VARIATION IN FLOWER MORPHOLOGY ENHANCES WILD BEE DIVERSITY IN

URBAN ECOSYSTEMS

Serena Sinno Hamid

A Thesis

in

The Department

of

Biology

Presented in Partial Fulfillment of the Requirements

For the Degree of Master of Science (Biology) at

Concordia University

Montreal, Quebec, Canada

December 2021

CONCORDIA UNIVERSITY
School of Graduate Studies

This is to certify that the thesis prepared

By: Serena Sinno

Entitled: Variation in flower morphology enhances wild bee diversity in urban environments
and submitted in partial fulfillment of the requirements for the degree of

Master of Science (Biology)

complies with the regulations of the University and meets the accepted standards with respect to
originality and quality.

Signed by the final Examining Committee:

Emma Despland
_____Chair

Dylan Fraser
_____ Examiner

Eric Pedersen
_____ Examiner

Carly Ziter
_____ Supervisor

Jean-Philippe Lessard
_____ Supervisor

Robert Weladji
Approved by _____
Chair of Department or Graduate Program Director

Pascale Sicotte
_____
Dean of Faculty

Abstract

VARIATION IN FLOWER MORPHOLOGY ENHANCES WILD BEE DIVERSITY IN

URBAN ECOSYSTEMS

Serena Sinno Hamid

Urbanization is a leading threat to biodiversity, but scientifically informed management of urban

ecosystems can mitigate negative impacts. For wild bees, which are declining worldwide, careful

consideration of flower choice in private and public green spaces could help preserve their

diversity. While floral density and species richness are both linked to wild bee diversity, the

mechanisms underlying these relationships remain poorly understood. Here, I tested two

hypotheses relating the influence of floral trait composition to bee species richness, which I have

termed the floral trait diversity and optimal floral trait hypotheses. To test my hypotheses, I

assessed whether within-site variation in bee richness relates to variation in floral trait

composition in urban green spaces across the city of Montreal, Canada. In addition to surveying

flower species richness and floral density, I measured two floral traits which relate to pollinator

feeding success, nectar sugar concentration and corolla length, as feeding is the main use of

flowers by bees and therefore likely to impact their communities. After accounting for variation

in floral density, I found that bee richness was positively related to community-wide variation in

corolla length, supporting the floral trait diversity hypothesis. These findings suggest that

although flower abundance and richness affect wild bee richness in urban ecosystems, the

composition of flower morphologies can further shape pollinator communities. I conclude that an

understanding of these mechanisms can positively impact conservation of urban wild bee

communities.

Keywords

Wild bee species richness, floral traits, urban green space, community ecology, community gardens, parks, cemeteries, pollinator conservation

Acknowledgements

I would first and foremost like to thank my supervisors, Carly Ziter and JP Lessard for mentoring me for the past two years, providing excellent guidance, supporting me along the way, and always answering my numerous questions. Thank you to my committee members, Emma Despland and Dylan Fraser, and Eric Pedersen, for helping me shape my work into what it is. Thank you to Gail MacInnis and Étienne Normandin for their invaluable knowledge and helping me identify many, many bees. Thank you to my research assistants for making my field season possible, and for all the laughs during long and hot field days. Thank you especially to each and every single one of my lab mates in the Ziter Urban Ecology Lab and the Biogeography and Community Ecology Lab at Concordia University. Kayleigh, Emily, Bella, Michael, Tonia, Javier, Gabriel, Victor, Isaac, Érik, and Dana – you've made the past few years some of the most memorable, and I'll always cherish all our lunches, outings, and chats about science and all else. Thank you for getting me through grad school. To my parents for providing a home and all the food I could ever want, being so proud of me, and alleviating so many worries, thank you, I love you. Thank you to my sister and brother, family, and friends for providing the same love and support, and also making fun of me just the right amount for studying bugs. Last but not least, I'd like to thank my partner, Costa, for everything.

Table of Contents

Introduction

Wild pollinator numbers are declining worldwide, making it pertinent to help conserve their populations (Potts et al. 2010, Cameron et al. 2011). Preserving bee diversity is important to ensure ecosystem resilience and to be able to sustain pollination services (Tilman 1996, Pennekamp et al. 2018). In addition to bee conservation in natural and agricultural landscapes, a rapidly growing area in bee ecology and conservation relates to how we can promote the maintenance of wild bee diversity in highly modified landscapes, such as cities (Hernandez et al. 2016). With over half of the world's human population living in cities, urban areas are the regions in which biodiversity encounters humans most frequently (Knapp et al. 2021, Spotswood et al. 2021). While urbanization poses a threat to bee diversity (Cardoso and Gonçalves 2018, Fenoglio et al. 2020), many urban areas are still able to sustain rich and abundant wild bee communities, largely from a great number of generalist species (Tonietto et al. 2011, Wray and Elle 2015, Theodorou et al. 2017). Some urban areas can be even richer in bee species than intensive agricultural and some natural ecosystems, owing to local habitat in cities consisting of a vast diversity of floral resources planted (Bates et al. 2011, Baldock et al. 2015, Hülsmann et al. 2015, Sirohi et al. 2015). However, to fully realize the potential of cities to serve as refuges for wild bee species (Hall et al. 2017), evidence-based management of urban green spaces is critical. Effective urban bee conservation thus requires an improved understanding of which environmental factors most strongly contribute to the maintenance of wild bee diversity in urban systems – including a better understanding of the mechanisms linking floral and bee communities.

The availability of food resources, flowers specifically, plays a large role in shaping the composition and richness of wild bee communities (Eltz and Brühl 2002, Potts et al. 2005,

Grundel et al. 2010, Murray et al. 2012, Pardee and Philpott 2014, Torné-Noguera et al. 2014). The availability and proximity of suitable resources is important because many wild bees have a short flight range (100 m to 1.5 km) and use resources within close proximity to their nests (Gathmann and Tscharntke 2002, Greenleaf et al. 2007, Zurbuchen et al. 2010). As such, attributes of the local floral community can influence bee diversity by at least two potential mechanisms: floral trait diversity and optimal floral traits. Floral trait diversity is defined here as the breadth of resource types or values available in a community and optimal floral traits as the abundance of an optimal resource in a community. On one hand, there has been much research suggesting that floral resource richness and abundance can increase pollinator diversity. On the other hand, there is also evidence that certain resources may be optimal, such that the presence or abundance of said resource would be even more crucial to preserve bee diversity (Roubik et al. 1995, Kim et al. 2011). Therefore, a floral community composed mainly of said optimal resources may have a strong influence on the richness of visiting pollinator species. The relative influence of floral trait diversity versus optimal floral traits on wild bee richness, however, remains poorly explored. This is highly relevant in urban ecosystems where humans play a large part in influencing what is planted and grows in local floral communities.

Within the floral community, floral characteristics that exert a strong influence on bee species richness are nutrition and morphology. Often land managers and decision-makers are given simplified recommendations to help wild bee communities, such as planting native flora, which may not always result in increased wild bee richness or abundance (Matteson and Langellotto 2011, Hanley et al. 2014, Salisbury et al. 2020). Public and private land managers are also told that planting a greater flower species richness helps support bee diversity, and although this is often true, less research has been done about exactly what it is about a high

2

flower species richness or abundance that promotes a high wild bee species richness, particularly in urban areas (Ebeling et al. 2008, Blaauw and Isaacs 2014). Therefore, assessing flower nutritional value and morphology through the lens of both trait diversity and optimal traits in urban environments may help increase the understanding of mechanisms underlying bee diversity, which can be implemented in pollinator protection plans and park management strategies (City of Toronto, 2021). This will then allow urban-decision makers and land managers to better conserve bee communities in cities, while enriching our mechanistic understanding of pollinator ecology and conservation more broadly.

The nutritional value of flowers to bees may be the most important trait to consider in studying the link between floral and bee communities, as it is the pollen and nectar that are produced by flowers that provide bees with sustenance for them and their brood. Nectar in particular is bees' primary source of energy, providing them with carbohydrates in the form of sugar (Pacini et al. 2003). However, not all flowers have the same reward value to bees, as the volume and concentration of nectar, as well as quantity of pollen varies widely among plant species (Bosch et al. 1997, Potts et al. 2003). Furthermore, not all bees have the same nutritional requirements. Larger and faster-flying bees often require more energy than smaller bees with lower metabolic demand, for example, so the diversity of rewards within floral communities may be a primary driver of bee diversity (Willmer 1988, Roubik et al. 1995, Potts et al. 2003, 2004). Alternatively, as proposed by the species richness-energy hypothesis, the abundance of high-quality resources may also influence how many bee species are able to be supported in local habitat patches, and how many species from within the landscape are attracted to a particular high reward patch (Brown 1981, Wright 1983). Often, pollinators will attempt to increase their energy consumption while minimizing the effort required to obtain this energy, and so an

optimal reward may exist that such that patches dominated by high quality nectar flowers may attract more species (Harder 1986, Kim et al. 2011).

In addition to nutritional rewards, the diversity of floral morphology in plant communities can also influence bee communities. Plant morphology may inhibit or facilitate resource use by bees based on the degree of functional trait matching. This is because bees and other pollinators may predominantly use flower species they've co-evolved with (Thompson 1989). These co-evolutions are termed pollination syndromes, which are collections of floral morphological traits that match with specific traits of pollinators (Ollerton et al. 2009). For example, resource-use often occurs based on size matching, where flower corollas are appropriately sized for a bee's proboscis to effectively collect nectar (Hobbs 1962, Borrell 2005, Stang et al. 2009, Klumpers et al. 2019), a diversity of corolla lengths in a community should correlate to richness of bee species, if diversity of tongue lengths correlates to number of bee species. However, considering most bees in cities are generalists and able to feed on a wide variety of flowers, a community composed mainly of short corollas may be able to support high bee species richness, as nectar resources will be accessible to bee species with varying proboscis lengths (Borrell 2005, Stang et al. 2006, Theodorou et al. 2017, 2020). I would expect the composition of morphological features within a floral community to influence the richness of wild bee communities under one of these scenarios, of either a diversity of corolla lengths or mostly short corolla lengths.

Here, I sampled 1935 bees across 16 urban sites to test the floral trait diversity and optimal floral trait hypotheses. Under the floral trait diversity hypotheses, I hypothesized that a greater diversity of nectar sugar concentration (H1) and a greater diversity of corolla lengths in a floral community (H2) will result in a greater bee species richness because there will be a greater

diversity of nutritional rewards that support wild bees with a diversity of nutritional requirements, and wild bee species with various tongue lengths, respectively. Alternatively, under the optimal floral trait hypothesis, I hypothesized that having a floral community dominated by plant species with high nectar sugar concentration ($H1_A$) will provide a greater amount of nutritional reward that will attract a greater richness of bee species regardless of their nutritional requirements. Again, under the optimal trait hypothesis, communities dominated by plant species with small corolla length ($H2_A$), which many bee species can use, regardless of their tongue length, will result in greater bee species richness.

