau D, Spivak M (2018) Wild, native bees and managed honey bees benefit from similar agricultural land uses. Agric Ecosyst Environ 268:162–170. https://doi.org/10.1016/J.AGEE.2018.09.014

Fitch G, Glaum P, Simao MC, et al (2019) Changes in adult sex ratio in wild bee communities are linked to urbanization. Sci Rep 9:1–10. https://doi.org/10.1038/s41598-019-39601-8

Fontaine C, Dajoz I, Meriguet J, Loreau M (2006) Functional diversity of plant–pollinator interaction webs enhances the persistence of plant communities. PLoS Biol 4:e1. https://doi.org/10.1371/journal.pbio.0040001

Forrest JRK, Thorp RW, Kremen C, Williams NM (2015) Contrasting patterns in species and functional-trait diversity of bees in an agricultural landscape. J Appl Ecol 52:706–715. https://doi.org/10.1111/1365-2664.12433

Fortel L, Henry M, Guilbaud L, et al (2014) Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. PLoS One 9:e104679. https://doi.org/10.1371/journal.pone.0104679

Frankie GW, Thorp RW, Hernandez J, et al (2009) Native bees are a rich natural resource in urban California gardens. Calif Agric 63:113–120

Geslin B, Le Féon V, Folschweiller M, et al (2016) The proportion of impervious surfaces at the landscape scale structures wild bee assemblages in a densely populated region. Ecol Evol 6:6599–6615. https://doi.org/10.1002/ece3.2374

Gibbs J, Brady SG, Kanda K, Danforth BN (2012) Phylogeny of halictine bees supports a shared origin of eusociality for *Halictus* and *Lasioglossum* (Apoidea: Anthophila: Halictidae). Mol Phylogenet Evol 65:926–939. https://doi.org/10.1016/j.ympev.2012.08.013

Glaum P, Simao M-C, Vaidya C, et al (2017) Big city *Bombus* : using natural history and land-use history to find significant environmental drivers in bumble-bee declines in urban development. R Soc Open Sci 4:170156. https://doi.org/10.1098/rsos.170156

Goddard MA, Dougill AJ, Benton TG (2010) Scaling up from gardens: biodiversity conservation in urban environments. Trends Ecol. Evol. 25:90–98

Goulson D, Peat J, Stout JC, et al (2002) Can alloethism in workers of the bumblebee, bombus terrestris, be explained in terms of foraging efficiency? Anim Behav 64:123–130. https://doi.org/10.1006/anbe.2002.3041

Goulson D, Sparrow KR (2009) Evidence for competition between honeybees and bumblebees; effects on bumblebee worker size. J Insect Conserv 13:177–181. https://doi.org/10.1007/s10841-008-9140-y

Graystock P, Yates K, Evison SEF, et al (2013) The Trojan hives: pollinator pathogens, imported and distributed in bumblebee colonies. J Appl Ecol 50:1207–1215. https://doi.org/10.1111/1365-2664.12134@10.1111/(ISSN)1365-2435.POLLINATOR

Greenleaf SS, Williams NM, Winfree R, Kremen C (2007) Bee foraging ranges and their relationship to body size. Oecologia 153:589–596. https://doi.org/10.1007/s00442-007-

0752-9

Grundel R, Jean RP, Frohnapple KJ, et al (2010) Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. Ecol Appl 20:1678–1692. https://doi.org/10.1890/08-1792.1

Gusachenko ON, Woodford L, Balbirnie-Cumming K, et al (2020) Evidence for and against deformed wing virus spillover from honey bees to bumble bees: a reverse genetic analysis. Sci Rep 10:1–10. https://doi.org/10.1038/s41598-020-73809-3

Hamblin AL, Youngsteadt E, Frank SD (2018) Wild bee abundance declines with urban warming, regardless of floral density. Urban Ecosyst 21:419–428. https://doi.org/10.1007/s11252-018-0731-4

Haydon DT, Laurenson MK, Sillero-Zubiri C (2002) Integrating epidemiology into population viability analysis: managing the risk posed by rabies and canine distemper to the Ethiopian Wolf. Conserv Biol 16:1372–1385. https://doi.org/10.1046/j.1523-1739.2002.00559.x

Hung KJ, Ascher JS, Davids JA, Holway DA (2019) Ecological filtering in scrub fragments restructures the taxonomic and functional composition of native bee assemblages. Ecology 100:e02654. https://doi.org/10.1002/ecy.2654

IUCN (2020) IUCN Red List of Threatened Species. https://www.iucnredlist.org/resources/summary-statistics. Accessed 28 Dec 2020

Jung M (2013) LecoS-A QGIS plugin for automated landscape ecology analysis. PeerJ Prepr 2:. https://doi.org/10.7287/peerj.preprints.116v2

Kendall LK, Rader R, Gagic V, et al (2019) Pollinator size and its consequences: Robust estimates of body size in pollinating insects. Ecol Evol 9:1702–1714. https://doi.org/10.1002/ECE3.4835

Kortright R, Wakefield S (2011) Edible backyards: A qualitative study of household food growing and its contributions to food security. Agric Human Values 28:39–53. https://doi.org/10.1007/s10460-009-9254-1

Krombein K V. (1967) Trap-nesting wasps and bees: life histories, nests, and associates. Smithsonian Press

Laliberte E, Legendre P (2010) A distance-based framework for measuring functional diversity from multiple traits. Ecology 91:299–305. https://doi.org/10.1890/08-2244.1

Lautenbach S, Seppelt R, Liebscher J, Dormann CF (2012) Spatial and temporal trends of global Ppllination benefit. PLoS One 7:e35954. https://doi.org/10.1371/journal.pone.0035954

Legendre P, Gallagher ED (2001) Ecologically meaningful transformations for ordination of species data. Oecologia 129:271–280. https://doi.org/10.1007/s004420100716

Lichtenberg EM, Kennedy CM, Kremen C, et al (2017) A global synthesis of the effects of diversified farming systems on arthropod diversity within fields and across agricultural landscapes. Glob Chang Biol 23:4946–4957. https://doi.org/10.1111/gcb.13714

Lindström SAM, Herbertsson L, Rundlöf M, et al (2016) Experimental evidence that honeybees depress wild insect densities in a flowering crop. Proc R Soc B 283:20161641. https://doi.org/10.1098/RSPB.2016.1641

Loreau M (1998) Biodiversity and ecosystem functioning: A mechanistic model. Ecology 95:5632–5636

MacInnis G, Buddle CM, Forrest JRK (2020) Small wild bee abundance declines with distance into strawberry crops regardless of field margin habitat. Basic Appl Ecol 44:14–23. https://doi.org/10.1016/j.baae.2020.02.007

Mallinger RE, Gaines-Day HR, Gratton C (2017) Do managed bees have negative effects on wild bees?: A systematic review of the literature. PLoS One 12:e0189268. https://doi.org/10.1371/journal.pone.0189268

Martins KT, Gonzalez A, Lechowicz MJ (2015) Pollination services are mediated by bee functional diversity and landscape context. Agric Ecosyst Environ 200:12–20. https://doi.org/10.1016/j.agee.2014.10.018

McCune F, Normandin É, Mazerolle MJ, Fournier V (2020) Response of wild bee communities to beekeeping, urbanization, and flower availability. Urban Ecosyst 23:39–54. https://doi.org/10.1007/s11252-019-00909-y

Michener CD (2000) The bees of the world. Johns Hopkins University Press, Baltimore MD

Mitchell TB (1962) Bees of the Eastern United States, Volume II. North Carolina Agricultural Experiment Station, Raleigh, NC

Mitchell TB (1960) The Bees of the Eastern United States, Volume I. North Carolina Agricultural Experiment Station

Mouillot D, Bellwood DR, Baraloto C, et al (2013) Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biol 11:e1001569. https://doi.org/10.1371/journal.pbio.1001569

Naimi B, Hamm NAS, Groen TA, et al (2014) Where is positional uncertainty a problem for species distribution modelling? Ecography 37:191–203. https://doi.org/10.1111/j.1600-0587.2013.00205.x

