

RESEARCH ARTICLE

# The Bees among Us: Modelling Occupancy of Solitary Bees

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**Citation:** MacIvor JS, Packer L (2016) The Bees among Us: Modelling Occupancy of Solitary Bees. PLoS ONE 11(12): e0164764. doi:10.1371/journal.pone.0164764

**Editor:** Nigel E. Raine, University of Guelph, CANADA

**Received:** October 6, 2015

**Accepted:** September 30, 2016

**Published:** December 2, 2016

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**Data Availability Statement:** All relevant data are within the paper and its Supporting Information files. The geographic locations of the sample sites are kept private as the majority are private residential homes. Coordinates can be obtained from the senior author upon request pending agreement from the landowners.

**Funding:** The first author was funded by a scholarship awarded by the Canadian National Science and Engineering Council (CGS D 408565) and an NSERC discovery grant funding awarded to the second author.

**Competing Interests:** No competing interests exist.

## Abstract

Occupancy modelling has received increasing attention as a tool for differentiating between true absence and non-detection in biodiversity data. This is thought to be particularly useful when a species of interest is spread out over a large area and sampling is constrained. We used occupancy modelling to estimate the probability of three phylogenetically independent pairs of native—introduced species [*Megachile campanulae* (Robertson)—*Megachile rotundata* (Fab.), *Megachile pugnata* Say—*Megachile centuncularis* (L.), *Osmia pumila* Cresson—*Osmia caerulescens* (L.)] (Apoidea: Megachilidae) being present when repeated sampling did not always find them. Our study occurred along a gradient of urbanization and used nest boxes (bee hotels) set up over three consecutive years. Occupancy modelling discovered different patterns to those obtained by species detection and abundance-based data alone. For example, it predicted that the species that was ranked 4<sup>th</sup> in terms of detection actually had the greatest occupancy among all six species. The native *M. pugnata* had decreased occupancy with increasing building footprint and a similar but not significant pattern was found for the native *O. pumila*. Two introduced bees (*M. rotundata* and *M. centuncularis*), and one native (*M. campanulae*) had modelled occupancy values that increased with increasing urbanization. Occupancy probability differed among urban green space types for three of six bee species, with values for two native species (*M. campanulae* and *O. pumila*) being highest in home gardens and that for the exotic *O. caerulescens* being highest in community gardens. The combination of occupancy modelling with analysis of habitat variables as an augmentation to detection and abundance-based sampling is suggested to be the best way to ensure that urban habitat management results in the desired outcomes.

## Introduction

### Detection probability

A persistent problem with understanding the results of repeated biodiversity surveys is that of false absence: when a species is present at the site but not detected in a sample [1]. This limitation is more readily assessed with repeated sampling at multiple locations or times where non-detections are interspersed among instances of detection; these patterns permit the estimation

of a detection probability per species and the proportion of non-detection that actually indicates true absences [1]. Interpreting non-detection as absence will underestimate a species' temporal and/or spatial distribution [2,3]. This can decrease the accuracy of habitat models [4] and may weaken the effectiveness of wildlife management recommendations [3,5–9]. The probability of detecting a species ( $p$ ) is related to species occupancy ( $\Psi$ ), a state variable that estimates the proportion of sites that are occupied by a species, whether or not it was detected in surveying [1]. Occupancy, as estimated with  $\Psi$ , does not consider abundance, only the presence or absence of a species at a site during sampling [10–12].

Occupancy models incorporate both  $\Psi$  and  $p$  and are especially useful for interpreting survey data of species that are difficult to sample, and/or where populations are common and/or widespread but extensive sampling is prohibitive in either cost or time [3]. These models permit the assessment of likelihood of the species being present at sites where the species of interest was not detected [13,14]. In sum, occupancy modelling should provide a more reliable picture of a species' presence among a series of samples irrespective of the proportion of times it was actually detected in sampling [2,14–18].

Welsh *et al.* (2013) argued that results from occupancy models can be highly variable depending on the number of individuals surveyed and that interpreting them can be as misleading as ignoring non-detection in abundance-based studies [9]. Here we present the results of occupancy modelling on the six most common bee species from trap nest surveys in a large urban landscape. Three are native and three introduced. We demonstrate that conclusions based on occupancy models are often different from those based upon sampled detection. Thus, we find that occupancy models provide additional insights into the determinants of bee occurrences in the urban milieu. Further, we argue that failure to detect a species in a sample when it might have been present should be acknowledged in ecological studies, and our data supports the notion that occupancy modelling produces meaningful results by partitioning true absence from false non-detection. Occupancy modelling should be added to the toolbox used by urban ecologists as it has implications for biodiversity management and planning of complementary urban green spaces, such as private home gardens or green roofs that can be difficult to access and sample repeatedly [19].

