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Response of wild bee communities to beekeeping, urbanization, and flower availability

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Abstract

Wild bees provide pollination services and are currently declining at the global scale. A potential cause for this decline is competitive interactions with domestic honey bees. Urban beekeeping, a fairly new activity, is rapidly gaining popularity. In contrast with agricultural and natural areas, the extent of competition between honey bees and wild bees in urban areas is unclear. The objectives of this study were to quantify the impact of honey bees, urbanization, and the availability of floral resources on wild bee communities. We hypothesized that honey bees exert negative impacts on wild bees, that floral resources favor wild bee communities and mitigate the negative impacts of competition with honey bees, and that the influence of heat islands, used as a proxy for urbanization, varies between wild bees with their functional traits (nesting behavior). We tested these hypotheses with a data set of 19 077 wild bee specimens collected using colored pan-traps at 25 urban sites in 2012 and 2013. We investigated community and population patterns after accounting for imperfect detection probability. We found no evidence of competition between wild and domesticated bees. Our analyses indicate mixed effects of urban heat islands across species and positive effects of floral resources. We conclude that cities can allow the coexistence of urban beekeeping and wild bees under moderate hive densities. However, it will remain crucial to further investigate the competitive interactions between wild and honey bees to determine the threshold of hive densities beyond which competition could occur.

Key words:

Pollinators, competition, *Apis mellifera*, hierarchical models, urbanization, solitary bees, flower diversity.

Introduction

Wild bees (Hymenoptera, Apoidea) and honey bees (*Apis (Apis) mellifera* L. 1758) are important pollinators of both natural and cultivated angiosperm plants (Garibaldi et al. 2013; Klein et al. 2007). Notably, 87 out of 115 major crops depend on bees for reproduction (Klein et al. 2007). Wild bees are superior to honey bees to improve fruit set in many crops (Garibaldi et al. 2013) and support the pollination of crops at global scales (Aizen and Harder 2009). However, pollination services are becoming threatened as wild bees are globally declining, mainly because of habitat loss, pathogens, and agrochemicals, and because honey bees are facing colony losses (Cameron et al. 2011; Potts et al. 2010a; Potts et al. 2010b).

Commercial pollinators potentially constitute an ecological threat. Negative impacts of the introduction or presence of honey bees include competition with wild pollinators for nesting and floral resources (Paini 2004; Stout and Morales 2009), introduction and proliferation of parasites and diseases (Goulson 2003; Graystock et al. 2014; Singh et al. 2010), and expansion of invasive plant species by an increase in pollination (Goulson and Derwent 2004). Domesticated pollinators have well-documented impacts on wild pollinators in agricultural and natural areas (Mallinger et al. 2017). The competition for floral resources might reduce wild bee diversity (Hudewenz and Klein 2013), abundance (Artz et al. 2011; Goulson et al. 2002), and fecundity (Paini and Roberts 2005). Over the last decade, urban beekeeping has gained a lot of popularity and is now a common practice in most major North American and European cities (Alton and Ratnieks 2016; Geslin et al. 2013). However, little is known on the coexistence of wild and domesticated bees in urban settings.

Urban expansion, characterised by high density of human population and built environment, is threatening habitats of some wild bee species, but provides many resources for others (Banaszak-Cibicka and Zmihorski 2012; Deguines et al. 2016; Geslin et al. 2013; Sirohi et al. 2015). The relative importance of floral and nesting resources for bees explains why some species can do very well in anthropic and fragmented landscapes such as urban environments (Frankie et al. 2005; Hülsmann et al. 2015; Matteson et al. 2008). Floral

resources are the most important factor structuring bee communities (Roulston and Goodell 2011). The richness and cover of floral species are often the main habitat variables affecting the richness of a pollinator community (Ebeling et al. 2008). Community gardens and flower beds in cities provide diverse native and exotic plant species, representing various sources of pollen and nectar (Ahrné et al. 2009; Matteson and Langellotto 2009). Besides floral resources, the availability and quality of nesting resources are also important factors. Nesting conditions in cities are favorable to cavity nesting bees (Lowenstein et al. 2014; Matteson et al. 2008). Those bees can use human structures like flower pots, fences, and wall mortar for nesting (Bates et al. 2011; Matteson et al. 2008; Sirohi et al. 2015). Impervious surfaces in the urban environment reduce the availability of bare ground essential to ground nesting bees (Cane 2005; Cane et al. 2006; Xie et al. 2013).

Urban expansion can also exert negative impacts. An urban heat island is an area that is significantly warmer than its surroundings (OECD 2010). With the reduction of vegetation cover (Jenerette et al. 2011) and the increase of impervious surfaces (Hart and Sailor 2009), temperatures in cities tend to be higher than in the landscape in their vicinity and create heat islands (OECD 2010). Differences up to 12°C have been observed between the center of a city and the agricultural surroundings (Angilletta et al. 2007; Voogt 2002). Because temperature is a cornerstone of virtually every biological process, heat islands could have strong impacts on ectotherms such as insects (Briere et al. 1999). Heat islands can change the phenology (Harrison et al. 2015), the development (Fründ et al. 2013), and the heat tolerance of insects (Angilletta et al. 2007), and thus their survival rate and fecundity (Sales et al. 2018). The response of bees to urbanization can be influenced by their level of specialisation (Geslin et al. 2013), their size (Geslin et al. 2016), their period of activity during the year, and their sociality (Banaszak-Cibicka and Zmihorski 2012).

Determining the impacts of competition and landscape factors in cities on bees is crucial as urbanization is expanding worldwide (United Nations 2014). The main objective of our study was to quantify the impact of urban beekeeping and urbanization on wild bee communities. We used the cover of heat islands throughout this paper as a proxy for urbanization. As heat islands result from the loss of vegetation (Jenerette et al. 2011), the proportion of cover of heat islands is highly correlated with the proportion of impervious

surfaces (Hart and Sailor 2009). The response of wild bees to urban heat islands could be a response to this increase in impervious surfaces as well as a response to the increase in temperature. We used a subset of an extensive data set (Normandin et al. 2017) to test three hypotheses. First, given that wild bees respond negatively to beekeeping in rural and natural settings (Artz et al. 2011; Goulson et al. 2002; Mallinger et al. 2017), we expected a similar pattern in urban habitats. Second, we expected the floral resources to have positive impacts on wild bees and to reduce the competition with honey bees (Ebeling et al. 2008). Finally, given that wild bee species respond to urbanization according to their functional traits, notably their nesting behavior, (Banaszak-Cibicka and Zmihorski 2012; Bates et al. 2011; Deguines et al. 2012), we expected the effects of the proportion of surface cover of urban heat islands within a 1500 m radius to vary across species. We tested these hypotheses by investigating the patterns of community composition of 166 species of wild bees, as well as the population patterns of 11 common wild bee species. This approach allowed us to investigate responses at both the population and the community levels.

Materials and Methods

Study sites and wild bee sampling

This study was conducted in the Montreal metropolitan area, Quebec, Canada (Fig. 1) (Normandin et al. 2017). Montreal is the second biggest city in Canada with a population of more than 4.1 million in the metropolitan area (Statistiques Canada 2018). A total of 25 sites were selected by Normandin et al. (2017) to sample bees in 2012 and 2013: five parks, nine cemeteries, and 11 community gardens. All 25 sites were used for the community-level analysis, whereas 15 sites were considered for the analysis of bee abundance relative to floral resources. Specifically, sites whose floral resources underwent major changes since 2013 were excluded for the survey of floral resources, as well as sites located in less urban settings and those with few floral resources. The 15 sites retained for the floral resource component of the study consisted of three parks, ten community gardens, and two cemeteries. The study area harbored 158 and 238 hives in 2012 and 2013, respectively (0.32 and 0.48 hives/km²) (Duchemin, 2018, personal communication), but this number

rapidly increased to more than 1000 hives in 2018 (2 hives/km²) (Duchemin, 2018, personal communication).