Nooten SS, Rehan SM (2019) Agricultural land use yields reduced foraging efficiency and unviable offspring in the wild bee *Ceratina calcarata*. Ecol Entomol 44:534–542. https://doi.org/10.1111/een.12730

Normandin É, Vereecken NJ, Buddle CM, Fournier V (2017) Taxonomic and functional trait diversity of wild bees in different urban settings. PeerJ 2017:e3051. https://doi.org/10.7717/peerj.3051

Ontario Ministry of Natural Resources and Forestry (2019) Southern Ontario Land Resource Information System (SOLRIS) Version 3.0: Data Specifications Contact

Packer L, Darla-West G (2021) Bees: How and why to sample them. In: Santos JC, Fernandes GW (eds) Measuring Arthropod Biodiversity: A Handbook of Sampling Methods. Springer Nature Switzerland

Packer L, Genaro JA, Sheffield CS (2007) The Bee Genera of Eastern Canada. Can J Arthropod Identif 3:1–32

Paini DR, Roberts JD (2005) Commercial honey bees (*Apis mellifera*) reduce the fecundity of an Australian native bee (Hylaeus alcyoneus). Biol Conserv 123:103–112. https://doi.org/10.1016/J.BIOCON.2004.11.001

Peters A, Patterson EI, Baker BGB, et al (2014) Evidence of Psittacine beak and feather disease virus spillover into wild critically endangered Orange-bellied parrots (*Neophema chrysogaster*). J Wildl Dis 50:288–296. https://doi.org/10.7589/2013-05-121

Plascencia M, Philpott SM (2017) Floral abundance, richness, and spatial distribution drive urban garden bee communities. Bull Entomol Res 107:1–10. https://doi.org/10.1017/S0007485317000153

Popic TJ, Davila YC, Wardle GM (2013) Evaluation of common methods for sampling invertebrate pollinator assemblages: Net sampling out-perform pan traps. PLoS One 8:e66665. https://doi.org/10.1371/journal.pone.0066665

Potts SG, Biesmeijer JC, Schweiger O, Kunin W (2010) Global pollinator declines: trends, impacts and drivers. Trends Ecol Evol 25:345–353. https://doi.org/10.1016/j.tree.2010.01.007

R Core Team (2020) R: A language and environment for statistical computing

Randall DA, Marino J, Haydon DT, et al (2006) An integrated disease management strategy for the control of rabies in Ethiopian wolves. Biol Conserv 131:151–162. https://doi.org/10.1016/j.biocon.2006.04.004

Renner SS, Graf MS, Hentschel Z, et al (2021) High honeybee abundances reduce wild bee abundances on flowers in the city of Munich. Oecologia 1:3. https://doi.org/10.1007/s00442-021-04862-6

Ribeiro MF (1994) Growth in bumble bee larvae: Relation between development time, mass, and amount of pollen ingested. Can J Zool 72:1978–1985. https://doi.org/10.1139/z94-270

Ropars L, Dajoz I, Fontaine C, et al (2019) Wild pollinator activity negatively related to honey bee colony densities in urban context. PLoS One 14:e0222316. https://doi.org/10.1371/journal.pone.0222316

Rushton SP, Lurz PWW, Gurnell J, et al (2006) Disease threats posed by alien species: The role of a poxvirus in the decline of the native red squirrel in Britain. Epidemiol Infect 134:521–533. https://doi.org/10.1017/S0950268805005303

Rust RW (1991) Size-Weight Relationships in *Osmia lignaria propinqua* Cresson (Hymenoptera: Megachilidae)

Santos PKF, Arias MC, Kapheim KM (2019) Loss of developmental diapause as prerequisite for social evolution in bees. Biol Lett 15:20190398. https://doi.org/10.1098/rsbl.2019.0398

Schönfelder ML, Bogner FX (2017) Individual perception of bees: Between perceived danger and willingness to protect. PLoS One 12:e0180168. https://doi.org/10.1371/journal.pone.0180168

Shavit O, Dafni A, Ne’eman G (2009) Competition between honeybees (*Apis mellifera*) and native solitary bees in the Mediterranean region of Israel—Implications for conservation. Isr J Plant Sci 57:171–183. https://doi.org/10.1560/IJPS.57.3.171

Sheffield CS, Pindar A, Packer L, Kevan PG (2013) The potential of cleptoparasitic bees as indicator taxa for assessing bee communities. Apidologie 44:501–510. https://doi.org/10.1007/s13592-013-0200-2

Sheffield CS, Ratti C, Packer L, Griswold T (2011) Leafcutter and mason bees of the genus *Megachile* Latreille (Hymenoptera: Megachilidae) in. Can J Arthropod Identif. https://doi.org/10.3752/cjai.2011.18

Shochat E, Lerman SB, Anderies JM, et al (2010) Invasion, competition, and biodiversity loss in urban ecosystems. Bioscience 60:199–208. https://doi.org/10.1525/bio.2010.60.3.6

Sirohi MH, Jackson J, Edwards M, Ollerton J (2015) Diversity and abundance of solitary and primitively eusocial bees in an urban centre: a case study from Northampton (England). J Insect Conserv 19:487–500. https://doi.org/10.1007/s10841-015-9769-2

Steffan-Dewenter I, Tscharntke T (2000) Resource overlap and possible competition between honey bees and wild bees in central Europe. Oecologia 122:288–296. https://doi.org/10.1007/s004420050034

Thomson D (2004) Competitive interactions between the invasive European honey bee and native bumble bees. Ecology 85:458–470

Thomson DM (2016) Local bumble bee decline linked to recovery of honey bees, drought effects on floral resources. Ecol Lett 19:1247–1255. https://doi.org/10.1111/ele.12659

Tonietto RK, Ascher JS, Larkin DJ (2017) Bee communities along a prairie restoration chronosequence: similar abundance and diversity, distinct composition. Ecol Appl 27:705–717. https://doi.org/10.1002/eap.1481

Torné-Noguera A, Rodrigo A, Osorio S, Bosch J (2016) Collateral effects of beekeeping: Impacts on pollen-nectar resources and wild bee communities. Basic Appl Ecol 17:199–209. https://doi.org/10.1016/j.baae.2015.11.004

Vierssen Trip N, MacPhail VJ, Colla SR, Olivastri B (2020) Examining the public’s awareness of bee (Hymenoptera: Apoidae: Anthophila) conservation in Canada. Conserv Sci Pract 2:. https://doi.org/10.1111/csp2.293

Visscher PK, Seeley TD (1982) Foraging strategy of honeybee colonies in a temperate deciduous. Ecology 63:1790–1801

Wcislo WT, Cane JH (1996) Floral resource utilization by solitary bees (Hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. Annu Rev Entomol 41:257–286. https://doi.org/10.1146/annurev.ento.41.1.257

Westphal C, Steffan-Dewenter I, Tscharntke T (2003) Mass flowering crops enhance pollinator densities at a landscape scale. Ecol Lett 6:961–965. https://doi.org/10.1046/j.1461-0248.2003.00523.x

Williams P, Thorp RW, Richardson L, Colla SR (2014) Bumble bees of North America: an identification guide. Princeton University Press

Willson MF, Bertin RI (1979) Flower-visitors, nectar production, and inflorescence size of *Asclepias syriaca*. Can J Bot 57:1380–1388. https://doi.org/10.1139/b79-172

Wilson JS, Griswold T, Messinger OJ (2008) Sampling bee communities (Hymenoptera: Apiformes) in a desert landscape: are pan traps sufficient? J Kansas Entomol Soc 81:288–300. https://doi.org/10.2317/JKES-802.06.1

Winfree R (2010) The conservation and restoration of wild bees. Ann N Y Acad Sci 1195:169–197. https://doi.org/10.1111/j.1749-6632.2010.05449.x

Winfree R, Williams NM, Gaines H, et al (2008) Wild bee pollinators provide the majority of crop visitation across land-use gradients in New Jersey and Pennsylvania, USA. J Appl Ecol 45:793–802. https://doi.org/10.1111/j.1365-2664.2007.01418.x