## Bees

Bees are essential pollinators in most terrestrial landscapes for both agricultural crops [20–22] and wild plants [23]. Consequently, they have been studied using a variety of abundance-based sampling techniques [24–28]. Discovery of bee declines has resulted in increased monitoring, conservation action, and public awareness [29–36].

Irrespective of sample size, bee surveys often contain many species represented as singletons [37,38] and it is difficult to measure species diversity accurately when many are rare [25]. Also, as bees forage away from their nest [39–41], their presence in samples may not be indicative of habitat suitability at the sample site *per se*. For example, individual bees may be just 'passing through' the habitat under investigation as they fly between their nest and floral resources [26].

Suitable foraging habitat for bees in urban landscapes is fragmented and heterogeneous, consisting of a mix of small and large patches supporting a diverse array of flowering plant species and varieties [42–44]. These patches can support urban pollinator diversity [45,46] but perhaps unsurprisingly, bee diversity generally declines with increasing urbanization [47,48] or exhibits no significant change [49,50]. However, one group, the cavity-nesting bees, seems to have a disproportionately higher representation in urban areas (except those where impervious surfaces extend beyond 50% of land cover) [43,51]. This is presumably because suitable nest sites are

more numerous due to increased numbers of cut plant stems, woody debris, home gardening structures (i.e. holes in garden sheds or fences) [43], and nest boxes [52]. Nest boxes are inexpensive to build and easy to monitor [19]. As they sample nests directly, nest boxes can be used to assess habitat quality because they do not include taxa that are merely passing through the area [53]. They are particularly useful for sampling large numbers of sites simultaneously as they are put out before seasonal bee activity begins and taken down after it ends.

In this study we use occupancy modelling to investigate differences in populations of native and introduced cavity-nesting bees in nest boxes at sites >250m apart throughout a large city over three years. We compare results among introduced and native species because: i) introduced bees can have negative impacts on both native bees [54–57] and pollination networks [58]; ii) they are increasingly represented in surveys of wild bees [26,51,59–61]; and iii) because introduced bees have been moved from one continent to another by human activity, a greater level of synanthropic adaptation might be found among them [62,63]. Consequently, our first hypothesis is that introduced species would have greater occupancy probabilities than native species. Detected bee species diversity declines towards those areas of cities where the proportion of buildings and impervious surfaces are highest [43,44,51]. Thus, our second hypothesis was that occupancy probabilities for all bees examined would decline with increasing urbanization as determined by the proportion of building footprint surrounding a site.

## Methods

### Sampling

Nest boxes were set up at sites throughout the city of Toronto and the surrounding region each year from 2011 to 2013 inclusive (S1 Fig). Four urban green space types (“type”) were differentiated: home gardens, community gardens, urban parks, and building rooftops. Permission was granted to sample in urban parks from the Toronto and Region Conservation Authority and city of Toronto park staff. Permission was also granted from homeowners, community gardeners, and building managers to sample in home gardens, community gardens and on rooftops, respectively. Home gardens were either front- or backyards occurring on privately owned property and maintained by a homeowner. Community gardens occupied a central location: i.e. a neighbourhood park, the grounds of an apartment complex, or a power line (hydro) corridor, where groups of people garden collectively. Urban parks were sites contained within the boundaries of named parks as designated by the City of Toronto and the Toronto and Region Conservation Authority (TRCA). These are usually grassy areas with sparse tree cover but usually with planted flowerbeds around the edges or along paths [64]. Building rooftop sites were atop single buildings upon which vegetation (i.e. planters, green roofs) had been installed [65]. Green roofs are increasingly common in Toronto where they are mandatory on new buildings of certain types [66].

Each nest box was constructed from a 30 cm piece of recyclable PVC pipe of 10 cm diameter with one end fitted with a covered pipe cap, the other with an open faceplate of insulation board with 30 cardboard tubes inserted. Cardboard tubes were of three different internal diameters (10 of each of: 3.4mm, 5.5mm and 7.6mm) to accommodate bees of different sizes and were each plugged with papier-mâché at the capped end of the pipe [19]. Nest boxes were set up facing southeast and attached using zip-ties to fixed features in the landscape. These included fence posts, exposed tree limbs, or other forms of urban infrastructure so that each nest box would not move, and was above the maximum height of any immediately surrounding vegetation (>1.2m off the ground).

Each year, all nest boxes were set up in April and taken down in October. Once recovered, the cardboard tubes were opened and the contents of each recorded. Altogether samples were

**Table 1. A list of the six bee species studied and the model equation used to fit the presence-absence data for each, as collected over the three-year study period.** The nesting tube diameters used (the preferred diameter in bold) and the observed frequency from the sample across all sites are also included.