Fig. 1 Map of 25 study sites of the Montreal metropolitan area. White triangles represent the 15 sites sampled for floral resources and black triangles represent the 10 remaining sites. Insert locates the study area in northeastern North America

Bee communities were surveyed in 2012 and 2013 using pan traps (Normandin et al. 2017). We used standard pan traps consisting of 400-ml bowls painted white, yellow or blue, such that each color was represented equally across the total number of bowls in each site. Pan traps were filled with soapy water and individually placed on a 60-cm wooden stick in order to be at the canopy level of the herbaceous vegetation. We deployed pan traps in clusters of three traps. Each cluster consisted of a trap of each color (white, yellow, and blue) spaced 1-m apart. Each cluster of pan traps was placed on a single transect at the interface of lawn and natural habitat for parks and cemeteries, and on the margin of flower beds and gardens for community gardens. We deployed a cluster for each 1 000 m² of site area up to a maximum of 15 clusters (i.e., 45 traps) in any given site. Sampling was performed twice a month, for 48 hours, from May to September. Overall, sites were sampled eight times in 2012 and seven times in 2013. Because the number of pan traps at a given site varied according to the size of the site, we used the number of pan traps of a given color deployed at a given site as a measure of sampling effort. We used the number of honey bees captured per sampling effort at each site for each year as a measure of competition associated with urban beekeeping, because information about hive densities and location in our study area was incomplete. This approach has limitations due to the long foraging distances of honey bees (Beekman and Ratnieks 2000; Seeley 1985) and the short time span of the study (Paini et al. 2005), but it enabled the estimation of the association between honey bee abundance and wild bee occupancy at each site.

Floral resource sampling

Floral resources were surveyed once a month, on 15 sites, during the flowering season (end of April to end of September), from June 2016 to May 2017 for a total of six sampling periods per site. We established 25-m long transects at the same position as the pan trap transects sampled by Normandin et al. (2017). Between one and three transects

were established for each site depending on the number of pan trap transects used by Normandin et al. (2017). All flowering plants one meter on each side of the transects were identified to the lowest possible taxonomic level and their percent cover was visually estimated for each meter of the transects. Floral diversity was quantified as the total number of flowering species sampled at a given site across the six sampling periods. Floral cover was quantified as the mean percent cover of all flowering species at a given site (mean of transects if more than one and mean of sampling periods).

Spatial analyses and urban heat islands

Buffers of 1500 m were created around each pan trap transect of each site using the buffer tool of ArcGIS software (ArcMAP 10.5). That distance corresponds to the flight foraging range of many wild bee species (Greenleaf et al. 2007). Buffers from sites with multiple pan trap transects were then merged to create only one buffer per site. The area (m²) of each garden, cemetery, and park calculated by Normandin et al. (2017) was log transformed. We used open source raster data on urban heat islands and cool areas for the Montreal metropolitan area available on Données Québec (Institut national de santé publique du Québec (INSPQ)) (Bouffroy et al. 2013). This raster mapping uses a classification of temperatures with nine levels, from cool areas to heat islands. Levels eight and nine in this classification correspond to heat islands. We summed the proportion of surface cover of these two temperature classes in each 1500 m buffer zone using ArcGIS to obtain the proportion of heat island cover in each buffer.

Statistical Analyses

It is often impossible to sample species with perfect detection probability (MacKenzie et al. 2006; Williams et al. 2002) due to factors such as variation in sampling effort, sampling method, weather conditions, date, habitat type, or species behavior. These factors complicate comparisons among sites, studies, and species. Recent methodological and analytical advances allow estimating state variables such as occupancy and abundance, after accounting for imperfect detection probability (Kéry and Royle 2016; Mazerolle et al. 2007; Williams et al. 2002). In this study, we used such approaches to estimate community

patterns as well as the abundance of 11 common species. We present each approach in turn below.

Community patterns

We investigated occupancy patterns in the entire bee community of the 166 species detected at least once in our traps and for which there was sufficient information on functional traits. Using the trap data for each visit at each site for all 25 sites sampled, we prepared detection histories for each species consisting of 1 (detected at least once in the traps of a given color) or 0 (not detected). Specifically, each detection history at a given site for a given date had a length of 3: one for each color of trap (blue, white, or yellow). For instance, a detection history of 010 for a species at a site indicated that the species was detected in a white trap, but not in either the blue or yellow pan traps. Individuals in the traps were collected for identification in the lab. Because this potentially resulted in modifying occupancy patterns across visits and because visits at the sites spanned across 6 months, we considered visits at a given site as replicates (i.e., time for space substitution, sensu Kéry and Royle (2016)).

Dorazio and Royle (2005); Royle and Dorazio (2008); Zipkin et al. (2009) extended the classic single season single species occupancy model of MacKenzie et al. (2002) for the analysis of an entire community of species. We modified the approach to our bee community data to test our hypotheses. The single species occupancy model of MacKenzie et al. (2002) includes two parameters. One parameter describes the biological process of interest, which is the probability of occurrence of the species (ψ), whereas the other parameter describes the observation process (p). To account for potential heterogeneity in either occupancy or detection probability, it is possible to include covariates on these parameters using a logit link function analogous to logistic regression. We built a community model and included random effects for each species on occupancy and detection probability to estimate these parameters separately for each species in the same model. Our community model included the following covariates on occupancy: log of site area (to account for differences in site area and thus sampling effort), the proportion of heat islands within 1500 m, and the honey bee capture rate. Specifically, this hierarchical model

included random intercepts and random slopes for each species, similar to a traditional generalized linear mixed model (Gelman and Hill 2007; Zuur et al. 2009). We also considered nesting behavior (cavity vs ground nesting) as a species functional trait that could influence species occupancy (Lowenstein et al. 2014; Matteson et al. 2008; Xie et al. 2013). All numeric variables were standardized to zero mean and unit variance before analysis.

We modeled the occupancy of species i at site j :

$$\log(\psi_{ij}/(1 - \psi_{ij})) = \varphi_i + \beta_{\log\text{Area } i} * \log\text{Area}_j + \beta_{\text{heat } i} * \text{heat}_j + \beta_{\text{beeCapture } i} * \text{beeCapture}_j + \beta_{\text{nesting}} * \text{nesting}_i$$

where φ_i corresponds to the random intercept of occupancy associated with species i , normally distributed with hyperparameters mean μ_φ and standard deviation σ_φ ($\varphi_i \sim N(\mu_\varphi, \sigma_\varphi)$). For random slopes of log Area and the proportion of heat islands within 1500 m, β_i denote the effects of a given variable on the occupancy of each species i , normally distributed with mean μ_β and standard deviation σ_β ($\beta_i \sim N(\mu_\beta, \sigma_\beta)$). In this model, we treated β_{nesting} as a fixed effect.

We modeled the detection probability of species i in site j of trap color k as a function of the number of traps of a given color (sampling effort), Julian date, Julian date squared, and pan trap color (blue, yellow, or white; blue being the reference level). We also included the inter-tegular distance as a species trait that could influence detection probability:

$$\log(p_{ijk}/(1 - p_{ijk})) = \alpha_i + \beta_{\text{effort } i} * \text{effort}_{ijk} + \beta_{\text{Jday } i} * \text{Jday}_{ijk} + \beta_{\text{Jday}^2 i} * \text{Jday}^2_{ijk} + \beta_{\text{color } i} * \text{color}_{ijk} + \beta_{\text{interteg}} * \text{interteg}_{ijk}$$

where α_i corresponds to the random intercept of detection probability associated with species i , normally distributed with hyperparameters mean μ_α and standard deviation σ_α ($\alpha_i \sim N(\mu_\alpha, \sigma_\alpha)$). As above, each β_i (i.e., effort, Jday, or Jday²) denotes the effect of a given

variable on the detection probability of species i distributed with mean μ_β and standard deviation σ_β ($\beta_i \sim N(\mu_\beta, \sigma_\beta)$). Inter-tegular distance was treated as a fixed effect on detection probability.