Wood TJ, Michez D, Paxton RJ, et al (2020) Managed honey bees as a radar for wild bee decline? Apidologie 51:1100–1116

Woodroffe R, Prager KC, Munson L, et al (2012) Contact with domestic dogs increases pathogen exposure in endangered African wild dogs (*Lycaon pictus*). PLoS One 7:e30099. https://doi.org/10.1371/journal.pone.0030099

Wright IR, Roberts SPM, Collins BE (2015) Evidence of forage distance limitations for small bees (Hymenoptera: Apidae). Eur J Entomol 112:303–310. https://doi.org/10.14411/eje.2015.028

Zanette LRS, Martins RP, Ribeiro SP (2005) Effects of urbanization on Neotropical wasp and bee assemblages in a Brazilian metropolis. Landsc Urban Plan 71:105–121. https://doi.org/10.1016/j.landurbplan.2004.02.003

Conclusion

The objective of my MSc research was to model floral resource requirements of honey bees (Chapter 1) and conduct a field study on the impacts of urban beehives on wild bee communities (Chapter 2), so that we can have a better understanding of whether honey bees are likely taking resources away from wild bees. The model I constructed to estimate honey bee resource requirements (i.e. number of flowers and area) to produce adequate amounts of honey for extraction in temperate climates had widely variable results, largely due to the variance in parameter estimates from published literature. However, the average estimated amount of area needed in agricultural landscapes was within the distance that honey bees are known to forage within resource limited landscapes (Couvillon et al. 2014, 2015a; Garbuzov et al. 2015b). In addition, both minimum calculations (agricultural and urban) for area requirements were within 1 km^2, which is the distance that honey bees are known to often travel (Couvillon et al. 2014, 2015a; Garbuzov et al. 2015a, b). All model outputs (minimum, average, and maximum) also showed that honey bees may require many more flowers for pollen collection compared to that for nectar or combined nectar and pollen collection. This model overall showed the need for further research in honey bee foraging behaviour, hive energy requirements (e.g. overwintering), and floral resource availability (e.g. floral density, and pollen and nectar available in the landscape) so that future models can more accurately predict the number of flowers and area a specific number of honey bee hives require in multiple landscapes. This model provides a starting point for future modelling, and local scale studies and improved models are likely required for policy implementation on optimal hive densities.

My field study investigated whether increasing urban honey bee abundance within the Greater Toronto Area negatively impacts wild bee communities. Overall, I found that increasing honey bee abundance may negatively impact wild bee communities in multiple ways, such as decreasing specific species abundances and body sizes, species richness, and functional diversity. These findings may have important implications for urban wild bees and urban pollination, since cities can sustain high bee diversity (Baldock et al. 2015b; Sirohi et al. 2015) and bee functional diversity has been linked to crop yield (Hoehn et al. 2008) and seed set (Martins et al. 2015) in agricultural landscapes. Future research should investigate further which species or genera may be more likely to be impacted by honey bees, as our research showed that certain groups may be more susceptible to negative impacts (i.e. *Nomada* spp.). As this was an observational study, experimental studies are needed to find causal mechanisms of negative impacts of honey bees on wild bees in urban landscapes, including floral resource competition (Mallinger et al. 2017) and pathogen spillover (Alger et al. 2019; Gusachenko et al. 2020). Overall, my research showed that honey bees may have the ability to deplete many resources in various landscapes (Ch. 1), and that they may be negatively impacting urban wild bee communities (Ch. 2). Wild bees need to be conserved to sustain pollination services in all landscapes, and conservation management plans should include managing for all potential stressors on wild bees, including the introduction of honey bees.

References

Alger SA, Burnham PA, Boncristiani HF, Brody AK (2019) RNA virus spillover from managed honeybees (*Apis mellifera*) to wild bumblebees (*Bombus spp*.). PLoS One 14:e0217822. https://doi.org/10.1371/journal.pone.0217822

Baldock KCR, Goddard MA, Hicks DM, et al (2015) Where is the UK's pollinator biodiversity?

The importance of urban areas for flower-visiting insects. Proc R Soc B 282:. https://doi.org/10.1098/rspb.2014.2849

Couvillon MJ, Riddell Pearce FC, Accleton C, et al (2015) Honey bee foraging distance depends on month and forage type. Apidologie 46:61–70. https://doi.org/10.1007/s13592-014-0302-5

Couvillon MJ, Schü Rch R, Ratnieks FLW (2014) Waggle dance distances as integrative indicators of seasonal foraging challenges. PLoS One 9:93495. https://doi.org/10.1371/journal.pone.0093495

Garbuzov M, Couvillon MJ, Schürch R, Ratnieks FLW (2015a) Honey bee dance decoding and pollen-load analysis show limited foraging on spring-flowering oilseed rape, a potential source of neonicotinoid contamination. Agric Ecosyst Environ 203:62–68. https://doi.org/10.1016/j.agee.2014.12.009

Garbuzov M, Schürch R, Ratnieks FLW (2015b) Eating locally: dance decoding demonstrates that urban honey bees in Brighton, UK, forage mainly in the surrounding urban area. Urban Ecosyst 18:411–418. https://doi.org/10.1007/s11252-014-0403-y

Gusachenko ON, Woodford L, Balbirnie-Cumming K, et al (2020) Evidence for and against deformed wing virus spillover from honey bees to bumble bees: a reverse genetic analysis. Sci Rep 10:1–10. https://doi.org/10.1038/s41598-020-73809-3

Hoehn P, Tscharntke T, Tylianakis JM, Steffan-Dewenter I (2008) Functional group diversity of bee pollinators increases crop yield. Proc R Soc B 275:2283–2291. https://doi.org/10.1098/rspb.2008.0405

Mallinger RE, Gaines-Day HR, Gratton C (2017) Do managed bees have negative effects on wild bees?: A systematic review of the literature. PLoS One 12:e0189268. https://doi.org/10.1371/journal.pone.0189268

Martins KT, Gonzalez A, Lechowicz MJ (2015) Pollination services are mediated by bee functional diversity and landscape context. Agric Ecosyst Environ 200:12–20. https://doi.org/10.1016/j.agee.2014.10.018

Sirohi MH, Jackson J, Edwards M, Ollerton J (2015) Diversity and abundance of solitary and primitively eusocial bees in an urban centre: a case study from Northampton (England). J Insect Conserv 19:487–500. https://doi.org/10.1007/s10841-015-9769-2

Appendices

Appendix A: Honey bee population dynamics and parameter sweep methods and results

Table 1. Honey bee colony population dynamics used for calculating honey consumption per colony per year (Farrar 1934; DeGrandi-Hoffman et al. 1989; Al-Ghamdi and Hoopingarner 2004; Schmickl and Crailsheim 2004; Harris 2008; Russell et al. 2013).

Month	Population of Workers	Honey needed per month (kg)
January	15000	1.10
February	15000	1.00
March	15000	1.10
April	30000	9.19
May	30000	9.50
June	60000	18.38
July	30000	9.50
August	30000	9.50
September	30000	9.19
October	30000	9.50
November	15000	1.07
December	15000	1.10
Sum		80.12

Table 2. Model output result changes from parameter sweeps. The maximum and minimum values represent the values that would result in the largest or smallest model output, respectively, not the values that are the largest or smallest.

Parameter	Change to maximum or minimum	∆ number of flowers for pollen collection	∆ total number of flowers, and agricultural and urban area
Mass of pollen collected per colony per year	Max	+33.11%	+30.83%
	Min	-25.22%	-23.49%
Mass of pollen per foraging trip	Max	0.00%	0.00%
	Min	0.00%	0.00%
Number of flowers visited per pollen forage bout	Max	0.00%	0.00%
	Min	0.00%	0.00%
Volume of pollen per flower	Max	+60518.46%	+56348.72%
	Min	-99.28%	-92.44%
Pollen density	Max	+2.36%	+2.20%
	Min	-2.26%	-2.10%
Overlap percentage	Max	+1.85%	+1.72%
	Min	-1.85%	-1.72%

References

DeGrandi-Hoffman G, Roth SA, Loper GL, Erickson EH. 1989. BEEPOP: A honeybee population dynamics simulation model. *Ecological Modelling* 45:133–150. DOI: 10.1016/0304-3800(89)90088-4.