Methods

Study system

The study took place on the Island of Montreal, Quebec, Canada. Montreal is Canada's second largest city, with a population of roughly 1.9 million people (Statistics Canada 2016). The city is located at the southwestern end of Quebec, situated in the St. Lawrence River, approximately at 45°30′32″ latitude and 73°33′42″ longitude. It is categorized as a humid continental climate by the Köppen-Geiger climate classification system, being relatively cold without a dry season, with warm summers (Peel et al. 2007). The city itself is composed of many high-rise and low-rise buildings, as well as a great amount of asphalt roads, with only approximately 12% of the Island classified as green space (Metson and Bennett 2015). Considering that the Island of Montreal is dominated by high levels of impervious surface, it can serve as an example for how to enhance biodiversity in other highly developed cities with limited green space.

I selected a total of 16 different sites on the Island of Montreal from a combination of different green space types (Fig. 1, Table S2) known to support pollinator communities in cities (Matteson and Langellotto 2010). I chose green spaces in urban centers as they support more pollinators than habitat that is dense in impervious surface (Baldock et al. 2018). The sites were composed of nine community gardens, three nature parks, and four cemeteries. The combination of different green space types resulted in diverse floral communities, due to differences in the floral resources that were planted and varying management strategies (Baldock et al. 2018). All sites were surrounded by an urban or suburban matrix to reduce the chance that differences in bee richness between sites is due to landscape factors. Sites range from approximately 1365 m^2 to 1 km^2. Sites were geographically distributed across the Island of Montreal and a minimum of 1 km away from one another, as many of the bee genera found in urban centers have foraging distances less than or around this range (Gathmann and Tscharntke 2002, Greenleaf et al. 2007, Zurbuchen et al. 2010, Normandin et al. 2017). Sampling public urban greenspaces will facilitate making recommendations for the city, as any recommendations resulting from this work can be directly applied to these sites, and similar surrounding areas. Furthermore, there is a high density of citizens and local organizations in the urban environment that may be inspired to implement the findings of this research on their property.

Wild bee collection

During July 2020, during peak bee foraging in Montreal, Quebec (Normandin et al. 2017), I sampled all sites twice, ensuring consecutive days with sunny weather, as bees do not forage during rainy weather conditions, and to be sure the bee community was as similar as possible during the days of sampling. Sampling took place from July 8 to July 10, and approximately

three weeks later from July 30 to July 31. The first sampling round consisted of three days, rather than two, to sweep net two sites that were missed the previous day. This was done to ensure that sites were only sampled between 8:00 AM and 5:00 PM, when sun and temperature are suitable for bee foraging (Nielsen et al. 2011, Hamblin et al. 2018). At each site, I established a total of eight observation plots. The centroids of all plots in a site were a minimum of 10 meters apart from one another to differentiate between floral patches. Each plot had dimensions of 2 meters x 2 meters. I placed the plots haphazardly in patches that were dense in flowers relative to the entire site. I determined the placement of the plots during each sampling repetition, only moving them from their original placement if it was no longer dense in flowers relative to the rest of the site. I sweep netted solely on the eight plots, with a cumulative time of one minute and 15 seconds spent on each plot to keep sampling time constant on each plot. The cumulative time of 10 minutes for each sampling repetition at a site was consistent with other studies sweep netting areas of this size (Cane et al. 2000, Potts et al. 2003). I split the sampling time for each plot in half and walked back and forth between the plots as some studies have found that passively waiting for long periods of time on observational plots is not optimal to estimate bee richness at a site (Westphal et al. 2008, Nielsen et al. 2011). Therefore, this proposed approach more closely resembles that of variable transect walks, where walking does not necessarily occur in a straight line, but rather where floral-dense patches occur (Westphal et al. 2008). Whenever a specimen was captured, I stopped the time to store the bee. I then took the specimens back to the lab for identification using several keys (Harder 1988, Gibbs 2010, Sheffield et al. 2011, Gibbs et al. 2013, Richardson and Williams 2013, Oram 2018).

In addition to sweep netting, which I performed during the collection of pan trap contents to reduce disturbance from the installation of the pan traps, I placed one pan trap within each of

the aforementioned plots for a total of 48 hours (Normandin et al. 2017). The protocol was composed of eight sets of pan traps at each site, a very common method for flying insect collection (Feinsinger 1994, Leong and Thorp 1999). This follows pan trap sampling protocol, which calls for pan traps to be spaced at least five meters apart, as that is approximately the minimum length where competition between pan trap bowls for bees ceases to exist (Droege et al. 2010). To maximize the likelihood of catching wild bees, I used pan traps that were elevated 60 cm above the ground, as pan traps positioned on the ground tend to be less effective (Cane et al. 2000). Also, elevated pan traps were closer in height to many of the flowering plant species at these sites, and therefore were in closer proximity to the bees' foraging height. Each pan trap set consisted of a blue, yellow, and white bowl to capture wild bees with different color preferences (Kirk 1984, Leong and Thorp 1999). Every bowl was filled with 2 cm of water, with a drop of soap to break surface tension (Quistberg et al. 2016, Bennett and Lovell 2019). By using a combination of both pan trapping and sweep netting, I could ensure a wide diversity of bees were caught, which better represents the bee community at a site, as pan traps and netting often capture different species (Cane et al. 2000, Grundel et al. 2011, Nielsen et al. 2011, Popic et al. 2013).

Flower identification and density measurements

I used the same 2-meter x 2-meter plots for flower identification as well as floral density measurements to directly assess the flower community that bees are using. This provided an accurate representation of the floral community at community gardens, as well as for the large sites, as there aren't extreme variations in the spatial patterns of the floral communities at large parks and cemeteries. For flower identification, I identified all the flower species currently

flowering in each plot to lowest taxonomic level possible, typically species, using iNaturalist, and often confirmed with the Fleurs des champs du Québec et des Maritimes (Parent et al. 2011). I quantified floral density by estimating the ratio between the area of flowering parts for each flower species and the total area of the plot. This was done to the nearest 5% density. If the density for a given flower species was less than 5%, I placed it in a less than 5% category - which was calculated as 2.5% for all analyses. In one instance, floral density was approximated to over 100%, so it was calculated as 100% for all analyses.

Floral traits

For every flower species I identified, I also took corolla length measurements. To do this, floral units for each flower species present were measured to the nearest hundredth millimeter using digital calipers. I took three measurements from the first plot a species was found in, unless there were less than three floral units present, and one additional measurement from each consecutive plot the flower species was growing in. Measurements were taken from every plot a species was found in, to account for variation in corolla length that may occur due to differences in microclimate or soil composition at smaller scales. This was done to be able to relate to the diversity of tongue length in wild bees at a site, which should correlate to the diversity of bee species, as bees often exhibit size matching with corolla length (Stang et al. 2009).

I also measured nectar sugar concentration for every flower species found in the plots using a Brix Bellingham + Stanley Ltd. refractometer (Willmer 1988, Roubik et al. 1995). I used microcapillary tubes to draw up nectar from flower corollas, and then ejected the nectar onto the refractometer to take sugar concentration percent measurements. At every site, I took one to two

sugar concentration measurements from one plant of each species from each plot which contained that species. I took measurements from more than one plot to account for variations in soil between the plots that may result in variations in sugar concentration, as well as the natural variation in nectar sugar concentrations (Petanidoua et al. 1999, Baude et al. 2011). Flower sampling occurred from 8:00 AM to 4:00 PM. I changed the sampling order of the sites for both sampling rounds to account for diurnal variation in nectar sugar concentration (Potts et al. 2001). The refractometer had a functioning range between 0% and 50% sugar. If a nectar measurement had a sugar concentration greater than or equal to 50%, it was placed in a 50%+ category - which was calculated as 50% for all analyses. This was rare, occurring for only 8 floral units out of 207 nectar concentration readings done in the field.

For 72 out of the 149 flower species identified, I was unable to obtain nectar sugar concentration readings in the field. This was often due to flowers not containing enough nectar for the refractometer to take a reading, or flowers already having been visited by nectar-feeding insects. For these flower species, I compiled information from already published data (Table S7) and was able to obtain nectar sugar concentration readings for 43 out of the 72 flower species that readings were not possible for in the field. To find this data, I used Google scholar to search key words such as "nectar sugar concentration", along with the flower species or genus. When published data existed in more than one study for a given species, I used a weighted average nectar concentration for my analyses, which was done for five of the species I used published data for. Each nectar concentration measurement was weighted by the number of flower individuals a reading was taken for in a study divided by the total number of flower individuals from all the studies that had readings for that species. In the event I was unable to find published nectar sugar concentrations for a given species in my study, I used non-weighted mean readings

from species in the same genus, as to give an equal weighting to each species. This was done for 17 flower species. However, if multiple published sources had measurements for the same species from the same genus that one of my species without a reading belonged to, then said species was weighted accordingly, as previously described. This was done for two flower species.

Floral trait metrics

To assess diversity of flower corolla lengths and nectar sugar concentration, I used an index of functional dispersion (Mason et al. 2003) – hereafter referred to as community weighted variance (CWV) for simplification – of corolla length and nectar sugar concentration:

$$CWV = \frac{2}{\pi} arctan(5V)$$

Let:

$$V = \sum_{i=1}^{N} w_i \left(\ln x_i - \overline{\ln x} \right)^2$$

Let: w_i = the relative abundance of species i, out of N species

x_i = the character value of species i

$\overline{\ln x}$ = the community weighted logarithmic mean, such that:

$$\overline{\ln x} = \sum_{i=1}^{N} w_i \times \ln x_i$$

A scaling factor of 5, followed by an arctan transformation, and scaled again by $\frac{2}{\pi}$ was used to be able to compress values between 0 and 1, to be able to usefully contextualize a value

of diversity (Mason et al. 2003). Note that the arctan transformation used to calculate CWV inflates large values towards the upper end of the function, and so data may be inflated towards values of higher diversity. However, the average CWV for corolla lengths in our data is approximately 0.417, so the data is not overly skewed towards large values.

To assess for an optimal corolla length and nectar sugar concentration, community weighted means (CWM) of these traits were used:

$$CWM = \sum_{i=1}^{N} w_i \times x_i$$

Where w_i = the relative abundance of species i, out of N species

x_i = the character value of species i

Both trait metrics were chosen due to being able to accommodate a low number of data points, i.e., low flower species richness at the plot level. Weighted metrics were used to account for differences in floral density among flower species. Finally, as my hypotheses consisted of different directional relationships for each trait, it was necessary to use metrics that only account for one trait at a time.

To calculate both floral trait metrics, I used mean values for each flower species at a plot. In the event a flower species at a plot didn't have a measurement for a given trait, I used an average value from all individuals of that species from the site it was identified at during the same sampling round. If the flower species had no measurements from any individuals at the site it was identified at, I used an average value of all the individuals of that species from all sites from both sampling rounds. If the flower species did not have any readings for nectar concentration in my dataset, I used data from published literature.