We estimated the parameters of the community model by adopting a Bayesian approach based on Markov chain Monte Carlo (MCMC) using five chains (Gelman et al. 2014). Each chain was run with 250 000 iterations, using 150 000 iterations as burn-in, and a thinning rate of 10. We used trace plots and the Brooks-Gelman-Rubin statistic to assess convergence. We used vague prior distributions for all parameters. Specifically, we used normal priors with $N(0, 1000)$ for the β parameters, and uniform priors $U(0, 10)$ for all standard deviation parameters. This model was implemented in JAGS 4.2.0 within R with the `jagsUI` and `coda` packages (Kellner 2017; Lunn et al. 2013; Plummer et al. 2006; R Core Team 2017). We reported means and 95% credible intervals for each parameter of interest, where intervals excluding 0 indicated that the effect of a variable differs from 0.

Abundance of common species

For the 15 sites sampled for floral resources, we analysed the abundance of 11 common species. The raw data for the abundance analysis consisted of the number of specimens of a given species at a given visit, yielding three counts at each site on a given date (i.e., one count for each of the three trap colors). We used N -mixture models, conducted separately for each species, to estimate the abundance and detection probability from our trapping data (Royle 2004). Specifically, we targeted 11 of the most abundant wild bee species in our study (*Hylaeus communis* ($n = 283$), *H. hyalinatus* ($n = 140$), *Agapostemon virescens* ($n = 672$), *Halictus ligatus* ($n = 412$), *Lasioglossum imitatum* ($n = 628$), *L. laevissimum* ($n = 1391$), *L. sagax* ($n = 264$), *L. versatum* ($n = 358$), *L. coriaceum* ($n = 133$), *Hoplitis producta* ($n = 407$), and *Ceratina calcarata* ($n = 326$)). We targeted these species because they were among the most abundant in our study and these species occurred at most sites. We quantified the effect of five environmental variables on abundance: floral diversity, floral cover, proportion of heat islands within 1500 m, honey bee capture rate, and log of site area. Because we expected that the relationship between the abundance of a given species and floral resources would depend on honey bee capture rate,

we also considered the potential effect of two interactions, 1) honey bee capture rate x floral diversity and 2) honey bee capture rate x floral cover (Table 1).

We built a set of candidate models based on our biological hypotheses and our knowledge of wild bee life history and the literature (Table 2). We included log of site area in every model to account for differences in the size of sampling sites. We quantified the effect of four variables on detection probability: Julian date, trap color (blue, yellow, or white; blue being the reference level), and number of transects sampled were systematically included in our models, whereas some models included the quadratic effect of Julian date to assess the potential non-linear effect of the date. As in the previous analysis, we standardized all numeric variables. We checked the collinearity among all numeric variables and we did not include variables with Pearson $|r| > 0.7$ in the same model. We used the same set of candidate models for each species.

Parameters were estimated using maximum likelihood implemented in the unmarked package in R (Fiske and Chandler 2011; R Core Team 2017). We used a model selection and multimodel inference approach based on Akaike's information criterion corrected for small samples (AIC_c) with the AICcmodavg package (Burnham and Anderson 2002; Mazerolle 2017). To quantify the effect of the parameters appearing in the top models, we used the shrinkage estimator for model averaging and computed 95% unconditional confidence intervals (Burnham and Anderson 2002; Lukacs et al. 2010). Intervals excluding 0 corresponded to a variable having an effect differing from 0. Model fit and overdispersion were assessed for the top-ranked model with a parametric bootstrap approach using 1000 bootstrap samples based on a χ^2 statistic. For species with high overdispersion ($1 < \hat{c} < 4$), we used the quasi-likelihood AIC_c ($QAIC_c$) to make our inferences. In cases where overdispersion exceeded 4, we used zero-inflated Poisson (ZIP) N -mixture models instead, provided the fit of the zero-inflated Poisson model was appropriate (assessed from the parametric bootstrap).

Results

Normandin et al. (2017) caught 19 077 specimens, representing 166 species across the 25 sites sampled. The proportion of surface cover of urban heat islands within a 1500 m radius varied from 4.32 to 66.40% (mean = 32.86, SD = 20.05). The honey bee capture rate varied from 0 to 17 honey bees captured per cluster of pan traps (mean = 2.67, SD = 3.87). For the 15 sites sampled for floral resources, the number of floral species/site varied from 10 to 69 species (mean = 34.68, SD = 18.50), and the floral cover varied from 3.60 to 18.16% (mean = 10.02, SD = 3.98).

Table 1 Covariates used in abundance models of 11 common species captured at urban sites in Montreal, QC in 2012 and 2013

Variables	Description	Number of sites for which the data were available
log area	log of area of a given site in m ²	25
Floral diversity	Diversity of floral species at a given site measured as the total number of floral species identified	15
Floral cover	Cover of floral species (%) at a given site measured as the mean cover of all species across all transects and all sampling periods	15
Honey bee capture rate	Capture rate of honey bees (total captured/sampling effort) (Normandin et al. 2017) at a given site on a given year	25
Heat islands proportion	Proportion of urban heat islands (%) within a 1500 m buffer zone around each site	25
Floral diversity X Honey bee capture rate	Interaction between the diversity of floral species and the capture rate of honey bees	15
Floral cover X Honey bee capture rate	Interaction between the cover of floral species and the capture rate of honey bees	15

Table 2 Biological hypotheses tested on abundance in the *N*-mixture models on wild bee capture data from urban sites in Montreal, QC in 2012 and 2013. Each scenario on abundance was tested on each of two scenarios on detection probability: 1) Sampling effort + Linear effect of Julian day + Method, 2) Sampling effort + Linear and quadratic effects of Julian day + Method. The null model consisted of log area on abundance and sampling effort on detection probability. Note that log area was included on abundance in all models to account for differences in site area

Candidate Models	Biological hypotheses on abundance
log area	Abundance varies with site area, but no other variable
log area + Floral diversity + Floral cover	Abundance varies with floral resources
log area + Floral diversity + Floral cover + Honey bee capture rate	Abundance varies with floral resources and competition with honey bees
log area + Floral diversity + Floral cover + Honey bee capture rate + Floral diversity X Honey bee capture rate	Abundance varies with floral cover, but the response to competition with honey bees depends on the floral diversity
log area + Floral diversity + Floral cover + Honey bee capture rate + Floral cover X Honey bee capture rate	Abundance varies with floral diversity, but the response to competition with honey bees depends on the floral cover
log area + Heat island proportion	Abundance varies with heat island proportion within 1500 m
log area + Floral diversity + Floral cover + Honey bee capture rate + Heat island proportion + Floral diversity X Honey bee capture rate	Abundance varies with heat island proportion within 1500 m and floral cover, but the response to competition with honey bees depends on floral diversity
log area + Floral diversity + Floral cover + Honey bee capture rate + Heat island proportion + Floral cover X Honey bee capture rate	Abundance varies with heat island proportion within 1500 m and floral diversity, but the response to competition with honey bees depends on floral cover

Community patterns

Our community analysis on the 25 sites revealed that only 46 out of 166 species responded to the proportion of urban heat islands (Table S1). The occupancy probability of 12 species increased with the proportion of urban heat islands within 1500 m, whereas the occupancy of 34 species decreased with the same explanatory variable (Fig. 2a). Twenty five percent of species (41) responded to the size of sites, and the occupancy of all these species increased with site area (Fig. 2b). A minority of species responded to honey bee capture rate (30 out of 166 species). For all of these species, the occupancy probability increased with the honey bee capture rate (Fig. 2c). Occupancy did not vary among nesting behaviors ($\beta_{\text{excavator}} = 0.25$; 95% credible interval: -0.32, 0.81). The bee species richness estimated at a site on a given visit was always substantially higher than the raw count of species for a given visit (Fig. S1).