Farrar C. 1934. Bees must have pollen. *Bee Culture* 62:276–278.

Ghamdi A Al, Hoopingarner R. 2004. Modeling of Honey Bee and Varroa Mite Population Dynamics. *Saudi Journal of Biological Sciences* 11.

Harris J. 2008. Effect of brood type on Varroa sensitive hygiene by worker honey bees (Hymenoptera: Apidae). *Entomological Society of America* 101: 1137–1144.

Russell S, Barron AB, Harris D. 2013. Dynamic modelling of honey bee (Apis mellifera) colony growth and failure. *Ecological Modelling* 265:158–169. DOI: 10.1016/j.ecolmodel.2013.06.005.

Schmickl T, Crailsheim K. 2004. Inner nest homeostasis in a changing environment with special emphasis on honey bee brood nursing and pollen supply. *Apidologie* 35:249–263. DOI: 10.1051/apido:2004019.

Appendix B: Full model

The final model for minimum, average, and maximum calculations is as follows:

$$AC=$$

$$\frac{\begin{array}{c}\left(\left(\frac{\frac{HP}{\left(\frac{NSC}{HSC}\right)}+(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_6])+(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_7])\ x\ 0.60)+([(ASH\ x\ 2)+(RSH\ x\ 22)]\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_7])\ x\ 0.40)+((\frac{A\ x\ D\ x\ NB\ x\ NF\ x\ NSF}{WC})x\ WH)}{NCFT}\times FVN\right)x\ (\frac{1}{NRR\ x\ FL\ x\ HBA})\ -\left(\left(\frac{\frac{HP}{\left(\frac{NSC}{HSC}\right)}+(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_6])+(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_7])\ x\ 0.60)+([(ASH\ x\ 2)+(RSH\ x\ 22)]\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_7])\ x\ 0.40)+((\frac{A\ x\ D\ x\ NB\ x\ NF\ x\ NSF}{WC})x\ WH)}{NCFT}\times FVN\right)x\ (\frac{1}{NRR\ x\ FL\ x\ HBA})\right)\ x\ OP\right)\\+\left(\left(\frac{PC}{PF}\times FTP\right)x\frac{1}{\left(\frac{PPF}{\left(\frac{PF}{FTP}\right)}\right)}-\left(\left(\frac{\frac{HP}{\left(\frac{NSC}{HSC}\right)}+(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_6])+(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_7])\ x\ 0.60)+([(ASH\ x\ 2)+(RSH\ x\ 22)]\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_7])\ x\ 0.40)+((\frac{A\ x\ D\ x\ NB\ x\ NF\ x\ NSF}{WC})x\ WH)}{NCFT}\times FVN\right)x(\frac{1}{NRR\ x\ FL\ x\ HBA})\right)\ x\ OP\right)\\+\left(\left(\frac{\frac{HP}{\left(\frac{NSC}{HSC}\right)}+(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_6])+(RS\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_7])\ x\ 0.60)+([(ASH\ x\ 2)+(RSH\ x\ 22)]\ x\ \frac{100}{HSc}\ x\ [(DMxW)_1+(DMxW)_2+\cdots(DMxW)_7])\ x\ 0.40)+((\frac{A\ x\ D\ x\ NB\ x\ NF\ x\ NSF}{WC})xWH)}{NCFT}\times FVN\right)x\ (\frac{1}{NRR\ x\ FL\ x\ HBA})\ x\ OP\right)\end{array}}{FD}$$

Appendix C: Bee species identification methods

Table 1. Identification methods used for each bee genus.

Family	Genus	Identifier(s)	Identification Method	Reference
Andrenidae	*Andrena*	Sarah MacKell/Sheila Dumesh	Unpublished key and Discover Life keys	Sheffield CS (2013) *Andrena* of Canada and Alaska (Hymenoptera: Andrenidae). Royal Saskatchewan Museum: Unpublished Key Larkin L, Andrus R, Droege S *Andrena* female identification guide - Discover Life. https://www.discoverlife.org/mp/20q?guide=Andrena_female. Accessed 2020 Larkin L, Andrus R, Droege S *Andrena* male identification guide - Discover Life. https://www.discoverlife.org/mp/20q?guide=Andrena_male. Accessed 2020
	Calliopsis	Sarah MacKell	Published key	Packer L, Genaro JA, Sheffield CS (2007) The bee genera of Eastern Canada. Can J Arthropod Identif 3:1–32
Apidae	*Anthophora*	Sarah MacKell/Hadil Elsayed	Published key	Packer L, Genaro JA, Sheffield CS (2007) The bee genera of Eastern Canada. Can J Arthropod Identif 3:1–32
	Bombus	Sheila Colla	Published key	Williams P, Thorp RW, Richardson L, Colla SR (2014) Bumble bees of North America: an identification guide. Princeton University Press
	Ceratina	Evan Kelemen	Published paper	*Ceratina dupla* species-group (Hymenoptera: Apidae: Xylocopinae) of eastern North America. Zootaxa 35–50. https://doi.org/10.11646/zootaxa.2873.1.3
	Epeolus	Sarah MacKell	Published key	Onuferko TM (2018) A revision of the cleptoparasitic bee genus *Epeolus* Latreille for nearctic species, north of Mexico (Hymenoptera, Apidae). Zookeys 755:1–185. https://doi.org/10.3897/zookeys.755.23939
	Holcopasites	Sarah MacKell/Hadil Elsayed	Published key	Packer L, Genaro JA, Sheffield CS (2007) The bee genera of Eastern Canada. Can J Arthropod Identif 3:1–32
	Melissodes	Sarah MacKell/Laurence Packer	Published key	LaBerge W (1961) A revision of the bees of the genus *Melissodes* in North and Central America. Part III (Hymenoptera, Apidae). Univ Kansas Sci Bulletin XLII:283–663
	Nomada	Katherine Odanaka	Published key and Discover Life keys	Mitchell TB (1962) Bees of the Eastern United States, Volume II. North Carolina Agricultural Experiment Station, Raleigh, NC NA *Nomada* female identification guide - Discover Life.https://www.discoverlife.org/mp/20q?guide=Nomada_female NA Accessed 2020

				Nomada male identification guide - Discover Life.https://www.discoverlife.org/mp/20q?guide=Nomada_male. Accessed 2020
	Peponapis	Laurence Packer	Published key	Packer L, Genaro JA, Sheffield CS (2007) The bee genera of Eastern Canada. Can J Arthropod Identif 3:1–32
	Triepeolus	Sarah MacKell/Thomas Onuferko	Published key	Rightmyer MG (2008) A review of the cleptoparasitic bee genus *Triepeolus* (Hymenoptera: Apidae). - Part 1. Zootaxa 1710:1–170
	Xylocopa	Sarah MacKell/Hadil Elsayed	Published key	Packer L, Genaro JA, Sheffield CS (2007) The bee senera of Eastern Canada. Can J Arthropod Identif 3:1–32
Colletidae	*Colletes*	Hadil Elsayed	Published key and Discover Life Keys	Romankova TG (2003) Bees of genus *Colletes* of Ontario (Hymenoptera, Apoidea, Colletidae). J Entomol Soc Ont 134: 91-106 Andrus R, Droege S, Griswold T *Colletes* female identification guide - Discover Life. https://www.discoverlife.org/mp/20q?guide=Colletes_female. Accessed 2020 Andrus R, Droege S, Griswold T *Colletes* male identification guide - Discover Life. https://www.discoverlife.org/mp/20q?guide=Colletes_male. Accessed 2020
	Hylaeus	Hadil Elsayed/Sheila Dumesh	Published key and Discover Life Keys	Romankova TG (2007) Bees of the genus *Hylaeus* of Ontario (Hymenoptera: Apoidea: Colletidae). J Entomol Soc Ont 138: 137-154. Andrus R, Droege S, Griswold T *Hylaeus* female identification guide - Discover Life. https://www.discoverlife.org/mp/20q?guide=Hylaeus_female. Accessed 2020 Andrus R, Droege S, Griswold T *Hylaeus* male identification guide - Discover Life. https://www.discoverlife.org/mp/20q?guide=Hylaeus_male. Accessed 2020
Halictidae	*Agapostemon*	Hadil Elsayed	Unpublished key	Arduser M (2019) *Agapostemon* of the tallgrass prairie region and eastern North America. National Biological Information Infrastructure: Unpublished key
	Augochlora	Sarah MacKell	Published key	Packer L, Genaro JA, Sheffield CS (2007) The bee genera of Eastern Canada. Can J Arthropod Identif 3:1–32
	Augochlorella	Sarah MacKell	Published key	Packer L, Genaro JA, Sheffield CS (2007) The bee genera of Eastern Canada. Can J Arthropod Identif 3:1–32
	Augochloropsis	Sarah MacKell	Published key	Packer L, Genaro JA, Sheffield CS (2007) The bee genera of Eastern Canada. Can J Arthropod Identif 3:1–32