Wild bee identification

Wild bees were dried, pinned, and identified to species level (Harder 1988, Sheffield et al. 2011, Gibbs et al. 2013, Høye et al. 2021).

Statistical analyses

1. Generalized Linear Mixed Models to assess the influence of floral traits on bee richness

To test my hypotheses linking bee richness to each floral trait, I used generalized linear mixed models. Specifically, to test the floral trait diversity hypotheses of both flower morphology and nectar reward, richness of wild bees was modelled against plot-level CWV of corolla length and nectar sugar concentration, respectively, in separate models. Then, to assess the optimal floral trait hypotheses of flower morphology and nectar reward, wild bee richness was modelled against plot-level CWM of corolla lengths and nectar sugar concentration. For all models, site was used as a random effect to account for multiple plots within the same site, and the biotic and abiotic conditions that may be similar within that site.

In addition to assessing the effect of trait metrics on bee richness, I assessed the fit of models that also included floral abundance and richness as fixed effects, as these variables are known to affect bee richness, and I wanted to assess whether average floral trait or floral trait diversity would explain bee richness beyond floral richness or density alone.

Sampling round was also included in each model in combination with the plant trait community metrics as fixed effects. For each combination of factors, GLMMs were tested where

all factors in the model were additive and where they were all interactive, to later be able to assess if factors interacting with one another provided a better fitting model.

I initially ran my models with a Poisson distribution for count data. To address overdispersion in these models (assessed using the check_overdispersion function from the performance package in R (version 0.8.0)), I re-ran all models with a negative binomial distribution. Models were then checked for under-dispersion using a Pearson chi-squared test using the testDispersion function from the DHARMa package in R (version 0.4.4) to confirm they were not zero-inflated. Model effects were checked to see if linearity assumption was met. Generalized linear mixed models were fit by maximum likelihood. All generalized linear mixed models were performed using the glmer function in the lme4 package (version 1.1-26) in R. Confidence intervals were calculated using the confint function in the stats package (version 4.0.5) in R. Effect sizes for predictor variables were calculated by exponentiating the estimate coefficients.

To ensure that any independent variables within the same model were not highly correlated, I assessed for collinearity among floral richness, density, and trait metrics using the rquery.cormat function in the corrplot package (version 0.90) in R (Fig. S1). Trait metrics or floral diversity metrics would be considered collinear at a correlation coefficient of 0.7. As no trait metrics were collinear, no changes were made to the analyses. I also checked whether bee richness and bee abundance were significantly correlated, to help contextualize whether bee abundance may be a key driver of changes in bee species richness (Fig. S2).

2. *Model comparison to test alternative hypotheses explaining variation in bee richness*

After GLMMs assessing wild bee species richness based on my hypotheses were run, model selection was used to determine the most parsimonious model relating community-wide floral characteristics to wild bee species richness. This was the primary method I used to assess predictors of bee richness. I followed this by also being sure to assess P-values of predictor variables to infer which had a significant effect on wild bee species richness. In my evaluation of best fit models, I only considered those models for which the floral trait metrics were significant.

Akaike's information criteria corrected (AICc) values were calculated for each model using combinations of the corresponding metrics for both plant traits, flower species richness and floral density, with models for each plant trait assessed separately (Table 1, 2, Table S3 - S6). I then determined the best-fitting model based on AICc values. Due to the GLMMs where all terms were additive consistently having lower AICc values than their corresponding GLMMs where all terms were interactive, as well as wanting to test the individual effects of the predictor variables, GLMMs with additive terms were considered in the final models. AICc values were calculated using the aictab function in the AICcmodavg (version 2.3-1) package in R.

Results

Biodiversity

I collected a total of 1935 wild bees coming from 105 different species from 21 different genera. I captured 701 individuals during the first sampling round and 1234 individuals during the second sampling round. Bee richness and abundance were positively correlated (Fig. S2, $P <$ 0.001). The three most common bee species were *Ceratina calcarata*, *Hylaeus communis* and *Lasioglossum laevissimum* representing 10.1%, 6.1% and 5.9% of total bees collected,

15

respectively. In addition, I identified flowers from a total of 148 species from 137 genera. During the first sampling round, I identified 96 flower species and 121 species during the second sampling round. The three most commonly occurring flower species were *Vicia villosa* (an introduced species comprising 4.0% of all flower observations), *Erigeron annuus* (a native species comprising 3.7% of all flower observations) and *Leucanthemum vulgare* (an introduced species comprising 3.6% of all flower observations). In terms of flower cover, the three flowers that occurred in the greatest proportions were *Erigeron annuus* (6.4% of the total floral cover), *Centaurea cyanus* (an introduced species comprising 4.2% of the total floral cover) and *Calendula officinalis* (an introduced species comprising 4.2% of the total floral cover).

The number of wild bee species was strongly positively corelated to the flower species richness at a plot, as well as floral density ($P < 0.001$; Table S1; for both flower species richness and floral density).

Effects of nectar sugar concentration on wild bee species richness

Diversity in nectar sugar concentration in a flower community (nectar concentration CWV) combined with floral density, as well as an optimal nectar sugar concentration (nectar concentration CWV) combined with floral density were the best predictors of wild bee species richness (Table 1). However, neither nectar concentration diversity or a high nectar sugar concentration had a significant effect on wild bee species richness ($P = 0.44$ and $P = 0.45$, respectively). No metric of nectar sugar concentration had a significant effect on wild bee species richness in any other model ($P > 0.05$; Table 1).

Effects of corolla length on wild bee species richness

According to the AIC comparisons, the model that best explains wild bee species richness is diversity in corolla length (corolla length CWV) in a flower community combined with floral density (Table 2). Corolla length CWM in addition to floral density improved the fit of the model more than floral density alone as a predictor of wild bee species richness. Diversity in corolla length (corolla length CWV) had a significant effect on wild bee species richness, with an increase of CWV from 0 to 1 increasing bee richness by 25% ($P < 0.05$; Table 3, Figure 1). Floral density had significant effect in this model ($P < 0.001$; Table 3), with an increase of floral density by 1% increasing wild bee richness by 0.9%. Sampling round was not significant in the top model ($P = 0.07$; Table 3). In the second-best model, with a community composed of an optimal trait (corolla length CWM) combined with floral density, corolla length CWM was not significant ($P = 0.07$; Table 3), but floral density and sampling round were ($P < 0.001$ and $P < 0.05$, respectively, Table 2).

Discussion

Our results confirm previous findings where an increase in floral richness (Lowenstein et al. 2014, Gerner and Sargent 2021) and density (Matteson and Langellotto 2010) resulted in an increase in wild bee species richness. However, my work also provided evidence that the diversity of flower morphology in a patch influences the species richness of visiting bees. Taken together, these findings suggest that urban management methods that maximize flower morphological diversity and floral density can help preserve bee diversity and the pollination services they provide.

This study was conducted in an urban environment to be able to better make recommendations to citizens and urban park and garden managers on how to best support bee diversity. Often, cities support higher bee diversity than agricultural areas or even natural habitats due to the many flower plantings by a diversity of urban stakeholders (Kaluza et al. 2016). Therefore, there is great potential to be able to support bees in these highly modified landscapes (Hall et al. 2017, Baldock 2020, Wenzel et al. 2020). With the numerous people living in urban environments, citizens can considerably contribute to wild bee conservation by incorporating the findings of this study to the gardens they manage.

Effects of corolla length community-wide variation on wild bee species richness

I found support for the floral trait diversity hypothesis for flower morphology, but not nectar sugar concentration. As expected, a greater diversity of corolla lengths in a floral community positively affects the species richness of visiting wild bees (Fig. 2, Table 3). A diversity in corolla lengths may be promoting bee diversity via trait-matching, where bee species are able to feed from flowers with corolla lengths that render nectar available to them based on their proboscis length (Stang et al. 2009). Recent work in natural areas shows that matching between corolla length and bee proboscis length predicts the frequency of plant-pollinator interactions (Klumpers et al. 2019). Pollinators often chose to feed on flowers that increase foraging efficiency, which occurs when a pollinator's proboscis is slightly longer than the corolla tube, due to a decrease in handling time. Similarly, the findings of Hobbs (1962) suggest that bumble bees choose to forage on flowers with longer corollas if they are long-tongued, and flowers with shorter corollas if they are short-tongued, as this likely facilitates nectar-extraction. Therefore, a

floral community with a diversity of corolla lengths allows efficient foraging for bees with various tongue lengths, supporting high bee species richness.

Floral communities with a high diversity of corolla lengths were visited by a greater number of wild bee species than what was expected based solely on the density of flowers. Therefore, we can infer that there are additional processes that occur that affect bee communities and support many bee species even when there is a high floral density. Of course, it is important to be sure to plant a high density of flowers as well, to ensure there are ample resources to both attract and support many bee species, as was also supported in urban environments by Quistberg et al. (2016).

Effects of community-wide average corolla length on wild bee species richness

In contrast to the floral trait diversity hypothesis for flower morphology, I did not find strong support for the optimal trait hypothesis. This is not in line with past research, which has shown that in floral communities with similar corolla lengths as the ones I analyzed, a smaller CWM of corolla length results in greater bee functional diversity in urban environments (Theodorou et al. 2020), and that flowers with shorter corollas had more observed pollinator species visiting them (Stang et al. 2006). As found by Stang et al. (2006), regardless of their proboscis length, both long-tongue and short-tongue bee species can reach the nectar in short corollas, whereas longer corollas will limit pollinators with short proboscis lengths due to the morphological constraint that results in difficult feeding. Although I did not find a significant relationship with average corolla length and wild bee species richness, it's possible that a floral community's average corolla length may have a greater effect on bee functional diversity than species richness. This is

because corolla lengths may create barriers to which bee functional groups are able to use a flower species, depending on the length of their proboscis.

Effects of nectar sugar concentration community-wide average on wild bee species richness

Based on species richness-energy theory, a community with a higher average nectar sugar concentration should result in a greater species richness of visiting wild bees, as more energy in a patch might optimize foraging and therefore attract more species. However, I did not find a relationship between average nectar sugar concentration and wild bee richness. This contrasts with another study showing that higher nectar sugar concentrations, between 35%-65%, are consumed by bee species more frequently, perhaps suggesting that more concentrated nectars are optimal for bees (Roubik et al. 1995). Other work provides support for bees foraging based on maximizing their energy intake rate through either selecting for flowers with nectar quantity above a certain threshold (Hodges 1981), or choosing inflorescences in close proximity to the one they had just used (Pyke 1979). Although both approaches to foraging efficiently minimize energy loss while feeding, there is evidence to support bees may also select flowers that maximize energy intake per unit time of feeding by other selection behaviours. As it was found that at higher nectar sugar concentrations, of around 55%, bumble bees acquire the greatest amount of energy per unit time of feeding, this may also support that a higher average nectar sugar concentration in a floral community should attract more bee species (Harder 1986).