Fig. 2 Beta estimate of occupancy of wild bee species for the proportion of heat island within 1500 m (a), site size (b), and honey bee capture rate (c) of 166 wild bee species captured in Montreal, QC in 2012 and 2013. Error bars denote 95% Bayesian credible intervals

Abundance of common species

The analysis of the 11 common wild bee species revealed that the most parsimonious model varied among species, but generally included the cover of urban heat islands, floral resources, and honey bee capture rate, with a honey bee x floral resource interaction (Table S2). The abundance of three species increased with the proportion of heat islands within 1500 m, whereas the abundance of one species decreased with the same variable (Table S3, Fig. 3ab). The abundance of five species increased with log area (Fig. 3cd). Floral diversity increased the abundance of two species (Fig. 4ab). The response of two species of wild bees to honey bee capture rate differed with floral diversity, but abundance tended to decrease with increasing honey bee captures under high floral diversity (Fig. 4cd). For the 11 common species we investigated, the abundance never varied with the main effects of floral cover or honey bee capture rate.

Fig. 3 Model-averaged predictions showing the effect of heat island proportion within 1500 m (ab, other species followed a pattern similar to *H. hyalinatus*) and the effect of log

area of size (cd, other species followed a similar pattern) on the abundance of common species captured in Montreal, QC in 2012 and 2013. Outer lines denote 95% confidence intervals

Fig. 4 Model-averaged predictions showing the effect of floral diversity (ab) and the effect of the interaction between floral diversity and honey bee capture rate (cd) on the abundance of common species captured in Montreal, QC in 2012 and 2013. Outer lines denote 95% confidence intervals

Detection probability

Detection probability was estimated separately in the analysis of community patterns and the analysis of the abundance of the common species. In both analyses, detection probability varied with the sampling effort, the Julian day, and the color of the pan traps. Detection probability increased with sampling effort for 17% of the 166 species of the community analysis (Fig. 5a) and 36% of the 11 common species in the abundance analysis (Table S4, Fig. 6ab). A single species responded negatively to sampling effort (*Megachile rotundata* in the community analysis). We found a positive quadratic relationship of detection probability with Julian day for two species in both analyses (Fig. 5b, Fig. 7), with a higher detection probability at the beginning or the end of the season. In contrast, the detection probability reached a maximum in the middle of the season for 54 species in the community analysis and for four common species in the abundance analysis, as indicated by the negative quadratic relationship with Julian day. Forty one species in the community analysis (Fig. 5c) and six common species in the abundance analysis (Fig. 6cd) had a greater detection probability in yellow bowls than blue bowls. In contrast, seven species in the community analysis and two common species in the abundance analysis were harder to detect with yellow bowls than blue bowls. The detection probability of 16 species in the community analysis (Fig. 3d) and four common species in the abundance analysis (Fig. 6cd) was higher in white bowls than blue bowls. Seven species in the community analysis and two common species in the abundance analysis had a lower detection probability in white bowls than blue bowls. Detection probability in the community analysis did not vary with inter-tegular distance (-0.05; 95% credible interval: -0.42, 0.33).

Fig. 5 Estimate of sampling effort (a), Julian day squared (b), yellow bowls compared to blue bowls (c), and white bowls compared to blue bowls (d) on detection probability

of 166 wild bee species captured in Montreal, QC in 2012 and 2013. Error bars denote 95% Bayesian credible intervals

Fig. 6 Model-averaged predictions showing the effect of sampling effort (ab, other species followed a similar pattern) and the effect of bowl color (cd, other species followed a similar pattern) on the detection probability of the common species captured in Montreal, QC in 2012 and 2013. Outer lines denote 95% confidence intervals

Fig. 7 Model-averaged predictions showing the effect of Julian day squared on the detection probability of the common species captured in Montreal, QC in 2012 and 2013. Outer lines denote 95% confidence intervals

Discussion

We studied the impacts of urban heat islands, honey bees, and floral resources on the occurrence and abundance of urban wild bees using a subset of an extensive dataset of 19 077 specimens captured in our study area (Normandin et al. 2017). To our knowledge, this is the first study on wild bees to use urban heat islands as a measure of urbanization. We found that the proportion of urban heat islands within 1500 m, used as a proxy for urbanization, had various effects on wild bees, with a majority of species responding negatively. Interestingly, we found no evidence of negative effects of urban beekeeping on wild bees. Our results therefore suggest that it is possible to conduct urban beekeeping in a sustainable way for wild bees. Finally, while floral resources had positive effects on wild bees, we did not observe the mitigating effect of floral resources we expected on competition from urban beekeeping.

Urbanization

The primary effect of urbanization, as assessed by the effect of urban heat islands, differed between the community and population analyses. Urban heat islands had more of a negative effect on the occurrence of species of wild bees (34) than a positive one (12), whereas 120 species did not respond to the amount of heat islands. In contrast, the analysis of abundance of the 11 common species revealed only a single species responding negatively to the proportion of cover of heat islands within 1500 m, whereas the abundance of three species increased with the same variable. The opposite patterns observed in the community and population analyses are probably due to the 11 species in the abundance analysis being common and well adapted to the urban environment (Verboven et al. 2014).

The three species whose abundance was favored by urbanization were *Hylaeus communis*, *Hylaeus hyalinatus*, and *Lasioglossum laevisimum*. Interestingly, *H. communis* is a newly introduced species in North America from Europe (Martins et al. 2017a; Martins et al. 2017b; Normandin et al. 2017) and could be favored by the urban landscape (Banaszak-Cibicka and Zmihorski 2012; Matteson et al. 2008).

Many studies found that more species of wild bees respond negatively to urbanization than positively (Bates et al. 2011; Deguines et al. 2016; Geslin et al. 2013; McIntyre and Hostetler 2001). This pattern is consistent with our community analysis based on our assessment of the proportion of heat islands within 1500 m. Wild bees seem to be globally suffering from the habitat transformation due to urbanization. Such declines may seem paradoxical, given that many studies found cities to harbour a higher diversity and abundance of wild bees than the surrounding landscape (Banaszak-Cibicka and Zmihorski 2012; Cane et al. 2006; Senapathi et al. 2015), even near our study area (Martins et al. 2017a). Furthermore, the responses to urbanization of some species were similar to those observed in other studies: positive for *H. hyalinatus* (Banaszak-Cibicka and Zmihorski 2012; Bates et al. 2011; Matteson et al. 2008) and negative for *H. affinis* and *L. versatum* (Martins et al. 2017a). In contrast, Martins et al. (2017a) reported patterns for *C. calcarata*, *A. pura*, and *A. virescens* opposite to those we observed for these species.

The impact of urbanization can be linked to the size of our sites, as both these impacts are related to the availability of floral and nesting resources. The proportion of urban heat islands and the size of a site can be considered measures of floral resources at larger spatial scales. In our community analysis, 41 out of 166 species responded positively to site size. We found no effect of site for the other 125 species. Regarding the abundance of the common species, no species responded negatively to the size of the site, but five out of the 11 species responded positively to the variable. Indeed, small fragmented patches usually hold less diverse and abundant bee communities (Hinnert et al. 2012). Those patches are presumably too small to contain all the resources essential to wild bees. However, this pattern has presumably weak effects on bee communities as they can travel across landscape barriers (Kennedy et al. 2013).