	Halictus	Sarah MacKell	Unpublished key	Arduser M (2019) *Halictus* of the tallgrass prairie region and eastern North America. National Biological Information Infrastructure: Unpublished key
	Lasioglossum	Hadil Elsayed/Sheila Dumesh	Published Keys	McGinley RJ (1986) Studies of Halictinae (Apoidea: Halictidae), I: Revision of New World *Lasioglossum* Curtis. Smithson Contr Zool 429: 1-294. Gibbs J (2010) Revision of the metallic species of *Lasioglossum* (Dialictus) in Canada (Hymenoptera, Halictidae, Halictini). Zootaxa 2591: 1–382. Gibbs J (2011) Revision of the metallic *Lasioglossum* (Dialictus) of eastern North America (Hymenoptera: Halictidae: Halictini). Zootaxa 3073: 1–216. Gibbs J, Packer L, Dumesh S, Danforth BN (2013) Revision and reclassification of *Lasioglossum* (Evylaeus), L. (Hemihalictus) and L. (Sphecodogastra) in eastern North America (Hymenoptera: Apoidea: Halictidae). Zootaxa 3672(1): 1–117.
	Sphecodes	Sarah MacKell/Laurence Packer	Discover Life keys	Arduser, M *Sphecodes* female identification guide - Discover Life. https://www.discoverlife.org/mp/20q?guide=Sphecodes_female. Accessed 2020 Arduser, M *Sphecodes* male identification guide - Discover Life.https://www.discoverlife.org/mp/20q?guide=Sphecodes_male. Accessed 2020
Megachilidae	*Anthidiellum*	Genevieve Rowe	Published keys	Miller SR, Gaebel R;, Mitchell RJ, Arduser M (2002) Occurrence of Two Species of Old World Bees, *Anthidium manicatum* and *A. Oblongatum* (Apoidea: Megachilidae), in Northern Ohio and Southern Michigan. Gt Lakes Entomol 35:1 Romankova T (2003) Ontario Nest-Building Bees of the Tribe Anthidiini (Hymenoptera, Megachilidae). J Entomol Soc Ontario 134:85–89
	Anthidium	Genevieve Rowe	Published key	Miller SR, Gaebel R, Mitchell RJ, Arduser M (2002) Occurrence of Two Species of Old World Bees, *Anthidium manicatum* and *A. Oblongatum* (Apoidea: Megachilidae), in Northern Ohio and Southern Michigan. Gt Lakes Entomol 35:1
	Chelostoma	Genevieve Rowe	Unpublished key (thesis)	Rowe G (2017) A taxonomic revision of the Canadian non-*Osmia* Osmiini (Hymenoptera: Megachilidae). York University
	Coelioxys	Genevieve Rowe	Unpublished key (thesis)	De Silva N (2012) Revision of the Cleptoparasitic Bee Genus *Coelioxys* (Hymenoptera: Megachilidae) in Canada. York University
	Heriades	Genevieve Rowe	Unpublished key (thesis)	Rowe G (2017) A taxonomic revision of the Canadian non-*Osmia* Osmiini (Hymenoptera: Megachilidae). York University

	Hoplitis	Genevieve Rowe	Unpublished key (thesis)	Rowe G (2017) A taxonomic revision of the Canadian non-*Osmia* Osmiini (Hymenoptera: Megachilidae). York University
	Megachile	Genevieve Rowe	Published key	Sheffield CS, Ratti C, Packer L, Griswold T (2011) Leafcutter and Mason Bees of the Genus *Megachile* Latreille (Hymenoptera: Megachilidae) in Canada and Alaska. Can J Arthropod Identif 18:1–107. https://doi.org/10.3752/cjai.2011.18
	Osmia	Genevieve Rowe	Mix of published key and Discover Life keys	Mitchell TB (1962) Bees of the Eastern United States, Volume II. North Carolina Agricultural Experiment Station, Raleigh, NC Griswold T, Ikerd H, Droege S, Pascarella JB, Pickering J *Osmia* female identification guide - Discover Life. https://www.discoverlife.org/mp/20q?guide=Osmia_female. Accessed 2020 Andrus R, Droege S, Griswold T (Accessed 2020) *Osmia* male identification guide - Discover Life. https://www.discoverlife.org/mp/20q?guide=Osmia_male. Accessed 2020
	Stelis	Genevieve Rowe	Published key	Mitchell TB (1962) Bees of the Eastern United States, Volume II. North Carolina Agricultural Experiment Station, Raleigh, NC
Melittidae	*Macropis*	Sarah MacKell	Published Key	Michez D, Patiny S (2005) World revision of the oil-collecting bee genus *Macropis* Panzer 1809 (Hymenoptera: Apoidea: Melittidae) with a description of a new species from Laos. Ann la Soc Entomol Fr 41:15–28. https://doi.org/10.1080/00379271.2005.10697439

Appendix D: Flowering species list for each site

Site	Flowering Plant Species
Centennial Park	*Alliaria petiolata* *Barbarea vulgaris* *Cirsium arvense* *Daucus carota* *Erigeron sp.* *Hesperis matronalis* *Lotus corniculatus* *Lythrum salicaria* *Taraxacum officinale* *Trifolium repens* *Veronica serpyllifolia* *Viola sp.*
Downsview Park	*Arctium lappa* *Carduus acanthoides* *Cirsium arvense* *Convolvulus arvensis* *Daucus carota* *Lotus corniculatus* *Medicago lupulina* *Taraxacum officinale* *Trifolium repens* *Vicia cracca*
Etobicoke Creek Trail	*Achillea millefolium* *Cirsiumarvense* *Daucus carota* *Lotus corniculatus* *Lythrum salicaria* *Securigera varia* *Taraxacum officinale* *Trifolium pratense* *Trifolium repens* *Vicia cracca*
G Ross Lord Park	*Arctium lappa* *Cichorium intybus* *Cirsiumarvense* *Daucus carota* *Erigeron sp.* *Lonicera tatarica* *Melilotus albus* *Potentilla sp.* *Taraxacum officinale* *Trifolium hybridum* *Trifolium repens* *Trifolium pratense* *Vicia cracca*
Northwood Park	*Anthemis sp.*

	Arctium lappa *Carduus acanthoides* *Cerastium fontanum* *Daucus carota* *Erigeron sp.* *Geum urbanum* *Glechoma hederacea* *Hydrophyllum viginianum* *Medicago lupulina* *Pastinaca sativa* *Prunella vulgaris* *Ranunclus acris* *Solanum dulcamara* *Taraxacum officinale* *Trifolium repens* *Veronica serpyllifolia* *Vicia cracca* *Viola sp.*
Serena Gundy Park	*Alliaria petiolata* *Cirsiumarvense* *Geum aleppicum* *Glechoma hederacea* *Hypericum perforatum* *Stellaria sp.* *Taraxacum officinale* *Trifolium repens* *Trifolium pratense* *Veronica serpyllifolia*
Toronto Botanical Garden	*Aguilegia canadensis* *Allium hollandicum* *Anemonastrum sp.* *Camassia leichtilinii* *Cirsium arvense* *Cornus sericea* *Echinacea sp.* *Echinacea purpurea* *Fragaria vesca* *Geranium sp.* *Geum sp.* *Helianthis divaricatus* *Heliopsis sp.* *Heliopsis helianthoides* *Hesperis matronalis* *Hibiscuis sp.* *Leucanthemum vulgare* *Lobelia siphilitica* *Monarda fistulosa* *Myosotis sp.* *Narcissus Accent'* *Paeonia tenuifolia* *Penstemon digitalis*