Effects of community-wide nectar sugar concentration variation on wild bee species richness

Diversity in nectar sugar concentrations did not influence wild bee species richness in my study. In other studies, an increase in nectar resource diversity or quality, both measured as the number and evenness of nectar volume and nectar concentration combinations present, resulted in bee species richness increasing (Potts et al. 2003, 2004). As neither nectar concentration diversity, nor a floral community composed of an optimal trait, had an effect on wild bee species richness in our study, this may suggest that nectar volume has a greater influence on bee species richness. Similarly, Potts et al. (2003) showed that nectar concentration only had an influence on bee community structure when assessed in combination with nectar volume. Furthermore, it is important to consider that nectar is not the only nutritional reward that may influence wild bee communities; pollen has also been shown to play a role in shaping bee communities and determining visitation, and so it may be important for future studies to also consider the effect of pollen quantity in combination with nectar on bee communities (Bosch et al. 1997, Potts et al. 2003, Rowe et al. 2020).

Several factors can affect nectar sugar concentrations and therefore, the conclusions of this study. Although we switched the order of sampling for our sites between both sampling rounds to account for changes in nectar sugar concentration throughout the day, nectar concentrations can still vary due to factors such as abiotic conditions and genetics (Pleasants 1983, Klinkhamer and van der Veen-van Wijk 1999). Furthermore, nectar quantities were often not enough to take sugar concentration readings for smaller flowers or flowers that were already visited by nectivorous insects earlier in the day. For these reasons, there may be a need for more nectar concentration measurements taken, and measurements taken at the same time of day, potentially after bagging flowers the day before, in studies going forward.

Implications

The findings of this study attest to the importance of flowers in helping shape wild bee communities in urban habitats (Martins et al. 2017, Lowenstein et al. 2019). Having a diversity in corolla lengths in a floral community is important for a high bee species richness. Our work also adds to the growing body of literature that shows floral abundance and flower species richness are important for bee communities (Matteson and Langellotto 2010, Lowenstein et al. 2014). When making recommendations for urban parks departments, garden managers, and citizens, it is still necessary to consider these measures of flower diversity, as it is important to plant a lot of flowers during the entire foraging season to help support urban bee communities. Furthermore, although we did not find a significant effect of nectar sugar concentration, it is still important to plant flowers that produce nectar, which is a necessary part of a bee's diet.

A few examples of common flower species in our study that would result in a diversity of corolla lengths were *Cosmos bipinnatus* (garden cosmos), *Echinacea purpurea* (echinacea) and *Phlox maculata* (meadow phlox), which have short, medium, and long corollas, respectively, and are all native to Eastern North America. They are all commonly found in planted city gardens and fare well in urban environments, and seeds can easily be found in greenhouses. Wild bees can benefit from these species if they are planted in managed areas in urban environments such as community parks, cemeteries, gardens, and sidewalk plantings. Additionally, some more common edible species that meet these criteria are thyme, cucumber and squash flowers, which can be planted in citizens' home flower beds or flower boxes, or in urban community gardens, to attract wild bee species.

It is also important to consider that there was a significant increase in wild bee species richness with increasing wild bee abundance, and so, wild bee richness may have been impacted by the abundance of bees caught. To further support wild bee conservation, future studies should assess the impact of floral traits, as well as floral density and richness on other aspects of bee diversity beyond the scope of this work, such as abundance or composition.

Conclusion

By assessing floral traits in addition to commonly assessed measures of flower communities such as density and richness, I was better able to explain wild bee species richness in an urban environment. This suggests that there are likely underlying mechanisms behind why bee species richness often increases with increasing floral richness and density. Although no metric of nectar sugar concentration influenced wild bee species richness, a community of diverse corolla lengths increased wild bee species richness. Therefore, park managers, cemetery landscapers, urban garden managers, and citizens should be sure to plant flower gardens with a diversity of corolla lengths. Doing so would support wild bee species richness in urban environments, which have been shown to act as a refuge for pollinators (Tommasi et al. 2004, Banaszak-Cibicka and Żmihorski 2012, Baldock et al. 2015, Hall et al. 2017). As pollinator populations are decreasing worldwide, implementing the findings of this study can help cities to play a larger role in pollinator conservation.

Works Cited

Baldock, K. C. 2020. Opportunities and threats for pollinator conservation in global towns and
cities. Current Opinion in Insect Science 38:63–71.

Baldock, K. C. R., M. A. Goddard, D. M. Hicks, W. E. Kunin, N. Mitschunas, H. Morse, L. M.
Osgathorpe, S. G. Potts, K. M. Robertson, A. V. Scott, P. P. A. Staniczenko, G. N. Stone, I.
P. Vaughan, and J. Memmott. 2018. A systems approach reveals urban pollinator hotspots
and conservation opportunities. Nature Ecology & Evolution.

Baldock, K. C. R., M. A. Goddard, D. M. Hicks, W. E. Kunin, N. Mitschunas, L. M. Osgathorpe,
S. G. Potts, K. M. Robertson, A. V. Scott, G. N. Stone, I. P. Vaughan, and J. Memmott.
2015. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-
visiting insects. Proceedings of the Royal Society B: Biological Sciences 282.

Banaszak-Cibicka, W., and M. Żmihorski. 2012. Wild bees along an urban gradient: Winners
and losers. Journal of Insect Conservation 16:331–343.

Bates, A. J., J. P. Sadler, A. J. Fairbrass, S. J. Falk, J. D. Hale, and T. J. Matthews. 2011.
Changing bee and hoverfly pollinator assemblages along an urban-rural gradient. PLoS
ONE 6.

Baude, M., J. Leloup, S. Suchail, B. Allard, D. Benest, J. Mériguet, N. Nunan, I. Dajoz, and X.
Raynaud. 2011. Litter inputs and plant interactions affect nectar sugar content. Journal of
Ecology 99:828–837.

Bennett, A. B., and S. Lovell. 2019. Landscape and local site variables differentially influence
pollinators and pollination services in urban agricultural sites. PLoS ONE 14:1–21.

Blaauw, B. R., and R. Isaacs. 2014. Larger patches of diverse floral resources increase insect
pollinator density, diversity, and their pollination of native wildflowers. Basic and Applied

Ecology 15:701–711.

Borrell, B. J. 2005. Long tongues and loose niches: Evolution of euglossine bees and their nectar flowers. Biotropica 37:664–669.

Bosch, J., J. Retana, and X. Cerda. 1997. Flowering phenology, floral traits and pollinator composition in a herbaceous Mediterranean plant community. Oecologia 109:583–591.

Brown, J. H. 1981. Two decades of homade to Santa Rosalia: toward a general theory of diversity. American Zoologist 21:877–888.

Cameron, S. A., J. D. Lozier, J. P. Strange, J. B. Koch, N. Cordes, L. F. Solter, and T. L. Griswold. 2011. Patterns of widespread decline in North American bumble bees. PNAS 108:662–667.

Cane, J. H., R. L. Minckley, and L. J. Kervin. 2000. Sampling bees (Hymenoptera: Apiformes) for pollinator community studies: pitfalls of pan-trapping. Journal of the Kansas Entomological Society 73:225–231.

Cardoso, M. C., and R. B. Gonçalves. 2018. Reduction by half: the impact on bees of 34 years of urbanization. Urban Ecosystems 21:943–949.

Droege, S., V. J. Tepedino, G. Lebuhn, W. Link, R. L. Minckley, Q. Chen, and C. Conrad. 2010. Spatial patterns of bee captures in North American bowl trapping surveys. Insect Conservation and Diversity 3:15–23.

Ebeling, A., A. M. Klein, J. Schumacher, W. W. Weisser, and T. Tscharntke. 2008. How does plant richness affect pollinator richness and temporal stability of flower visits? Oikos 117:1808–1815.

Eltz, T., and C. A. Brühl. 2002. Determinants of stingless bee nest density in lowland dipterocarp forests of Sabah, Malaysia. Oecologia 131:27–34.

Feinsinger, P. 1994. Habitat fragmentation, native insect pollinators, and feral honey bees in Argentine "Chaco Serano." Ecological Applications 4:378–392.

Fenoglio, M. S., M. R. Rossetti, and M. Videla. 2020. Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. Global Ecology and Biogeography 29:1412–1429.

Gathmann, A., and T. Tscharntke. 2002. Foraging ranges of solitary bees. Journal of Animal Ecology 71:757–764.

Gerner, E. E., and R. D. Sargent. 2021. Local plant richness predicts bee abundance and diversity in a study of urban residential yards. Page Basic and Applied Ecology. Elsevier GmbH.

Gibbs, J. 2010. Revision of the metallic species of Lasioglossum (Dialictus) in Canada (Hymenoptera, Halictidae, Halictini). Zootaxa 2591: 1–382 (2010).

Gibbs, J., L. Packer, S. Dumesh, and B. N. Danforth. 2013. Revision and reclassification of Lasioglossum (Evylaeus), L. (Hemihalictus) and L. (Sphecodogastra) in eastern North America (Hymenoptera: Apoidea: Halictidae). Page Zootaxa.

Greenleaf, S. S., N. M. Williams, R. Winfree, and C. Kremen. 2007. Bee foraging ranges and their relationship to body size. Oecologia 153:589–596.

Grundel, R., K. J. Frohnapple, R. P. Jean, and N. B. Pavlovic. 2011. Effectiveness of bowl trapping and netting for inventory of a bee community. Environmental Entomology 40:374–380.

Grundel, R., R. P. Jean, K. J. Frohnapple, G. A. Glowacki, P. E. Scott, and N. B. Pavlovic. 2010. Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. Ecological Applications 20:1678–1692.

Hall, D. M., G. R. Camilo, R. K. Tonietto, J. Ollerton, K. Ahrné, M. Arduser, J. S. Ascher, K. C.

R. Baldock, R. Fowler, G. Frankie, D. Goulson, B. Gunnarsson, M. E. Hanley, J. I. Jackson, G. Langellotto, D. Lowenstein, E. S. Minor, S. M. Philpott, S. G. Potts, M. H. Sirohi, E. M. Spevak, G. N. Stone, and C. G. Threlfall. 2017. The city as a refuge for insect pollinators. Conservation Biology 31:24–29.

Hamblin, A. L., E. Youngsteadt, and S. D. Frank. 2018. Wild bee abundance declines with urban warming, regardless of floral density:419–428.

Hanley, M. E., A. J. Awbi, and M. Franco. 2014. Going native? Flower use by bumblebees in English urban gardens. Annals of Botany 113:799–806.

Harder, L. D. 1986. Effects of nectar concentration and flower depth on flower handling efficiency of bumble bees. Oecologia 69:309–315.

Harder, L. D. 1988. The bumble bees of eastern canada. The Canadian Entomologist 120:965–987.

Hernandez, J. L., G. W. Frankie, and R. W. Thorp. 2016. Ecology of Urban Bees: A Review of Current Knowledge and Directions for Future Study. Cities and the Environment 2:1–15.