The nesting behaviour of wild bees did not influence the probability of occupancy of species in our community analysis: ground nesters did not differ in occupancy relative to cavity nesters. This was surprising, given that cities are characterised by high proportions of impervious surfaces or soils degraded by compaction and erosion (Cane 2005; Cane et al. 2006). Ground nesting bees need soft and bare ground to establish their nest (Cane et al. 2006; Xie et al. 2013) and should be affected by urbanization more than cavity nesting bees (Geslin et al. 2016; Lowenstein et al. 2014; Matteson et al. 2008). A potential explanation of the lack of difference in occupancy between cavity nesters and other species is that the urban parks, gardens, and cemeteries of our study area hold interesting nesting resources for both ground and cavity nesting bees. The high heterogeneity of urban patches can provide diversified resources and accommodate both functional groups.

Competition with honey bees

In contrast to what we expected according to the literature (Mallinger et al. 2017), we did not observe a negative impact of honey bees on wild bees. The occupancy of 30 species of wild bees in our community analysis increased with honey bee capture rate, whereas the other 136 species did not vary with honey bee capture rate. This suggests either no or weak competition between honey bee and wild bee species. We hypothesized that the competition with honey bees is mediated by the availability of floral resources. However, we found no evidence in support of this hypothesis in our study. Three criteria must be present for competition to occur between two species: the niche of both species must be overlapping, this overlap must lead to a decrease in the capacity of one or both species to acquire resources, and this decrease must cause a decrease in reproductive rate or fitness of one or both species (Paini 2004; Stout and Morales 2009). Therefore, an absence of effect could indicate that either the niches of wild and honey bees are not overlapping, the resources are not limited in our setting, or there is no decrease in reproduction of wild bees even with rarefied resources.

Wild and honey bees both consume mainly nectar and pollen, and, to a lesser extent, honeydew, plant sap, waxes, resins and water (Goulson 2003). Their niches in flower usage overlap between 17 and 97% (Goulson et al. 2002; Paini and Roberts 2005; Steffan-

Dewenter and Tschardt 2000). It is very unlikely that the niches of the species in our system are not overlapping. Floral resources may have been sufficient to support both honey bees and wild bees. Cities harbour diversified and abundant floral communities usually composed of native and exotic floral species. Densely populated neighborhoods have a very high diversity of flowers (Lowenstein et al. 2014; Matteson et al. 2013). Again, the high heterogeneity of urban landscapes might promote the diversification and abundance of resources for bees (Williams and Kremen 2007) and mitigate competition (Herbertsson et al. 2016). Systems in which resources are not limited (Minckley et al. 2003) or where honey bee density is low (Roubik 1983) can allow cohabitation between wild and honey bees. Hive densities in our study area (0.32 – 0.48 hives/km²) were lower than those reported in other cities such as Paris and London with 9.5 and 2.23 hives/km² (Alton and Ratnieks 2016; Rubin 2018). Studies conducted in natural or agricultural settings found negative effects of competition with honey bees at hive densities much higher than those in our study with 4.53 and 200 hives/km² (Dupont et al. 2004; Lindström et al. 2016).

The occupancy of 30 species increased with honey bee abundance. We believe that it is unlikely that honey bees have a positive impact on wild bees. Even if there were no associations between the floral resources and the abundance of honey bees, sites of better quality could still have attracted more honey bees as well as a greater abundance of wild bees. To the best of our knowledge, the only other case of positive effect of honey bees on wild bees is the synchronous increase in visitation rates of wild bees and honey bees to *Echium plantagineum* (Nielsen et al. 2012). Nonetheless, it is difficult to draw conclusions on the population dynamics of wild bees, because our study was purely correlative. Experimental manipulations of honey bee hive densities are required to better understand the potential effects of this commercial species in North American cities (Goulson et al. 2002). In addition, estimation of wild bee fecundity, fitness, or survival would provide superior measures to inform potential impacts of competition on demographic parameters (Paini 2004).

Honey bees and urban beekeeping can represent a threat to wild bees (Mallinger et al. 2017). However, our results indicate that cities can allow the coexistence of honey bees and wild bees under moderate hive densities or high floral resources. Beekeeping in cities

and protected areas should not be seen as a biological conservation approach (Geldmann and González-Varo 2018). Wild bees are at least as important as honey bees to provide the pollination services. The key to ensure wild bee persistence is to maintain and manage an abundance of flowers (Roulston and Goodell 2011).

Floral resources

Floral resources are expected to have positive impacts as both diversity and cover of floral communities are positively related with pollinator community richness (Ebeling et al. 2008; Grundel et al. 2010). Floral resources had a rather positive effect on the abundance of some of the most common bee species of our study. Three species responded positively to floral diversity. On the other hand, the abundance of one species (*L. laevissimum*) decreased with increasing floral cover. We speculate that *L. laevissimum* may be limited by another factor, such as the availability of nesting resources. The negative impact of floral cover for this species may also result from the use of pan traps. Indeed, pan traps are known to become less attractive to bees in flower-rich habitats (Plascencia and Philpott 2017). Thus, a high cover of flowers can lead to a reduction in the number of bees that are caught by pan traps.

A potential shortcoming of our study was that three years had elapsed between the sampling of bees and of floral resources. To reduce this problem, floral sampling excluded sites that had undergone important changes in management practices between 2013 and 2016. Thus, we are confident that the floral communities we sampled were very similar to those of 2012 and 2013. The nature of the study sites also supports that notion. For instance, community gardens are often managed year after year by the same gardeners harvesting the same plant groups. Furthermore, transects in cemeteries and parks were located on the edge of forest patches and grass, where weeds and herbaceous plants maintain their populations over time. We believe that our results are representative of the situation in North American cities with similar hive densities and could help understand the ecology of wild bees in many urban settings.

Detection probability

Both the community and abundance analyses show that the probability of detection of many species varied with the sampling effort, the linear or quadratic effect of Julian day, or the bowl color. This result highlights the importance of explicitly modeling detection probability to estimate occupancy or abundance, because detection probability is neither constant across the season nor close to 1. Obviously, in the community analysis, sampling effort had a much more positive effect (28 species) than a negative one (one species). The species being negatively affected by sampling effort, *Megachile rotundata*, is a common cavity nesting bee. This negative link with sampling effort could be due to its high abundance in some small sized gardens and parks and its absence or lower abundance in large size parks and cemeteries.

The relationship with the detection probability and the Julian day is the result of variations in the period of activities of the different bee species within the season. Some species are indeed active later or sooner in the season (Normandin et al. 2017). Variations in the detection probability during the season for many species could also be linked to the reduced attractiveness of pan traps when flowers are abundant (Plascencia and Philpott 2017). Yellow was the most attractive color overall and agrees with Hall (2016), but contrasts with previous studies where blue traps were more effective at attracting bees (Campbell, 2007), or where all colors had similar attractiveness (Toler, 2005). Nevertheless, our results indicate that a combination of all three colors is essential to thoroughly assess bee communities. Because it is impossible to standardise traps and their efficiency between dates and sites, estimating detection probability is essential to obtain abundance and occupancy estimates that can be compared between studies.

Conclusion

We did not find evidence of a relationship between wild bees and honey bees in our urbanized landscape. However, we found strong relationships of bee occupancy and abundance with urbanization as measured by the proportion of urban heat islands within 1500 m and the availability of floral resources, indicating that those factors are the main drivers of wild bee communities in our urban system. Our results suggest that cities can harbor important wild bee communities when floral resources are abundant and urban

beekeeping is maintained at a moderate level. Management practices should aim at increasing the floral resources and maintaining the urban beekeeping under densities where competition could occur, and manipulative field studies should investigate this threshold.