	Penstemon sp. *Prunus serotina* *Pyrus salicifolia* *Rudbeckia hirta* *Salvia sp.* *Symphyotrichum novae-angliae* *Taraxacum officinale* *Tulipa Queen of Night'* *Tulipa Pink Vision'* *Tulipa Negrita Parrot'* *Verbena hastata* *Vernonia sp.* *Viburnum sp.* *Zizia aurea*
University of Toronto Scarborough	*Cerastium fontanum* *Daucus carota* *Erigeron sp.* *Glechoma hederacea* *Leucanthemum sp.* *Leucanthemum vulgare* *Prunella vulgaris* *Ranunculus aris* *Solidago sp.* *Stelleria sp.* *Taraxacum officinale* *Trifolium repens* *Trifolium pratense* *Tussilago farfara*
Wanita Park	*Cornus sericea* *Daucus carota* *Glechoma hederacea* *Impatiens capensis* *Prunella vulgaris* *Ranunculus aris* *Rubus sp.* *Solanum dulcamara* *Solidago sp.* *Stelleria sp.* *Taraxacum officinale* *Trifolium repens* *Tussilago farfara* *Verbena sp.* *Veronica serpyllifolia*
Macola Garden (York University)	*Alliaria petiolata* *Arctium lappa* *Cichorium intybus* *Cirsium arvense* *Convolvulus arvensis* *Daucus carota* *Leonurus cardiaca* *Lotus corniculatus*

	Rumex crispus *Taraxacum officinale* *Trifolium repens* *Vicia cracca*

Appendix E: RDA plots and scores

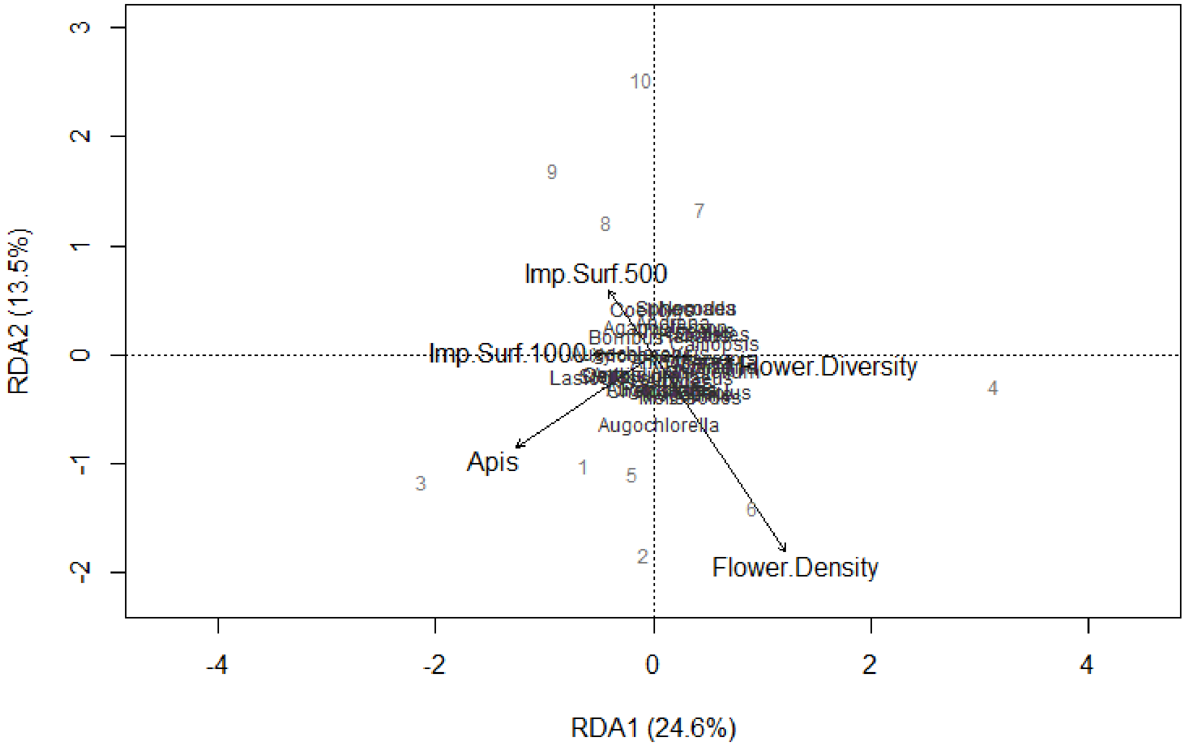


Figure 1. Biplot of genera RDA to investigate which genera potentially had a significant relationship with honey bee relative abundance.

Table 1. RDA scores for each genus for RDA1 and RDA2. The biplot scores for *Apis* were: -0.4664, -0.313721, for RDA1 and RDA2, respectively. Bolded biplot scores and genus names indicate which genera were chosen to be further investigated for possibly negative (i.e. biplot scores with the opposite signs) or positive associations (i.e. biplot scores with the same signs) with relative honey bee abundance.

Genus	RDA1	RDA2
Agapostemon	**0.124354**	**0.248887**
Andrena	**0.179398**	**0.307711**
Anthidiellum	0.477722	-0.140365
Anthidium	**-0.14449**	**-0.163112**
Anthophora	0.278164	-0.061877
Augochlora	0.029181	-0.319473
Augochlorella	0.056767	-0.645903
Augochloropsis	-0.109371	0.01123
Bombus	-0.237891	0.177279
Calliopsis	**0.573246**	**0.09571**
Ceratina	0.612556	-0.085979
Chelostoma	0.077933	-0.316539
Coelioxys	**0.002061**	**0.419198**
Colletes	**0.551593**	**0.211268**
Epeolus	0.568165	-0.349339
Halictus	**0.387775**	**0.192487**
Heriades	0.184806	-0.232954
Holcopasites	0.588047	-0.03765
Hoplitis	0.418426	-0.113218
Hylaeus	0.421669	-0.205174

Lasioglossum	**-0.352503**	**-0.209395**
Macropis	0.588047	-0.03765
Megachile	0.316777	-0.354743
Melissodes	0.345531	-0.368757
Nomada	**0.407992**	**0.44207**
Osmia	**-0.361942**	**-0.161274**
Peponapis	0.149628	-0.313623
Sphecodes	**0.319672**	**0.430116**
Stelis	**-0.436751**	**-0.177089**
Triepeolus	**0.326342**	**0.222439**
Xylocopa	**-0.183951**	**-0.004412**

Table 2. Best GLMs for predicting either genus or species level abundance relationships with honey bee relative abundance. No value means that the predictor was not included in the best model, which was based on AIC_c or quasi-AIC_c values depending on the distribution of the GLM. Light grey indicates a significantly positive association, and darker grey indicates a significantly negative association. (a) indicates a Poisson distribution, (b) indications a quasi-Poisson distribution (based on overdispersion test).