Hobbs, G. A. 1962. Further Studies on the Food-Gathering Behaviour of Bumble Bees (Hymenoptera: Apidae). The Canadian Entomologist 94:538–541.

Hodges, C. M. 1981. Optimal foraging in bumblebees: Hunting by expectation. Animal Behaviour 29:1166–1171.

Høye, T. T., S. Loboda, A. M. Koltz, M. A. K. Gillespie, J. J. Bowden, and N. M. Schmidt. 2021. Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. Proceedings of the National Academy of Sciences of the United States of America 118.

Hülsmann, M., H. von Wehrden, A. M. Klein, and S. D. Leonhardt. 2015. Plant diversity and

composition compensate for negative effects of urbanization on foraging bumble bees. Apidologie 46:760–770.

Kaluza, B. F., H. Wallace, T. A. Heard, A. M. Klein, and S. D. Leonhardt. 2016. Urban gardens promote bee foraging over natural habitats and plantations. Ecology and Evolution 6:1304–1316.

Kim, W., T. Gilet, and J. W. M. Bush. 2011. Optimal concentrations in nectar feeding. PNAS 108:16618–16621.

Kirk, W. D. J. 1984. Ecologically selective coloured traps. Ecological Entomology 9:35–41.

Klinkhamer, P. G. L., and C. A. M. van der Veen-van Wijk. 1999. Genetic variation in floral traits of Echium vulgare. Oikos 85:515.

Klumpers, S. G. T., M. Stang, and P. G. L. Klinkhamer. 2019. Foraging efficiency and size matching in a plant–pollinator community: the importance of sugar content and tongue length. Ecology Letters 22:469–479.

Knapp, S., M. F. J. Aronson, E. Carpenter, A. Herrera-Montes, K. Jung, D. J. Kotze, F. A. La Sorte, C. A. Lepczyk, I. Macgregor-Fors, J. S. Macivor, M. Moretti, C. H. Nilon, M. R. Piana, C. C. Rega-Brodsky, A. Salisbury, C. G. Threlfall, C. Trisos, N. S. G. Williams, and A. K. Hahs. 2021. A Research Agenda for Urban Biodiversity in the Global Extinction Crisis. BioScience 71:268–279.

Leong, J. M., and R. W. Thorp. 1999. Colour-coded sampling: the pan trap colour preferences of oligolectic and nonoligolectic bees associated with a vernal pool plant. Ecological Entomology 24:329–335.

Lowenstein, D. M., K. C. Matteson, and E. S. Minor. 2019. Evaluating the dependence of urban pollinators on ornamental, non-native, and 'weedy' floral resources. Urban Ecosystems

22:293–302.

Lowenstein, D. M., K. C. Matteson, I. Xiao, A. M. Silva, and E. S. Minor. 2014. Humans, bees, and pollination services in the city: The case of Chicago, IL (USA). Biodiversity and Conservation 23:2857–2874.

Martins, K. T., A. Gonzalez, and M. J. Lechowicz. 2017. Patterns of pollinator turnover and increasing diversity associated with urban habitats. Urban Ecosystems 20:1359–1371.

Mason, N. W. H., K. MacGillivray, J. B. Steel, and J. B. Wilson. 2003. An index of functional diversity. Journal of Vegetation Science 14:571–578.

Matteson, K. C., and G. A. Langellotto. 2010. Determinates of inner city butterfly and bee species richness. Urban Ecosystems 13:333–347.

Matteson, K. C., and G. A. Langellotto. 2011. Small scale additions of native plants fail to increase beneficial insect richness in urban gardens. Insect Conservation and Diversity 4:89–98.

Metson, G. S., and E. M. Bennett. 2015. Phosphorus cycling in Montreal's food and urban agriculture systems. PLoS ONE 10:1–18.

Murray, T. E., Ú. Fitzpatrick, A. Byrne, R. Fealy, M. J. F. Brown, and R. J. Paxton. 2012. Local-scale factors structure wild bee communities in protected areas. Journal of Applied Ecology 49:998–1008.

Nielsen, A., I. Steffan-Dewenter, C. Westphal, O. Messinger, S. G. Potts, S. P. M. Roberts, J. Settele, H. Szentgyörgyi, B. E. Vaissière, M. Vaitis, M. Woyciechowski, I. Bazos, J. C. Biesmeijer, R. Bommarco, W. E. Kunin, T. Tscheulin, E. Lamborn, and T. Petanidou. 2011. Assessing bee species richness in two Mediterranean communities: Importance of habitat type and sampling techniques. Ecological Research 26:969–983.

Normandin, É., N. J. Vereecken, C. M. Buddle, and V. Fournier. 2017. Taxonomic and

    functional trait diversity of wild bees in different urban settings. PeerJ 5:e3051.

Ollerton, J., R. Alarcon, N. M. Waser, M. V. Price, S. Watts, L. Cranmer, A. Hingston, C. I.

    Peter, and J. Rotenberry. 2009. A global test of the pollination syndrome hypothesis. Annals

    of Botany 103:1471–1480.

Oram, R. J. 2018. Revision of the Genus Hylaeus Fabricius (Hymenoptera : Colletidae) in

    Canada A Thesis Submitted to the Faculty of Graduate Studies and Research In Partial

    Fulfillment of the Requirements For the Degree of Master of Science in Biology University

    of Regin:175.

Pacini, E., M. Nepi, and J. L. Vesprini. 2003. Nectar biodiversity: a short review. Plant

    Systematics and Evolution 238:7–21.

Pardee, G. L., and S. M. Philpott. 2014. Native plants are the bee's knees: local and landscape

    predictors of bee richness and abundance in backyard gardens. Urban Ecosystems 17:641–

    659.

Parent, S., M. J. Simard, and M. Leboeuf. 2011. Fleurs des champs du Québec et des Maritimes.

    Éditions M. Quintin.

Peel, M. C., B. L. Finlayson, and T. A. Mcmahon. 2007. Updated world map of the Köppen-

    Geiger climate classification. Hydrology and Earth System Sciences 11:1633–1644.

Pennekamp, F., M. Pontarp, A. Tabi, F. Altermatt, R. Alther, Y. Choffat, E. A. Fronhofer, P.

    Ganesanandamoorthy, A. Garnier, J. I. Griffiths, S. Greene, K. Horgan, T. M. Massie, E.

    Mächler, G. M. Palamara, M. Seymour, and O. L. Petchey. 2018. Biodiversity increases and

    decreases ecosystem stability. Nature 563:109–112.

Petanidoua, T., V. Goethals, and E. Smets. 1999. The effect of nutrient and water availability on

nectar secretion and nectary structure of the dominant Labiatae species of phrygana 244:233–244.

Pleasants, J. M. 1983. Nectar Production Patterns in Ipomopsis Aggregata (Polemoniaceae). American Journal of Botany 70:1468–1475.

Popic, T. J., Y. C. Davila, and G. M. Wardle. 2013. Evaluation of Common Methods for Sampling Invertebrate Pollinator Assemblages: Net Sampling Out-Perform Pan Traps. PLoS ONE 8:1–9.

Potts, S. G., J. C. Biesmeijer, C. Kremen, P. Neumann, O. Schweiger, and W. E. Kunin. 2010. Global pollinator declines: Trends, impacts and drivers. Trends in Ecology and Evolution 25:345–353.

Potts, S. G., A. Dafni, and G. Ne'Eman. 2001. Pollination of a core flowering shrub species in Mediterranean phrygana: Variation in pollinator diversity, abundance and effectiveness in response to fire. Oikos 92:71–80.

Potts, S. G., B. Vulliamy, A. Dafni, G. Ne'eman, and P. G. Willmer. 2003. Linking bees and flowers: how do floral communities structure pollinator communities? Ecology 84:2628–2642.

Potts, S. G., B. Vulliamy, S. Roberts, C. O'Toole, A. Dafni, G. Ne'eman, and P. Willmer. 2005. Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. Ecological Entomology 30:78–85.

Potts, S. G., B. Vulliamy, S. Roberts, C. O. Toole, A. Dafni, G. Ne, and P. G. Willmer. 2004. Nectar resource diversity organises flower-visitor community structure. Entomologia Experimentalis et Applicata 113:103–107.

Pyke, G. H. 1979. Optimal foraging in bumblebees: Rule of movement between flowers within

inflorescences. Animal Behaviour 27:1167–1181.

Quistberg, R. D., P. Bichier, and S. M. Philpott. 2016. Landscape and local correlates of bee
abundance and species richness in urban gardens. Environmental Entomology 45:1–10.

Richardson, L., and P. Williams. 2013. Bumblebees of the eastern United States.

Roubik, D. W., D. Yanega, M. A. S, S. L. Buchmann, and D. W. Inouye. 1995. On optimal
nectar foraging by some tropical bees (Hymenoptera: Apidae). Apidologie 26:197–211.

Rowe, L., D. Gibson, C. A. Bahlai, J. Gibbs, D. A. Landis, and R. Isaacs. 2020. Flower traits
associated with the visitation patterns of bees. Oecologia 193:511–522.

Salisbury, A., S. Al-Beidh, J. Armitage, S. Bird, H. Bostock, A. Platoni, M. Tatchell, K.
Thompson, and J. Perry. 2020. Enhancing gardens as habitats for soil-surface-active
invertebrates: should we plant native or exotic species? Biodiversity and Conservation
29:129–151.

Schoener, T. W. 1971. Theory of Feeding Strategies. Annual Review of Ecology and
Systematics 2:369–404.

Sheffield, C. S., C. Ratti, L. Packer, and T. Griswold. 2011. Leafcutter and Mason Bees of the
Genus Megachile Latreille (Hymenoptera: Megachilidae) in Canada and Alaska. Canadian
Journal of Arthropod Identification 18:1–107.

Sirohi, M. H., J. Jackson, M. Edwards, and J. Ollerton. 2015. Diversity and abundance of solitary
and primitively eusocial bees in an urban centre : a case study from Northampton (England
). Journal of Insect Conservation:487–500.

Spotswood, E. N., E. E. Beller, R. Grossinger, J. L. Grenier, N. E. Heller, and M. F. J. Aronson.
2021. The Biological Deserts Fallacy: Cities in Their Landscapes Contribute More than We
Think to Regional Biodiversity. BioScience 71:148–160.

Stang, M., P. G. L. P. G. L. Klinkhamer, and E. V. D. E. V. Der Meijden. 2006. Size constraints and flower abundance determine the number of interactions in a plant-flower visitor web. Oikos 112:111–121.

Stang, M., P. G. L. Klinkhamer, N. M. Waser, I. Stang, and E. van der Meijden. 2009. Size-specific interaction patterns and size matching in a plant–pollinator interaction web. Annals of Botany 103:1459–1469.

Theodorou, P., K. Albig, R. Radzevičiūtė, J. Settele, O. Schweiger, T. E. Murray, and R. J. Paxton. 2017. The structure of flower visitor networks in relation to pollination across an agricultural to urban gradient. Functional Ecology 31:838–847.