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Supplementary material

Fig. S1 Estimated species richness of 166 wild bee species captured in Montreal, QC in 2012 and 2013. Error bars denote 95% Bayesian credible intervals

Table S1 List of species for the community analysis sorted by phylogenetic order. These numbers identify species on the x axis of figures 2 -- 8

	Species
1	<i>Colletes simulans</i> Cresson, 1868
2	<i>Hylaeus (Hylaeus) annulatus</i> (Linnaeus, 1758)
3	<i>Hylaeus (Hylaeus) communis</i> Nylander, 1852
4	<i>Hylaeus (Hylaeus) leptcephalus</i> (Morawitz, 1871 [“1870”])
5	<i>Hylaeus (Hylaeus) mesillae</i> (Cockerell, 1896)
6	<i>Hylaeus (Prosopis) affinis</i> (Smith, 1853)
7	<i>Hylaeus (Prosopis) modestus</i> Say, 1837
8	<i>Hylaeus (Prosopis) nelumbonis</i> (Robertson, 1890)
9	<i>Hylaeus (Spatulariella) hyalinatus</i> Smith, 1842
10	<i>Hylaeus (Spatulariella) punctatus</i> (Brullé, 1832)
11	<i>Augochloropsis (Paraugochloropsis) metallica</i> (Fabricius, 1793)
12	<i>Augochlorella aurata</i> (Smith, 1853)
13	<i>Augochlora (Augochlora) pura pura</i> (Say, 1837)
14	<i>Agapostemon (Agapostemon) texanus</i> Cresson, 1872
15	<i>Agapostemon (Agapostemon) virescens</i> (Fabricius, 1775)
16	<i>Sphecodes carolinus</i> Mitchell, 1956
17	<i>Sphecodes clematidis</i> Robertson, 1897
18	<i>Sphecodes cressonii</i> (Robertson, 1903)
19	<i>Sphecodes dichrous</i> Smith, 1853
20	<i>Sphecodes ranunculi</i> Robertson, 1897
21	<i>Halictus (Odontalictus) ligatus</i> Say, 1837
22	<i>Halictus (Protohalictus) rubicundus</i> (Christ, 1791)
23	<i>Halictus (Seladonia) confusus confusus</i> Smith, 1853
24	<i>Lasioglossum (Dialictus) asteris</i> (Mitchell, 1960)

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- 25 *Lasioglossum (Dialictus) cephalotes* (Dalla Torre, 1896)
26 *Lasioglossum (Dialictus) coeruleum* (Robertson, 1893)
27 *Lasioglossum (Dialictus) cressonii* (Robertson, 1890)
28 *Lasioglossum (Dialictus) dreisbachi* (Mitchell, 1960)
29 *Lasioglossum (Dialictus) ephialtum* Gibbs, 2010
30 *Lasioglossum (Dialictus) heterognathum* (Mitchell, 1960)
31 *Lasioglossum (Dialictus) hitchensi* Gibbs, 2012
32 *Lasioglossum (Dialictus) imitatum* (Smith, 1853)
33 *Lasioglossum (Dialictus) laevissimum* (Smith, 1853)
34 *Lasioglossum (Dialictus) leucocomum* (Lovell, 1908)
35 *Lasioglossum (Dialictus) lineatulum* (Crawford, 1906)
36 *Lasioglossum (Dialictus) michiganense* (Mitchell, 1960)
37 *Lasioglossum (Dialictus) nigroviride* (Graenicher, 1911)
38 *Lasioglossum (Dialictus) oblongum* (Lovell, 1905)
39 *Lasioglossum (Dialictus) paradmirandum* (Knerer & Atwood, 1966)
40 *Lasioglossum (Dialictus) pilosum* (Smith, 1853)
41 *Lasioglossum (Dialictus) planatum* (Lovell, 1905)
42 *Lasioglossum (Dialictus) sagax* (Sandhouse, 1924)
43 *Lasioglossum (Dialictus) smilacinae* (Robertson, 1897)
44 *Lasioglossum (Dialictus) tegulare* (Robertson, 1890)
45 *Lasioglossum (Dialictus) tenax* (Sandhouse, 1924)
46 *Lasioglossum (Dialictus) trigeminum* Gibbs, 2011
47 *Lasioglossum (Dialictus) versans* (Lovell, 1905)
48 *Lasioglossum (Dialictus) versatum* (Robertson, 1902)
49 *Lasioglossum (Dialictus) viridatum* (Lovell, 1905)
50 *Lasioglossum (Dialictus) zephyrum* (Smith, 1853)
51 *Lasioglossum (Evylaeus) cinctipes* (Provancher, 1888)
52 *Lasioglossum (Hemihalictus) birkmanni* (Crawford, 1906)
53 *Lasioglossum (Hemihalictus) foxii* (Robertson, 1895)
54 *Lasioglossum (Hemihalictus) macoupinense* (Robertson, 1895)
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- 55 *Lasioglossum (Lasioglossum) athabascense* (Sandhouse, 1933)
56 *Lasioglossum (Lasioglossum) coriaceum* (Smith, 1853)
57 *Lasioglossum (Leuchalictus) zonulum* (Smith, 1848)
58 *Lasioglossum (Leuchalictus) leucozonium* (Schrank, 1781)
59 *Lasioglossum (Sphecogastra) comagenense* (Knerer & Atwood, 1964)
60 *Lasioglossum (Sphecogastra) quebecense* (Crawford, 1907)
61 *Lasioglossum (Sphecogastra) oenotherae* (Stevens, 1920)
62 *Andrena (Andrena) clarkella* (Kirby, 1802)
63 *Andrena (Andrena) frigida* Smith, 1853
64 *Andrena (Andrena) mandibularis* Robertson, 1892
65 *Andrena (Andrena) milwaukeensis* Graenicher, 1903
66 *Andrena (Andrena) rufosignata* Cockerell, 1902
67 *Andrena (Cnemiandrena) chromotricha* Cockerell, 1899
68 *Andrena (Cnemiandrena) hirticincta* Provancher, 1888
69 *Andrena (Cnemiandrena) nubecula* Smith, 1853
70 *Andrena (Euandrena) geranii* Robertson, 1891
71 *Andrena (Gonandrena) integra* Smith, 1853
72 *Andrena (Gonandrena) persimulata* Viereck, 1917
73 *Andrena (Holandrena) cressonii cressonii* Robertson, 1891
74 *Andrena (Larandrena) miserabilis* Cresson, 1872
75 *Andrena (Leucandrena) erythronii* Robertson, 1891
76 *Andrena (Melandrena) carlini* Cockerell, 1901
77 *Andrena (Melandrena) commoda* Smith, 1879
78 *Andrena (Melandrena) dunningi* Cockerell, 1898
79 *Andrena (Melandrena) nivalis* Smith, 1853
80 *Andrena (Melandrena) vicina* Smith, 1853
81 *Andrena (Micrandrena) ziziae* Robertson, 1891
82 *Andrena (Micrandrena) nigrae* Robertson, 1905
83 *Andrena (Plastandrena) crataegi* Robertson, 1893
84 *Andrena (Ptilandrena) distans* Provancher, 1888
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- 85 *Andrena (Ptilandrena) erigeniae* Robertson, 1891
- 86 *Andrena (Rhacandrena) robertsonii* Dalla Torre, 1896
- 87 *Andrena (Scrapteropsis) imitatrix* Cresson, 1872
- 88 *Andrena (Scrapteropsis) morrisonella* Viereck, 1917
- 89 *Andrena (Simandrena) nassonii* Robertson, 1895
- 90 *Andrena (Simandrena) wheeleri* Graenicher, 1904
- 91 *Andrena (Taeniandrena) wilkella* (Kirby, 1802)
- 92 *Andrena (Thysandrena) w-scripta* Viereck, 1904
- 93 *Andrena (Thysandrena) bisalicis* Viereck, 1908
- 94 *Andrena (Trachandrena) ceanothi* Viereck, 1917
- 95 *Andrena (Trachandrena) forbesii* Robertson, 1895
- 96 *Andrena (Trachandrena) hippotes* Robertson, 1895
- 97 *Andrena (Trachandrena) rugosa* Robertson, 1891
- 98 *Andrena (Trachandrena) sigmundi* Cockerell, 1902
- 99 *Andrena (Trachandrena) spiraeana* Robertson, 1895
- 100 *Andrena (Tylandrena) erythrogaster* (Ashmead, 1890)
- 101 *Andrena (Tylandrena) perplexa* Smith, 1853
- 102 *Calliopsis (Calliopsis) andreniformis* Smith, 1853
- 103 *Pseudopanurgus parvus* (Robertson, 1892)
- 104 *Anthidium (Anthidium) manicatum* Linnaeus, 1758
- 105 *Anthidium (Anthidium) florentinum* Fabricius, 1775
- 106 *Anthidium (Proantidium) oblongatum* (Illiger, 1806)
- 107 *Heriades (Neotrypetes) carinata* Cresson, 1864
- 108 *Heriades (Neotrypetes) leavitti* Crawford, 1913
- 109 *Hoplitis (Hoplitis) anthocopoides* Schenck, 1853
- 110 *Hoplitis (Alcidamea) pilosifrons* (Cresson, 1864)
- 111 *Hoplitis (Alcidamea) producta producta* (Cresson, 1864)
- 112 *Hoplitis (Alcidamea) spoliata* (Provancher, 1888)
- 113 *Osmia (Diceratosmia) conjuncta* Cresson, 1864
- 114 *Osmia (Melanosmia) albiventris* Cresson, 1864
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- 115 *Osmia (Melanosmia) atriventris* Cresson, 1864
116 *Osmia (Melanosmia) pumila* Cresson, 1864
117 *Osmia (Melanosmia) simillima* Smith, 1853
118 *Osmia (Osmia) lignaria* Say, 1837
119 *Osmia (Osmia) taurus* Smith, 1873
120 *Chelostoma (Foveosmia) campanularum* (Kirby, 1802)
121 *Chelostoma (Gyrodromella) rapunculi* (Lepeletier, 1841)
122 *Chelostoma (Prochelostoma) philadelphi* (Robertson, 1891)
123 *Megachile (Chelostomoides) campanulae* (Robertson, 1903)
124 *Megachile (Eutricharaea) rotundata* (Fabricius, 1787)
125 *Megachile (Litomegachile) brevis* Say, 1837
126 *Megachile (Litomegachile) mendica* Cresson, 1878
127 *Megachile (Litomegachile) texana* Cresson, 1878
128 *Megachile (Megachile) centuncularis* (Linnaeus, 1858)
129 *Megachile (Megachile) lapponica* Thomson, 1872
130 *Megachile (Megachile) inermis* Provancher, 1888
131 *Megachile (Megachile) relativa* Cresson, 1878
132 *Megachile (Xanthosarus) frigida* Smith, 1853
133 *Megachile (Xanthosarus) gemula* Cresson, 1878
134 *Megachile (Xanthosarus) latimanus* Say, 1823
135 *Megachile (Sayapis) pugnata* Say, 1837
136 *Coelioxys (Boreocoelioxys) octodentata* Say, 1824
137 *Coelioxys (Boreocoelioxys) porterae* Cockerell, 1900
138 *Ceratina (Zadontomerus) calcarata* Robertson, 1900
139 *Ceratina (Zadontomerus) dupla* Say, 1837
140 *Ceratina (Zadontomerus) mikmaqi* Rehan & Sheffield, 2011
141 *Nomada bethunei* Cockerell, 1903
142 *Nomada cressonii* Robertson, 1893
143 *Nomada denticulata* Robertson, 1902
144 *Nomada luteoloides* Robertson, 1895
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145	<i>Nomada maculata</i> Cresson, 1863
146	<i>Nomada pygmaea</i> Cresson, 1963
147	<i>Nomada vicina</i> Cresson, 1863
148	<i>Epeolus scutellaris</i> Say, 1824
149	<i>Triepeolus pectoralis</i> (Robertson, 1897)
150	<i>Holcopasites calliopsidis</i> (Linsley, 1943)
151	<i>Mellisodes (Eumelissodes) druriella</i> (Kirby, 1802)
152	<i>Melissodes (Eumelissodes) subillata</i> LaBerge, 1961
153	<i>Melissodes (Eumelissodes) illata</i> Lovell & Cockerell, 1906
154	<i>Melissodes (Eumelissodes) trinodis</i> Robertson, 1901
155	<i>Melissodes (Heliomelissodes) desponsa</i> Smith, 1854
156	<i>Peponapis (Peponapis) pruinosa</i> (Say, 1837)
157	<i>Anthophora (Clisodon) terminalis</i> Cresson, 1869
158	<i>Bombus (Bombus) terricola</i> Kirby, 1837
159	<i>Bombus (Psithyrus) citrinus</i> (Smith, 1854)
160	<i>Bombus (Thoracobombus) fervidus</i> (Fabricius, 1798)
161	<i>Bombus (Cullumanobombus) rufocinctus</i> Cresson, 1863
162	<i>Bombus (Cullumanobombus) griseocollis</i> (DeGeer, 1773)
163	<i>Bombus (Pyrobombus) bimaculatus</i> Cresson, 1863
164	<i>Bombus (Pyrobombus) impatiens</i> Cresson, 1863
165	<i>Bombus (Pyrobombus) vagans vagans</i> Smith, 1854
166	<i>Apis (Apis) mellifera</i> Linnaeus, 1758