	Flower Density			***Flower Diversity***			***Relative Apis***			***Imp.Surface.1000***			***Imp.Surface.500***		
Species/Genus	**Res. Dev**	**Z (a) /T (b)**	**Est.**	**Res. Dev**	**Z (a) /T (b)**	**Est.**	**Res. Dev**	**Z (a) /T (b)**	**Est.**	**Res. Dev**	**Z (a) /T (b)**	**Est.**	**Res. Dev**	**Z (a) /T (b)**	**Est.**
Agapostemon (b)													390.94	0.31	0.394
Agapostemon virescens (b)													136.29	1.504	2.230
Andrena (b)							314.63	-1.461	-2.602						
Andrena imitatrix (a)	39.861	-0.975	-0.002	38.228	2.007	0.41109	34.534	-2.363	-2.067	30.701	-2.344	-8.744	26.909	1.812	3.426
Andrena nasonii (b)							220.45	-0.846	-2.2387						
Anthidium (b)							222.13	1.185	3.768						
Anthidium oblongatum (b)							212.92	1.265	4.018						
Colletes inaequalis (a)				360.79	10.67	1.713***				21.74	-10.7	-21.583***			
Halictus (b)				287.6	1.66	0.506				215.05	-1.491	-4.240			
Halictus confusus (b)										194.65	-1.515	-5.71			
Halictus ligatus (b)				91.242	3.216	0.547*									
Lasioglossum (a)	543.82	0.05	0.001	480.67	-1.45	-0.469	438.88	-1.082	-1.565	437.73	4.017	10.755	60.61	-5.099	-7.1594*
Lasioglossum imitatum (a)	38.226	6.514	0.019***										27.464	-3.313	-2.398**
Lasioglossum leucozonium (b)										28.993	-1.862	-4.76			
Lasioglossum mitchelli (a)				466.38	-8.019	-1.746***	439.02	-6.577	-7.998***	419.83	10.195	22.407***	8.28	-15.661	-15.075***
Lasioglossum paradmirandum (a)				135.121	-3.681	-1.244***				121.464	7.139	23.966***	4.331	-8.213	-14.388***
Lasioglossum weemsi (a)				57.044	-3.272	-0.867**				54.389	5.406	16.037	8.906	-6.382	-9.530***

Nomada (b)							310.78	-1.629	-4.898						
Nomada bethunei (a)							57.183	-6.622	-9.390***	37.416	-4.719	-30.877***	11.02	4.305	11.545***
Osmia (a)	92.07	-0.75	-0.001	83.762	-0.702	-0.104*	83.754	0.946	0.758	83.288	5.083	7.901	38.087	-6.755	-5.771***
Osmia albiventris (a)										212.92	-1.658	-2.434			
Osmia conjuncta (b)	190.996	0.491	0.012				186.122	0.899	13.608	184.544	2.636	18.126	51.351	-2.305	-17.063*
Xylocopa (b)	192.13	-1.143	-0.014	163.18	1.527	1.345							120.41	-1.334	-4.133

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

Appendix F: FDis GLM Results

Table 1. All FDis GLM results. No value means that the predictor was not included in the best model, which was based on AIC$_c$ values. Light grey indicates a significantly positive association, and darker grey indicates a significantly negative association.

Trait	***Flower Density***			***Flower Richness***			***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.**
Body Size										0.001	0.422	0.015			
Diet							0.045	-1.939	-0.396^{N}						
Sociality	0.013	-4.281	-0.001**	0.012	4.102	0.039							0.002	-5.462	-0.224***
Seasonality				0.004	2.367	0.017*									
Type of nesting				0.012	1.258	0.015									
Tongue Length				0.003	1.464	0.009									
Nest Building				0.015	0.832	0.011									
Pollen Strategy	0.010	2.162	0.001*												
All Traits							0.005	-2.64	-0.175*	0.004	-1.695	-0.124^{N}			

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

Appendix F: Body size GLMs results

Table 1. All body size GLM results. F is for female, M is for Male, T is for thorax, and H is for head. No value means that the predictor was not included in the best model, which was based on AIC$_c$ values. Light grey indicates a significantly positive association, and darker grey indicates a significantly negative association.

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.**
Agapostemon virescens	F	T				4.988	-1.202	-0.073	4.982	1.004	0.208	4.937	0.920	1.405	4.914	-0.692	-0.515
Agapostemon virescens	F	H				1.628	-2.251	-0.077	1.628	1.190	0.139	1.605	1.731	1.495	1.573	-1.461	-0.615
Agapostemon virescens	M	T										10.359	3.698	5.672***	9.694	-2.645	-3.133^{N}
Agapostemon virescens	M	H										4.248	3.618	3.562***	3.954	-2.741	-2.084*
Andrena imitatrix	M	T	4.334	-3.684	-0.002*	4.066	2.263	0.092	3.985	1.137	0.278						
Andrena imitatrix	M	H	3.296	-3.921	-0.003^{N}	2.984	2.747	0.150^{N}				2.874	0.978	1.255	2.765	-1.500	-1.075
Andrena nasonii	F	T										4.115	-3.149	-0.523	3.964	3.421	0.356**
Andrena nasonii	F	H	2.171	-1.902	-0.001**				2.154	-1.289	-0.066	2.139	-0.429	-0.100	2.134	0.803	0.106
Anthidium oblongatum	F	T				5.439	2.536	0.158^{N}				5.435	-1.485	-1.538	5.321	1.508	0.672
Anthidium oblongatum	F	H				2.660	1.672	0.040							2.638	0.946	0.125
Anthidium oblongatum	M	T	14.062	1.754	0.001										13.955	-0.932	-0.306
Anthidium oblongatum	M	H	7.186	2.159	0.001^{N}							7.186	0.861	0.475	7.056	-1.443	-0.440
Augochlorella aurata	F	T	2.692	0.651	0.001				2.576	0.430	0.205^{N}	2.539	2.639	0.900	2.442	-2.265	-0.671^{N}
Augochlorella aurata	F	H	1.016	-4.340	-0.001				0.896	-5.246	-0.780***	0.837	3.026	0.387*			
Bombus bimaculatus	F	T				7.092	-0.150	-0.006	7.075	0.368	0.159						
Bombus bimaculatus	F	H	2.405	1.364	0.001	2.356	-1.086	-0.033									