Theodorou, P., S. C. Herbst, B. Kahnt, P. Landaverde-González, L. M. Baltz, J. Osterman, and R. J. Paxton. 2020. Urban fragmentation leads to lower floral diversity, with knock-on impacts on bee biodiversity. Scientific Reports 10:1–11.

Thompson, J. N. 1989. Concepts of coevolution. Trends in Ecology and Evolution 4:179–183.

Tilman, D. 1996. Biodiversity: population versus ecosystem stability. Ecology 77:350–363.

Tommasi, D., A. Miro, H. A. Higo, and M. L. Winston. 2004. Bee diversity and abundance in an urban setting. Canadian Entomologist 136:851–869.

Tonietto, R., J. Fant, J. Ascher, K. Ellis, and D. Larkin. 2011. A comparison of bee communities of Chicago green roofs, parks and prairies. Landscape and Urban Planning 103:102–108.

Torné-Noguera, A., A. Rodrigo, X. Arnan, S. Osorio, H. Barril-graells, L. Correia da Rocha-Filho, and J. Bosch. 2014. Determinants of spatial distribution in a bee community: nesting resources, flower resources, and body size. PLOS ONE 9:1–10.

Wenzel, A., I. Grass, V. V. Belavadi, and T. Tscharntke. 2020. How urbanization is driving pollinator diversity and pollination – A systematic review. Biological Conservation

241:108321.

Westphal, C., R. Bommarco, G. Carré, E. Lamborn, N. Morison, T. Petanidou, S. G. Potts, S. P.
M. Roberts, H. Szentgyörgyi, T. Tscheulin, B. E. Vaissière, M. Woyciechowski, J. C.
Biesmeuer, W. E. Kunin, J. Settele, and I. Steffan-Dewenter. 2008. Measuring bee diversity
in different European habitats and biogeographical regions. Ecological Monographs
78:653–671.

Willmer, P. G. 1988. The role of insect water balance in pollination ecology: Xylocopa and
Calotropis. Oecologia 76:430–438.

Wray, J. C., and E. Elle. 2015. Flowering phenology and nesting resources influence pollinator
community composition in a fragmented ecosystem. Landscape Ecology 30:261–272.

Wright, D. H. 1983. Species-energy theory: an extension of species-area theory. Oikos 3:496–
506.

Zurbuchen, A., L. Landert, J. Klaiber, A. Müller, S. Hein, and S. Dorn. 2010. Maximum foraging
ranges in solitary bees: only few individuals have the capability to cover long foraging
distances. Biological Conservation 143:669–676.

Figures

Figure 1. Map of all sites sampled on the Island of Montreal. Blue points represent cemeteries, green sites represent natural parks, and purple points represent urban community gardens.
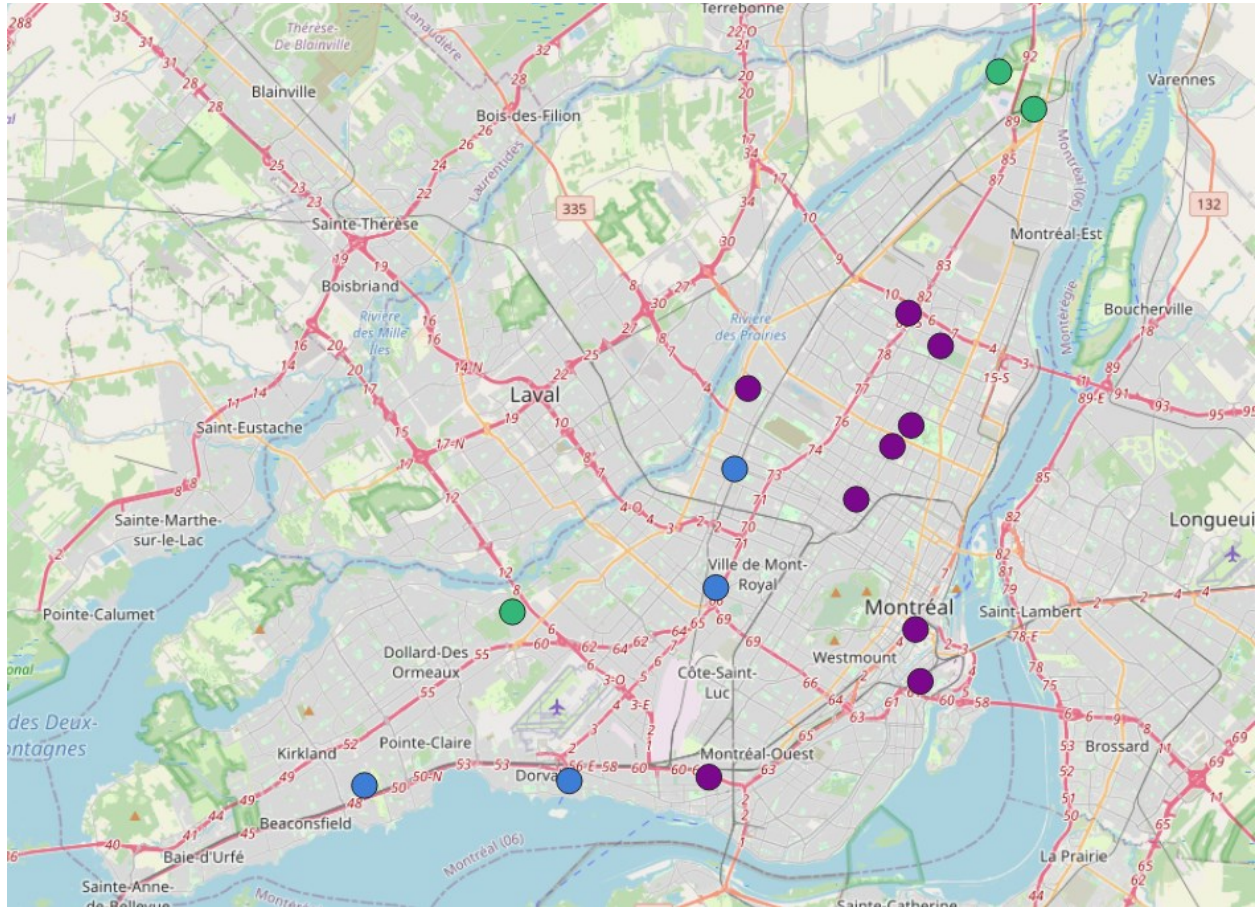
Figure 2. (a) Generalized linear mixed model of relationship between wild bee species richness of early July 2020 sampling and late July 2020 sampling and floral density of early July 2020 sampling and late July 2020 sampling. Model includes site as a random effect. (b) Residuals of bee richness and floral density plotted against CWV of corolla length for early July 2020 sampling and late July 2020 sampling. For both a and b, each point on the graph represents a plot. Black points and the solid black line represent the first sampling round, and white points and the dashed line represent the second sampling round.
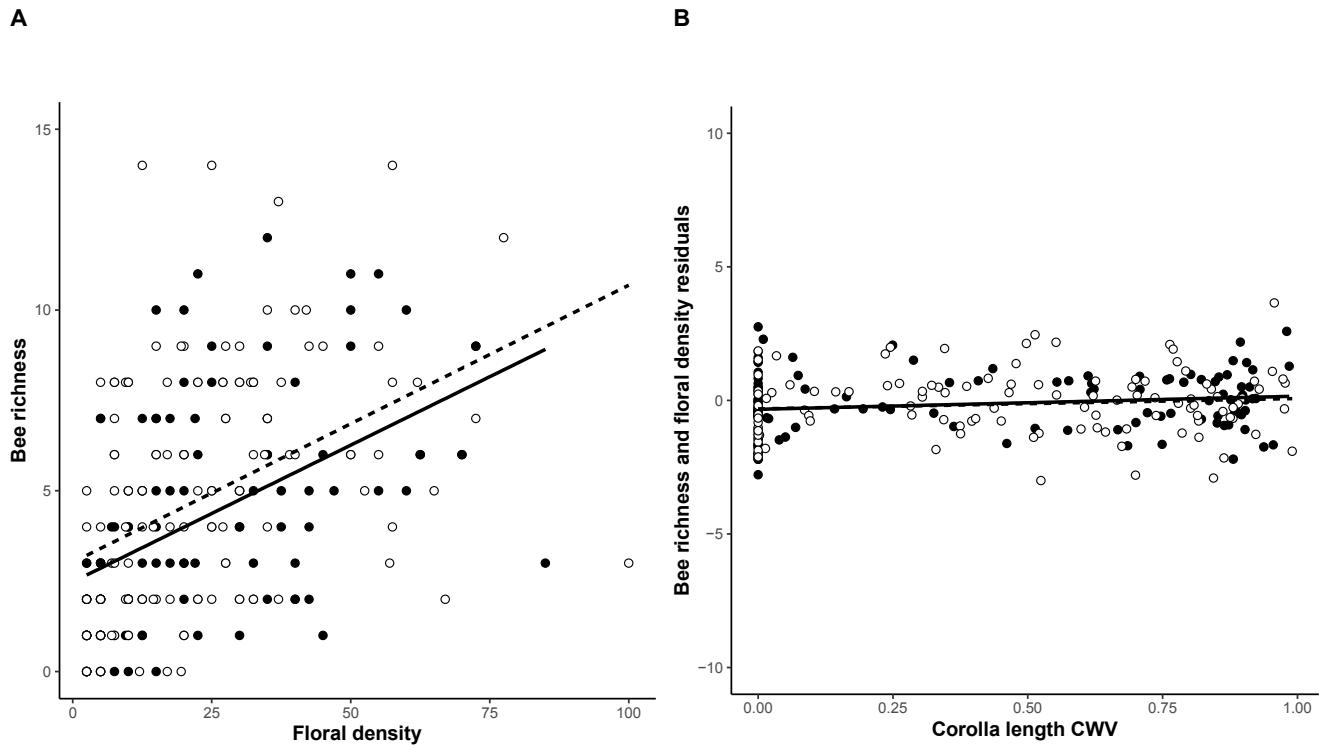
Tables

Table 1. Nectar concentration hypothesis table. All significant terms are shown in bold. Site is included in each model as a random effect.

	Model	AICc
Trait diversity hypothesis + floral density	Wild bee species richness ~ **floral density** + nectar concentration CWV + sampling round	1075.15
Optimal trait hypothesis + floral density	Wild bee species richness ~ **floral density** + nectar concentration CWM + **sampling round**	1075.19
Optimal trait hypothesis + floral richness	Wild bee species richness ~ **floral richness** + nectar concentration CWM + sampling round	1082.93
Trait diversity hypothesis + floral richness	Wild bee species richness ~ **floral richness** + nectar concentration CWV + sampling round	1084.30
H1$_A$. Optimal trait hypothesis	Wild bee species richness ~ nectar concentration CWM + **sampling round**	1090.01
H1. Trait diversity hypothesis	Wild bee species richness ~ nectar concentration CWV + sampling round	1098.25
Trait diversity + optimal trait	Wild bee species richness ~ nectar concentration CWV + nectar concentration CWM + **sampling round**	1097.98
Floral density	Wild bee species richness ~ **floral density** + sampling round	1119.52
Floral richness	Wild bee species richness ~ **floral richness** + sampling round	1128.14

Table 2. Corolla length hypothesis table. All significant terms are shown in bold. Site is included in each model as a random effect.