Table S2 Model selection based on QAIC_c of *N*-mixture models used to estimate the abundance of the common species captured in Montreal, QC in 2012 and 2013. Only models with $\Delta\text{QAIC}_c < 4$ are shown for brevity. Note that explanatory variables on abundance are designated between parentheses in lambda(), whereas variables tested on detection probability are shown between parentheses in p(). Estimate of overdispersion (c-hat) is shown in parentheses for each species

	K	QAIC _c	ΔQAIC_c	QAIC _c Wt
<i>Hylaeus communis</i> (c-hat = 5.16)				
lambda(log area + floral diversity + floral cover +	14	455.91	0.00	0.64

honey bee capture rate + heat island proportion + floral diversity X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)				
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral cover X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	14	457.12	1.20	0.35
<i>Agapostemon virescens</i>				
lambda(log area + floral diversity + floral cover + honey bee capture rate + floral diversity X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	14	618.45	0.00	0.25
lambda(log area + floral diversity + floral cover + honey bee capture rate + floral diversity X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	13	618.63	0.18	0.23
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral diversity X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	15	619.66	1.22	0.13
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral diversity X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	14	619.96	1.52	0.12
lambda(log area + floral diversity + floral cover + honey bee capture rate + floral cover X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	13	620.02	1.57	0.11
lambda(log area + floral diversity + floral cover + honey bee capture rate + floral cover X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	14	620.28	1.83	0.10
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral cover X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	14	622.24	3.79	0.04

***Ceratina calcarata* (c-hat = 3.49)**

lambda(log area + floral diversity + floral cover + 15 413.49 0.00 0.92
honey bee capture rate + heat island proportion +
floral cover X honey bee capture rate) p(sampling
effort + Julian day + Julian day² + pan trap color)

***Hylaeus hyalinatus* (c-hat = 3.17)**

lambda(log area + floral diversity + floral cover + 14 391.48 0.00 0.54
honey bee capture rate + heat island proportion +
floral cover X honey bee capture rate) p(sampling
effort + Julian day + Julian day² + pan trap color)

lambda(log area + floral diversity + floral cover + 14 391.80 0.31 0.46
honey bee capture rate + heat island proportion +
floral diversity X honey bee capture rate) p(sampling
effort + Julian day + Julian day² + pan trap color)