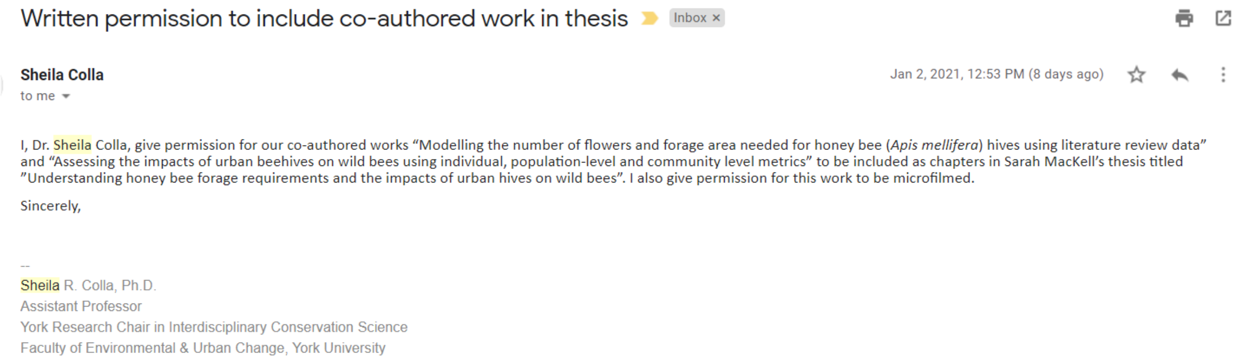
Bombus griseocollis	F	T	28.389	3.572	0.004^{N}	23.298	-1.777	-0.203***				23.297	2.247	2.918	19.848	-3.681	-2.151**
Bombus griseocollis	F	H	9.191	3.146	0.003^{N}	7.876	-1.669	-0.111**				7.865	2.459	1.859	6.719	-3.648	-1.240**
Bombus griseocollis	M	T				9.796	1.803	0.059	8.964	2.567	1.669^{N}						
Bombus griseocollis	M	H				3.091	2.368	0.044	2.956	1.803	0.673						
Bombus impatiens	F	T	167.560	2.090	0.001	148.340	-2.588	-0.122***	147.790	0.905	0.211				146.110	-2.486	-0.494^{N}
Bombus impatiens	F	H	70.499	1.811	0.001	62.477	-2.481	-0.076***	61.937	1.663	0.2513^{N}				61.261	-2.432	-0.313^{N}
Bombus impatiens	M	T	6.499	-1.212	-0.001							6.490	1.278	2.168	6.375	-1.236	-1.161
Bombus impatiens	M	H	3.289	-1.874	-0.001	3.280	-1.572	-0.070				3.274	3.068	4.281	2.915	-3.214	-2.304*
Bombus rufocinctus	F	T	63.764	2.296	0.001				63.008	2.052	0.480						
Bombus rufocinctus	F	H	23.212	1.625	0.000				22.866	2.305	0.325^{N}						
Bombus rufocinctus	M	T							28.694	3.599	1.879**	28.495	2.081	2.751	27.907	-1.909	-1.580
Bombus rufocinctus	M	H							7.116	2.271	0.594^{N}	7.036	1.171	0.775	7.001	-0.928	-0.384
Colletes inaequalis	F	T				3.388	2.441	0.469	3.273	-1.397	-0.801	3.190	-2.302	-12.921	2.994	2.413	6.711^{N}
Colletes inaequalis	F	H	14572.500	-3.760	-0.189	8894.700	8.398	27.042***	7570.600	3.945	74.641**						
Halictus confusus	F	T										4.703	1.009	0.252	4.698	-0.489	-0.077
Halictus confusus	F	H	3.595	-1.468	0.000				3.594	0.561	0.053	3.588	1.425	0.466	3.559	-1.294	-0.233
Halictus confusus	M	T				1.814	0.429	0.017				1.809	0.619	0.415	1.793	-0.864	0.415
Halictus confusus	M	H				0.800	1.449	0.036	0.794	0.923	0.133	0.791	-0.504	-0.083			
Halictus ligatus	F	T	8.902	1.278	0.000	8.769	-1.093	-0.028	8.698	1.088	0.227	8.697	-0.808	-0.546	8.658	0.891	0.310
Halictus ligatus	F	H	9.834	1.172	0.000	9.735	-1.488	-0.036							9.702	0.773	0.084
Megachile rotundata	F	T	6.111	-2.457	-0.002^{N}							5.790	1.793	1.002			
Megachile rotundata	F	H	3.007	-1.623	-0.001^{N}				2.930	0.317	0.108	2.781	1.748	0.768			
Megachile rotundata	M	T				3.771	1.725	0.112	3.618	2.270	0.895	3.420	-1.847	-0.816			
Megachile rotundata	M	H							2.517	1.653	0.386	2.424	-1.521	-0.382			

Nomada bethunei	F	T	7.146	1.763	0.004	7.026	-2.157	-0.452	6.376	-2.125	-0.917^{N}	2.317	2.167	5.779^{N}			
Nomada bethunei	F	H	5.154	1.761	0.003*	5.027	-2.250	-0.394	4.666	-1.799	-0.649	4.030	2.864	2.237*			
Xylocopa viriginica	F	T	20.41	-0.602	-0.001	20.111	-0.973	-0.053	19.804	-1.331	-1.123						
Xylocopa viriginica	F	H	10.658	-1.684	-0.001				10.312	-1.965	-1.160						

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

Appendix G. Co-author written permissions for inclusion of manuscripts in the dissertation

Chapters 1 and 2: Dr. Sheila Colla



Written permission to include co-authored work in thesis

Sheila Colla

to me

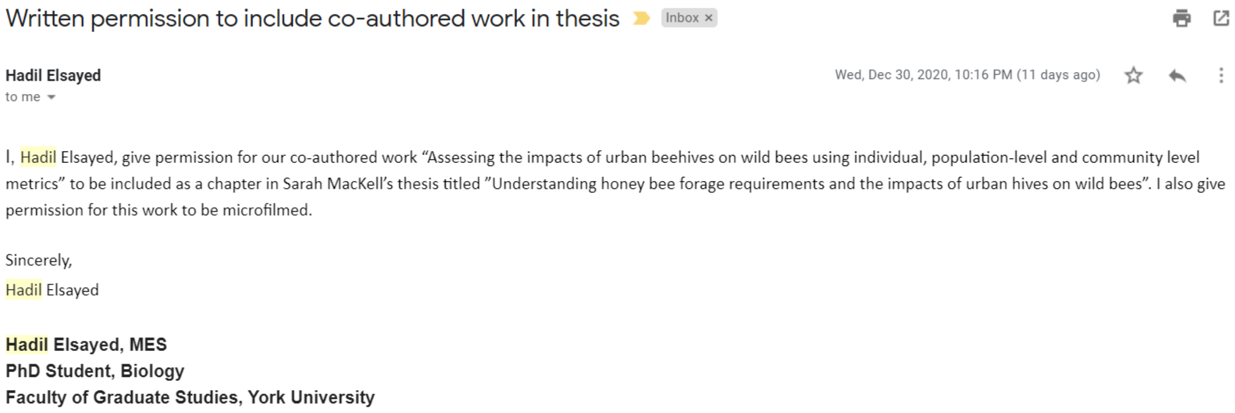
Jan 2, 2021, 12:53 PM (8 days ago)

I, Dr. Sheila Colla, give permission for our co-authored works "Modelling the number of flowers and forage area needed for honey bee (*Apis mellifera*) hives using literature review data" and "Assessing the impacts of urban beehives on wild bees using individual, population-level and community level metrics" to be included as chapters in Sarah MacKell's thesis titled "Understanding honey bee forage requirements and the impacts of urban hives on wild bees". I also give permission for this work to be microfilmed.

Sincerely,

--
Sheila R. Colla, Ph.D.
Assistant Professor
York Research Chair in Interdisciplinary Conservation Science
Faculty of Environmental & Urban Change, York University

Chapter 2: Hadil Elsayed



Written permission to include co-authored work in thesis

Hadil Elsayed

to me

Wed, Dec 30, 2020, 10:16 PM (11 days ago)

I, Hadil Elsayed, give permission for our co-authored work "Assessing the impacts of urban beehives on wild bees using individual, population-level and community level metrics" to be included as a chapter in Sarah MacKell's thesis titled "Understanding honey bee forage requirements and the impacts of urban hives on wild bees". I also give permission for this work to be microfilmed.

Sincerely,
Hadil Elsayed

Hadil Elsayed, MES
PhD Student, Biology
Faculty of Graduate Studies, York University

Appendix H. Candidate’s contribution to co-authored work

Statement of Sarah MacKell’s contribution to co-authored works included in the dissertation titled “Modeling honey bee hive forage requirements in multiple landscapes and assessing impacts of urban beehives on wild bees”.

Chapter 1: Modelling the number of flowers and forage area needed for honey bee (*Apis mellifera*) hives using literature review data

Sarah E. MacKell, Sheila R. Colla

This chapter will be submitted for publication to a peer-reviewed journal.

<u>Candidate’s Contributions:</u>

Sarah MacKell and Dr. Colla conceived of the ideas for this manuscript. Sarah MacKell conducted the literature review, processed all articles, extracted relevant data from articles retained for the review, constructed the model, and summarized and analyzed the results. Sarah MacKell led the writing of the manuscript, and both Sarah MacKell and Dr. Colla contributed to editing the article. Both Sarah MacKell and Dr. Colla gave permission for this article to be submitted to a peer-reviewed journal (at a future date) and for inclusion of the manuscript in the dissertation.

Chapter 2: Assessing the impacts of urban beehives on wild bees using individual, population-level and community level metrics

Sarah E. MacKell, Hadil L. Elsayed, and Sheila R. Colla

This chapter will be submitted for publication to a peer-reviewed journal.

Candidate’s Contributions:

Sarah MacKell and Dr. Colla, conceived of the ideas. Sarah MacKell led the development of the field methodology. Sarah MacKell and Hadil Elsayed contributed equally to the collection of data in the field and processing of samples (i.e. identifying and measuring). Sarah MacKell led the data analysis, but Hadil Elsayed conducted the trait composition analysis. Sarah MacKell led the writing of the manuscript. All authors contributed to editing and gave permission for this article to be submitted to a peer-reviewed journal (at a future date) and for inclusion of the manuscript in the dissertation.