	Model	AICc
Trait diversity hypothesis + floral density	Wild bee species richness ~ **floral density** + **corolla length CWV** + sampling round	1117.36
Optimal trait hypothesis + floral density	Wild bee species richness ~ **floral density** + corolla length CWM + **sampling round**	1118.30
Floral density	Wild bee species richness ~ **floral density** + sampling round	1123.98
Optimal trait hypothesis + floral richness	Wild bee species richness ~ **floral richness** + **corolla length CWM** + sampling round	1124.32
Trait diversity + optimal trait	Wild bee species richness ~ **corolla length CWV** + **corolla length CWM** + sampling round	1126.82
Trait diversity hypothesis + floral richness	Wild bee species richness ~ **floral richness** + corolla length CWV + sampling round	1129.02
H2. Trait diversity hypothesis	Wild bee species richness ~ **corolla length CWV** + sampling round	1131.49
H2$_A$. Optimal trait hypothesis	Wild bee species richness ~ **corolla length CWM** + **sampling round**	1132.52
Floral richness	Wild bee species richness ~ **floral richness** + sampling round	1135.12

Table 3. Results from generalized linear mixed model using negative binomial family to assess influence of plot-level corolla length community-weighted variance and floral density (in percent cover) on wild bee species richness. Study site was set as a random effect, with a standard deviation of 0.402. Bold P-values are significant.

	Estimate	Standard Error	z-value	95% CI	P-value
Intercept	1.009	0.130	7.774	(0.269, 0.627)	**< 0.001**
Corolla length CWV	0.227	0.110	2.070	(0.012, 0.442)	**< 0.05**
Floral density	0.009	0.002	4.134	(0.748, 1.275)	**< 0.001**
Sampling round	0.127	0.069	1.831	(-0.009, 0.263)	0.07

Supplementary Material

Figure S1. Pearson correlation matrix showing correlations between floral community metrics. Color opaqueness is proportional to the correlation coefficients, with red being a positive correlation and blue being a negative correlation.
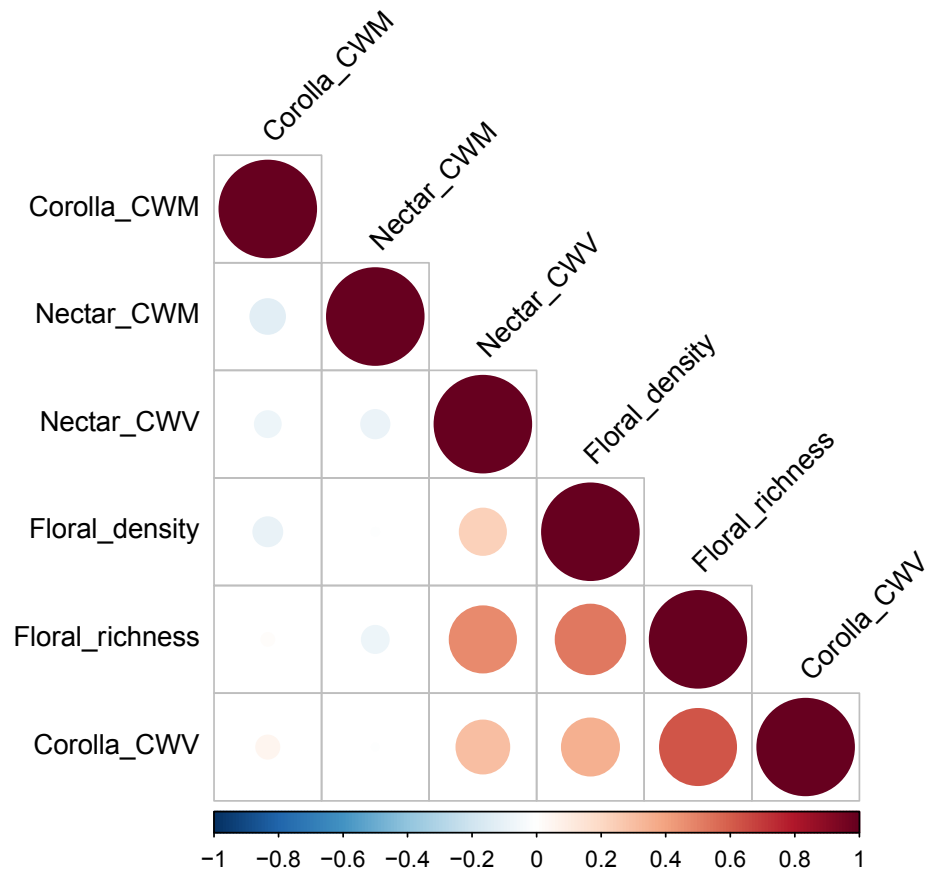
Figure S2. Relationship between bee richness and bee abundance of both sampling rounds, early and late July 2020. Bee abundance is a significant factor.
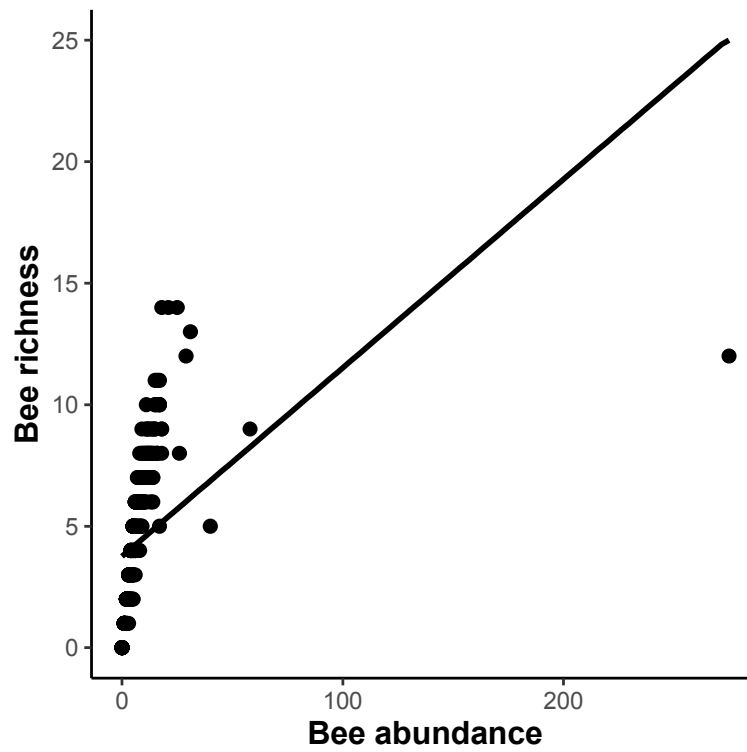
Table S1. Results from generalized linear mixed model using negative binomial family to assess influence of plot-level flower species richness and floral density on wild bee species richness. Study site was set as a random effect. Bold P-values are significant.

	Estimate	Standard Error	z-value	P-value
Intercept	0.718	0.160	4.504	**< 0.001**
Floral richness	0.169	0.050	3.391	**< 0.001**
Floral density	0.017	0.004	4.416	**< 0.001**
Sampling round	0.112	0.071	1.571	0.116
Floral richness:floral density	-0.003	0.001	-2.916	**< 0.01**

Table S2. Each site sampled, including latitude and longitude, as well as site type. Min bee richness and max bee richness are the minimum and maximum wild bee species richness captured at a plot during either sampling round in early July 2020 or late July 2020. Mean bee richness is the average bee richness captured from all plots during both sampling rounds in early July 2020 and late July 2020.

Name	Area (m^2)	Latitude	Longitude	Type	Min bee richness	Max bee richness	Mean bee richness
Shaare Zion	16483	45.550315	-73.655244	Cemetery	0	8	2.81
Urgel Bougie	62100	45.509662	-73.664437	Cemetery	0	6	2.50
Lakeview	147000	45.441835	-73.836624	Cemetery	0	5	1.44
La Presentation	13005	45.443412	-73.736278	Cemetery	0	5	1.25
Etienne-Desmarteaux	5149	45.558046	-73.577985	Garden	5	13	7.75
Prieur	4221	45.577859	-73.648734	Garden	0	10	4.44
Pere-Marquette	3180	45.539918	-73.595684	Garden	3	14	7.69
Roseraie	2117	45.592415	-73.554373	Garden	1	14	4.44
Rosemont-Eglantier	7514	45.565208	-73.568768	Garden	2	9	5.63
Réal Gareau	960	45.444694	-73.667889	Garden	2	11	7.44

Bois-de-Liesse	1716	45.501337	-73.76413	Park	4	14	6.75
Pointe-aux-Prairies Marais	9211	45.686168	-73.525811	Park	0	7	2.00
52e Ave	10,962	45.673354	-73.508691	Park	0	6	2.38
Georges Vanier	957	45.495318	-73.566644	Garden	2	8	4.44
Pointe-vert	836	45.477523	-73.56429	Garden	0	11	4.94
Laurendeau	2320	45.603646	-73.570105	Garden	0	8	3.69

Table S3. Nectar concentration hypothesis table. Site is included in each model as a random effect.

	Model	AICc
Trait diversity hypothesis * floral density	Wild bee species richness ~ floral density * nectar concentration CWV * sampling round	1085.48
Optimal trait hypothesis * floral density	Wild bee species richness ~ floral density * nectar concentration CWM * sampling round	1087.62
Optimal trait hypothesis * floral richness	Wild bee species richness ~ floral richness * nectar concentration CWM * sampling round	1088.95
Trait diversity hypothesis * floral richness	Wild bee species richness ~ floral richness * nectar concentration CWV * sampling round	1094.24
$H1_A$. Optimal trait hypothesis	Wild bee species richness ~ nectar concentration CWM * sampling round	1099.18
H1. Trait diversity hypothesis	Wild bee species richness ~ nectar concentration CWV * sampling round	1100.04
Trait diversity * optimal trait	Wild bee species richness ~ nectar concentration CWV * nectar concentration CWM * sampling round	1101.18
Floral density	Wild bee species richness ~ floral density * sampling round	1121.62
Floral richness	Wild bee species richness ~ floral richness * sampling round	1135.37

Table S4. Corolla length hypothesis table. Site is included in each model as a random effect.