***Halictus ligatus* (c-hat = 3.67)**

lambda(log area + floral diversity + floral cover + 13 531.45 0.00 0.26
honey bee capture rate + heat island proportion +
floral diversity X honey bee capture rate) p(sampling
effort + Julian day + pan trap color)

lambda(log area + floral diversity + floral cover + 12 532.35 0.90 0.17
honey bee capture rate + floral cover X honey bee
capture rate) p(sampling effort + Julian day + pan
trap color)

lambda(log area + floral diversity + floral cover + 13 532.43 0.98 0.16
honey bee capture rate + heat island proportion +
floral cover X honey bee capture rate) p(sampling
effort + Julian day + pan trap color)

lambda(log area + floral diversity + floral cover + 14 533.71 2.26 0.08
honey bee capture rate + heat island proportion +
floral diversity X honey bee capture rate) p(sampling
effort + Julian day + Julian day² + pan trap color)

lambda(log area + floral diversity + floral cover + 11 533.87 2.42 0.08
honey bee capture rate) p(sampling effort + Julian
day + pan trap color)

lambda(log area + floral diversity + floral cover + 13 534.57 3.12 0.05
honey bee capture rate + floral cover X honey bee

capture rate) p(sampling effort + Julian day + Julian day² + pan trap color)

lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral cover X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	14	534.68	3.23	0.05
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lambda(log area + floral diversity + floral cover) p(sampling effort + Julian day + pan trap color)	10	534.93	3.48	0.05
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lambda(log area + floral diversity + floral cover + honey bee capture rate + floral diversity X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	12	535.02	3.57	0.04
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***Hoplitis producta* (c-hat = 4.61)**

lambda(log area + floral diversity + floral cover) p(sampling effort + Julian day + Julian day ² + pan trap color)	12	358.11	0.00	0.42
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lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral diversity X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	15	359.76	1.65	0.18
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lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral cover X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	15	359.99	1.88	0.16
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lambda(log area + floral diversity + floral cover + honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	13	360.23	2.12	0.14
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***Lasioglossum coriaceum* (c-hat = 2.03)**

lambda(log area + honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	10	346.54	0.00	0.70
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lambda(log area + floral diversity + floral cover + honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	12	350.47	3.92	0.10
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***Lasioglossum imitatum* (c-hat = 4.34)**

lambda(log area + floral diversity + floral cover) p(sampling effort + Julian day + Julian day ² + pan trap color)	11	630.71	0.00	0.31
lambda(log area + floral diversity + floral cover) p(sampling effort + Julian day + pan trap color)	10	631.06	0.35	0.26
lambda(log area + floral diversity + floral cover + honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	12	632.79	2.08	0.11
lambda(log area + floral diversity + floral cover + honey bee capture rate) p(sampling effort + Julian day + pan trap color)	11	632.96	2.24	0.10
<i>Lasioglossum laevissimum</i> (c-hat = 7.70)				
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral diversity X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	15	885.38	0.00	1.00
<i>Lasioglossum sagax</i> (c-hat = 5.39)				
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral diversity X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	15	348.53	0.00	0.35
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral diversity X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	14	349.76	1.23	0.19
lambda(log area + floral diversity + floral cover + honey bee capture rate + floral diversity X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	14	350.20	1.67	0.15
lambda(log area + floral diversity + floral cover + honey bee capture rate + floral diversity X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	13	350.59	2.06	0.13
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral cover X honey bee capture rate) p(sampling	15	351.38	2.85	0.08

effort + Julian day + Julian day ² + pan trap color)				
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral cover X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	14	351.80	3.26	0.07
<i>Lasioglossum versatum</i> (c-hat = 4.11)				
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral diversity X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	13	368.42	0.00	0.61
lambda(log area + floral diversity + floral cover + honey bee capture rate + heat island proportion + floral diversity X honey bee capture rate) p(sampling effort + Julian day + Julian day ² + pan trap color)	14	370.28	1.86	0.24
lambda(log area + floral diversity + floral cover + honey bee capture rate + floral diversity X honey bee capture rate) p(sampling effort + Julian day + pan trap color)	12	371.95	3.54	0.11

Table S3 Model-averaged estimates and 95% confidence intervals of parameters on abundance of common species captured in Montreal, QC in 2012 and 2013. Only estimates for which 95% confidence interval excludes 0 are shown

Parameter	Species	Model-averaged estimate*	95% CI
Floral diversity	<i>H. hyalinatus</i>	0.84	[0.02, 1.67]
Floral diversity	<i>H. producta</i>	0.82	[0.08, 1.57]
Heat proportion	island <i>H. communis</i>	0.6	[0.31, 0.9]
Heat proportion	island <i>H. hyalinatus</i>	1.00	[0.66, 1.35]
Heat proportion	island <i>L. laevissimum</i>	0.66	[0.48, 0.84]
Heat proportion	island <i>C. calcarata</i>	-0.92	[-1.47, -0.37]
Floral diversity x honey bee capture rate interaction	<i>L. laevissimum</i>	-0.54	[-0.79, -0.29]
Floral diversity x honey bee capture rate interaction	<i>L. versatum</i>	-0.90	[-1.34, -0.45]
log area	<i>H. communis</i>	0.77	[0.17, 1.38]
log area	<i>H. ligatus</i>	0.82	[0.19, 1.44]
log area	<i>L. imitatum</i>	0.62	[0.25, 1]
log area	<i>L. laevissimum</i>	0.90	[0.55, 1.25]
log area	<i>L. coriaceum</i>	1.14	[0.66, 1.61]

*shrinkage estimator used for main effects of variables not involved in interactions, model-averaged effect size for unit change of 1 reported otherwise.

Table S4 Model-averaged estimates and 95% confidence intervals of parameters on detection probability of 11 common species captured in Montreal, QC in 2012 and 2013. Only estimates for which 95% confidence interval excludes 0 are shown

Parameter	Species	Model-averaged estimate	95% CI
Julian day squared	<i>H. hyalinatus</i>	-0.85	[-1.21, -0.5]
Julian day squared	<i>H. communis</i>	-0.62	[-0.97, -0.26]
Julian day squared	<i>L. laevissimum</i>	-0.30	[-0.45, -0.16]
Julian day squared	<i>L. coriaceum</i>	0.91	[0.34, 1.47]
Julian day squared	<i>H. producta</i>	-4.59	[-6.02, -3.17]
Julian day squared	<i>C. calcarata</i>	0.52	[0.28, 0.75]
Sampling effort	<i>H. hyalinatus</i>	1.99	[1.37, 2.61]
Sampling effort	<i>L. laevissimum</i>	0.92	[0.65, 1.19]
Sampling effort	<i>L. sagax</i>	1.28	[0.51, 2.05]
Sampling effort	<i>H. producta</i>	0.83	[0.4, 1.26]
White vs blue bowls	<i>H. hyalinatus</i>	1.34	[0.6, 2.08]
White vs blue bowls	<i>A. virescens</i>	-0.92	[-1.3, -0.54]
White vs blue bowls	<i>L. imitatum</i>	0.96	[0.51, 1.4]
White vs blue bowls	<i>L. laevissimum</i>	0.63	[0.35, 0.9]
White vs blue bowls	<i>L. coriaceum</i>	-0.75	[-1.46, -0.04]
White vs blue bowls	<i>H. producta</i>	0.43	[0.05, 0.82]
Yellow vs blue bowls	<i>H. hyalinatus</i>	1.69	[0.97, 2.41]
Yellow vs blue bowls	<i>A. virescens</i>	-0.52	[-0.86, -0.17]
Yellow vs blue bowls	<i>H. ligatus</i>	0.51	[0.06, 0.95]
Yellow vs blue bowls	<i>L. imitatum</i>	1.21	[0.77, 1.65]
Yellow vs blue bowls	<i>L. laevissimum</i>	1.02	[0.75, 1.28]
Yellow vs blue bowls	<i>L. sagax</i>	1.31	[0.79, 1.84]
Yellow vs blue bowls	<i>L. versatum</i>	1.16	[0.52, 1.8]
Yellow vs blue bowls	<i>H. producta</i>	-0.50	[-0.97, -0.03]

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