	Model	AICc
Trait diversity hypothesis * floral density	Wild bee species richness ~ floral density * corolla length CWV * sampling round	1124.22
Floral density	Wild bee species richness ~ floral density * sampling round	1126.05
Optimal trait hypothesis * floral density	Wild bee species richness ~ floral density * corolla length CWM * sampling round	1127.48
Trait diversity hypothesis * floral richness	Wild bee species richness ~ floral richness * corolla length CWV * sampling round	1134.34
Optimal trait hypothesis * floral richness	Wild bee species richness ~ floral richness * corolla length CWM * sampling round	1135.14
Floral richness	Wild bee species richness ~ floral richness * sampling round	1135.37
Trait diversity * optimal trait	Wild bee species richness ~ corolla length CWV * corolla length CWM * sampling round	1136.41
H2. Trait diversity hypothesis	Wild bee species richness ~ corolla length CWV * sampling round	1141.32
H2$_A$. Optimal trait hypothesis	Wild bee species richness ~ corolla length CWM * sampling round	1141.52

Table S5. Nectar concentration hypothesis table. All significant terms are shown in bold. Site is included in each model as a random effect. Model comparisons exclude sampling rounds.

	Model	AICc
Trait diversity hypothesis + floral density	Wild bee species richness ~ **floral density** + nectar concentration CWV	1076.78
Optimal trait hypothesis + floral density	Wild bee species richness ~ **floral density** + nectar concentration CWM	1076.87
Optimal trait hypothesis + floral richness	Wild bee species richness ~ **floral richness** + nectar concentration CWM	1082.26
Trait diversity hypothesis + floral richness	Wild bee species richness ~ **floral richness** + nectar concentration CWV	1083.26
H1$_A$. Optimal trait hypothesis	Wild bee species richness ~ nectar concentration CWM	1091.32
H1. Trait diversity hypothesis	Wild bee species richness ~ nectar concentration CWV	1091.66
Trait diversity + optimal trait	Wild bee species richness ~ nectar concentration CWV + nectar concentration CWM	1092.49
Floral density	Wild bee species richness ~ **floral density**	1121.17
Floral richness	Wild bee species richness ~ **floral richness**	1127.16

Table S6. Corolla length hypothesis table. All significant terms are shown in bold. Site is included in each model as a random effect. Model comparisons exclude sampling rounds.

	Model	AICc
Trait diversity hypothesis + floral density	Wild bee species richness ~ **floral density** + **corolla length CWV**	1118.58
Optimal trait hypothesis + floral density	Wild bee species richness ~ **floral density** + corolla length CWM	1120.51
Optimal trait hypothesis + floral richness	Wild bee species richness ~ **floral richness** + **corolla length CWM**	1123.74
Floral density	Wild bee species richness ~ **floral density**	1127.08
Trait diversity hypothesis + floral richness	Wild bee species richness ~ **floral richness** + corolla length CWV	1128.25
Trait diversity + optimal trait	Wild bee species richness ~ **corolla length CWV** + **corolla length CWM**	1128.44
H2. Trait diversity hypothesis	Wild bee species richness ~ **corolla length CWV**	1132.37
H2$_A$. Optimal trait hypothesis	Wild bee species richness ~ **corolla length CWM**	1134.54
Floral richness	Wild bee species richness ~ **floral richness**	1134.64

Table S7. Table including all flower species sampled during the study. Sources column indicates literature sources nectar sugar concentration readings were taken from. If no literature was present, or if nectar readings were taken during the study, it is indicated in the Sources column.

Species	Sources
Achillea millefolium	Day, 2020
Ageratum houstonianum	No reading possible, no literature found
Alcea rosea	Nectar readings taken
Alliaria petiolata	Cruden et al., 1996
Allium ampeloprasum	Hagler et al., 1990; Kumar and Gupta, 1993; Farkas et al. 2012; Baude et al., 2016; Pamminger et al., 2019
Allium cepa	Hagler et al., 1990; Kumar and Gupta, 1993; Baude et al., 2016; Pamminger et al., 2019
Anemone hupehensis	Bayton and Maughan, 2017
Anethum graveolens	No reading possible, no literature found
Antirrhinum majus	Nectar readings taken
Aquilegia vulgaris	Nectar readings taken
Arabis alpina	Strzalkowska-Abramek et al., 2016
Arctium lappa	Nectar readings taken
Asclepias tuberosa	Arnold and Michaels, 2017
Astrantia major	No reading possible, no literature found
Begonia cucullata	No reading possible, no literature found
Borage officinalis	Nectar readings taken
Brassica rapa	Baude et al., 2016; Pamminger et al., 2019
Calendula arvensis	Nectar readings taken
Calendula officinalis	Nectar readings taken
Calibrachoa parviflora	No reading possible, no literature found
Campanula latifolia	Denisow et al., 2018; Strzalkowska-Abramek et al., 2018
Campanula persicifolia	Strzalkowska-Abramek et al., 2018
Campanula rapunculoides	No reading possible, no literature found
Capsicum annuum	Rabinowitch et al., 1993; Pamminger et al., 2019
Centaurea cyanus	Nectar readings taken
Centaurea jacea	Nectar readings taken
Centaurea montana	No reading possible, no literature found
Chamaesyce hypericifolia	No reading possible, no literature found
Chelidonium majus	No reading possible, no literature found
Cichorium intybus	Nectar readings taken
Convolvulus arvensis	Nectar readings taken

Coreopsis grandiflora	Day, 2020
Coriandrum sativum	Sivaram, 2001
Cosmos bipinnatus	Nectar readings taken
Cosmos sulphureus	Biroki, 2021
Crocosmia aurea	Nectar readings taken
Cucumis sativus	Nectar readings taken
Cucurbita pepo	Nectar readings taken
Dasiphora fruticosa	No reading possible, no literature found
Daucus carota	Abrol, 2006
Delphinium elatum	Waser, 1978; Pleasants, 1981
Dianthus armeria	Erhardt, 1998; Erhardt, 1990; Erhardt and Jäggi, 1995
Dianthus plumaris	Nectar readings taken
Dianthus plumarius	Nectar readings taken
Digitalis purpurea	Percival and Morgan, 1965; Baude et al., 2016
Echinacea purpurea	Nectar readings taken
Erigeron annuus	Hocking, 1968
Erysimum cheiri	Nectar readings taken
Erysimum odoratum	Tew et al., 2021
Filipendula rubra	No reading possible, no literature found
Gaillardia pulchella	No reading possible, no literature found
Galinsoga parviflora	No reading possible, no literature found
Galinsoga quadriradiata	No reading possible, no literature found
Geranium sylvaticum	Konarska and Masierowska, 2020; Tew et al., 2021
Gladiolus communis	Nectar readings taken
Glebionis segetum	No reading possible, no literature found
Gomphrena globosa	No reading possible, no literature found
Gypsophila elegans	No reading possible, no literature found
Heliopsis helianthoides	Nectar readings taken
Hemerocallis fulva	Nectar readings taken
Hemerocallis lilioasphodelus	Nectar readings taken
Hesparis matronalis	Nectar readings taken
Hosta plantaginea	Nectar readings taken
Hyacinthoides hispanica	Nectar readings taken
Hydrangea arborescens	Wong Sato and Kato, 2019
Hypericum perforatum	Nectar readings taken
Hypericum scouleri	Tew et al., 2021

Hypochaeris radicata	No reading possible, no literature found
Impatiens hawkeri	Nectar readings taken
Impatiens walleriana	Nectar readings taken
Lactuca sativa	No reading possible, no literature found
Lamium maculatum	Nectar readings taken
Lantana camara	Nectar readings taken
Lavandula angustifolia	Nectar readings taken
Leucanthemum vulgare	Nectar readings taken
Liatris aspera	Nectar readings taken
Liatris spicata	Arnold and Michaels, 2017
Lilium bulbiferum	Nectar readings taken
Lotus corniculatus	Nectar readings taken
Lunaria annua	No reading possible, no literature found
Lycium barbarum	Nectar readings taken
Lythrum salicaria	Nectar readings taken
Malva alcea	No reading possible, no literature found
Matricaria chamomilla	No reading possible, no literature found
Medicago sativa	Nectar readings taken
Melilotus albus	Pamminger et al., 2019
Melilotus officinalis	Montgomery, 1958
Mentha spicata	Duffy and Stout, 2008
Monarda didyma	Whitten, 1981
Nepeta racemosa	Nectar readings taken
Ocimum basilicum	Nectar readings taken
Ocimum minimum	Nectar readings taken
Oenothera biennis	Nectar readings taken
Oenothera fruticosa	Chalcoff et al., 2006; Veits et al. 2019
Origanum vulgare	Nectar readings taken
Oxalis stricta	Luo et al., 2015
Papaver rhoeas	No reading possible, no literature found
Papaver somniferum	Nectar readings taken
Pastinaca sativa	No reading possible, no literature found
Pelargonium x hortorum	Nectar readings taken
Pelargonium zonale	Nectar readings taken
Perilla frutescens	No reading possible, no literature found
Petunia axillaris	Nectar readings taken

Petunia violacea	Nectar readings taken
Petunia x hybrida	Nectar readings taken
Phaseolus coccineus	Nectar readings taken
Phaseolus vulgaris	Nectar readings taken
Phlox drummondii	Suni et al., 2020
Phlox maculata	Nectar readings taken
Phlox paniculata	Nectar readings taken
Potentilla recta	McIver and Erickson, 2012
Prunella vulgaris	Baude et al., 2016
Rorippa sylvestris	Jachula et al., 2021
Rosa chinensis	White and Stiles, 1985
Rosa cinnamomea	White and Stiles, 1985
Rosa gallica	White and Stiles, 1985
Rosa moyesii	White and Stiles, 1985
Rosa rugosa	White and Stiles, 1985
Rubus idaeus	Pamminger et al., 2019
Rudbeckia fulgida	No reading possible, no literature found
Rudbeckia laciniata	No reading possible, no literature found
Salvia farinacea	Nectar readings taken
Salvia rosmarinus	Nectar readings taken
Saponaria officinalis	Nectar readings taken
Satureja montana	Nectar readings taken
Sedum acre	Nectar readings taken
Sempervivum tectorum	Nectar readings taken
Silene vulgaris	Baude et al., 2016
Sinapis arvensis	Nectar readings taken
Solanum dulcamara	Nectar readings taken
Solanum lycopersicum	Nectar readings taken
Sonchus oleraceus	Nectar readings taken
Spiraea japonica	No reading possible, no literature found
Tagetes erecta	Nectar readings taken
Tagetes patula	Nectar readings taken
Tagetus erecta	Nectar readings taken
Tanacetum parthenium	No reading possible, no literature found
Tanacetum vulgare	Nectar readings taken
Thymus vulgaris	Nectar readings taken

Trifolium dubium	No reading possible, no literature found
Trifolium repens	Southwick and Southwick, 1986; Baude et al., 2016; Pamminger et al., 2019
Tropaeolum majus	Nectar readings taken
Valeriana officinalis	Nectar readings taken
Verbena rigida	Nectar readings taken
Vicia villosa	Nectar readings taken
Viola tricolor	Nectar readings taken
Viola x wittrockiana	Nectar readings taken
Weigela florida	Nectar readings taken
Zinnea elegans	Nectar readings taken