Species	Nest Diameter	Actual Site Occupancy	Model Equation
Native			
<i>Megachile campanulae</i> (Robertson)	5.5, 7.6	0.286	$\Psi(\text{site}), p(\cdot)$
<i>Megachile pugnata</i> Say	5.5, <b>7.6</b>	0.045	$\Psi(\text{foot}, \text{site}), p(\text{site})$
<i>Osmia pumila</i> Cresson	<b>3.4</b> , 5.5	0.322	$\Psi(\text{site}), p(\cdot)$
Introduced			
<i>Megachile rotundata</i> (Fabricius)	3.4, <b>5.5</b> , 7.6	0.337	$\Psi(\text{site}), p(\text{foot}, \text{site})$
<i>Megachile centuncularis</i> (Linnaeus)	5.5, <b>7.6</b>	0.176	$\Psi(\text{foot}), p(\cdot)$
<i>Osmia caerulea</i> Linnaeus	3.4, <b>5.5</b>	0.342	$\Psi(\text{site}), p(\text{foot}, \text{site})$

doi:10.1371/journal.pone.0164764.t001

taken from 199 sites. Bees were kept in cold storage (October–March) before transfer to a growth chamber where they were incubated and reared to adulthood for identification. From a total of 36 bee species found, six megachilids were selected for occupancy modelling because they were common and widespread [3] (Table 1). For each of the six species, the total number of brood cells constructed was recorded as the abundance per site, and the total number of nesting tubes colonized was also recorded from each sampling site/year. Since the differences in response to urbanization between native and introduced bees might be phylogenetically constrained, we grouped the native and introduced bees [67,68] into pairs that exhibit reciprocal monophyly. Based upon available phylogenies [69], the species pairs are as follows (native species first within each pair): *Megachile campanulae* (Robertson) + *M. rotundata* (Fab.); *M. pugnata* Say + *M. centuncularis* (L.); *Osmia pumila* Cresson + *O. caerulea* L.

## Analysis

City of Toronto spatial reference data shapefiles (RMSI, Toronto, Ontario) were examined using geospatial tools in ArcGIS v.10 (ESRI, Toronto, Canada). To determine site variables potentially impacting bee presence, the proportion of building footprint ( $\text{m}^2$ ) (hereafter referred to as ‘foot’) within a 300m radius around each site was determined. We used this radius for two reasons: i) local habitat structure has a greater impact upon bees than does landscape-scale structure [39] and ii) small to medium-sized solitary bees that use nest boxes rarely travel further than 300m from their nest [40,41]. The proportion of area covered by buildings is a good indicator of urbanization [70] and is applicable citywide across different land use types [71], consequently, building footprint was summed for all building types. This metric was extracted using the buffer and clip tools in ArcGIS within the 300m radius surrounding each site. Z-scores were calculated to standardize the building footprint values prior to statistical testing.

Presence/absence data for the six bee species were recorded from nest boxes at each site for each year and analysed using the program, PRESENCE [3]. This program permits the user to estimate the proportion of sites occupied ( $\Psi$ ) and the detection probability per site ( $p$ ) for specific taxa in relation to different site variables. To interpret  $\Psi$  from each site over the three years, each year was considered a single sample, and a single season model in PRESENCE was used to examine each species independently. Nest boxes provided data on annual detection of bee species; the bees are collected once per year after the nest box is opened, and not returned to the site from which they were collected, hence, each site/year is a closed sample in which a species is recorded as either present or absent. As a result, data for each species were collapsed into the single-season feature in PRESENCE, which is conventionally used to fit multiple

samples from a single season, rather than a multiple-season model requiring multiple samples for each season [3]. To further comply with the model assumptions, we had three consecutive samples per site, which is the minimum required to eliminate biases associated with false absences [4,5] and allow for interpretation of spatial occupancy patterns not apparent from detection or abundance data alone [1]. All possible combinations of urban green space site type ('site') and building footprint ('foot') were fit to  $\Psi$  and  $p$  parameters and each model equation was applied to the presence data for each species separately (S1 Table). The model of best fit was determined using AIC model selection [72] for each species (Table 1).

To quantify any uncertainty in our occupancy estimates and assess model convergence, Markov chain Monte Carlo (MCMC) algorithms were implemented using the Gibbs sampling program JAGS and the accompanying program rjags [73] in RStudio v0.98 [74]. For each model, we ran three chains with 10,000 iterations each for 30,000 total. We used the Gelman-Rubin convergence diagnostic to assess model convergence with potential scale reduction factor (PSRF) values approaching 1 (and no higher than 1.1) considered acceptable [75].

A Pearson's correlation test was used to determine whether  $\Psi$  estimates were correlated with species detection, species abundance or the number of nesting tubes colonized over all sampling sites/years for all four models and for each of the six species (see Fig 1). Using estimates from the model equation  $\Psi(\text{site}), p(\cdot)$ , linear regression analysis ( $\alpha = 0.05$ ) was used to compare individual species'  $\Psi$ , site abundance and the number of nesting tubes colonized against building footprint and the coefficients qualitatively compared among the six species. For each species, an analysis of variance (ANOVA) was used to test for significant differences in species'  $\Psi$  among the four urban green space types defined.

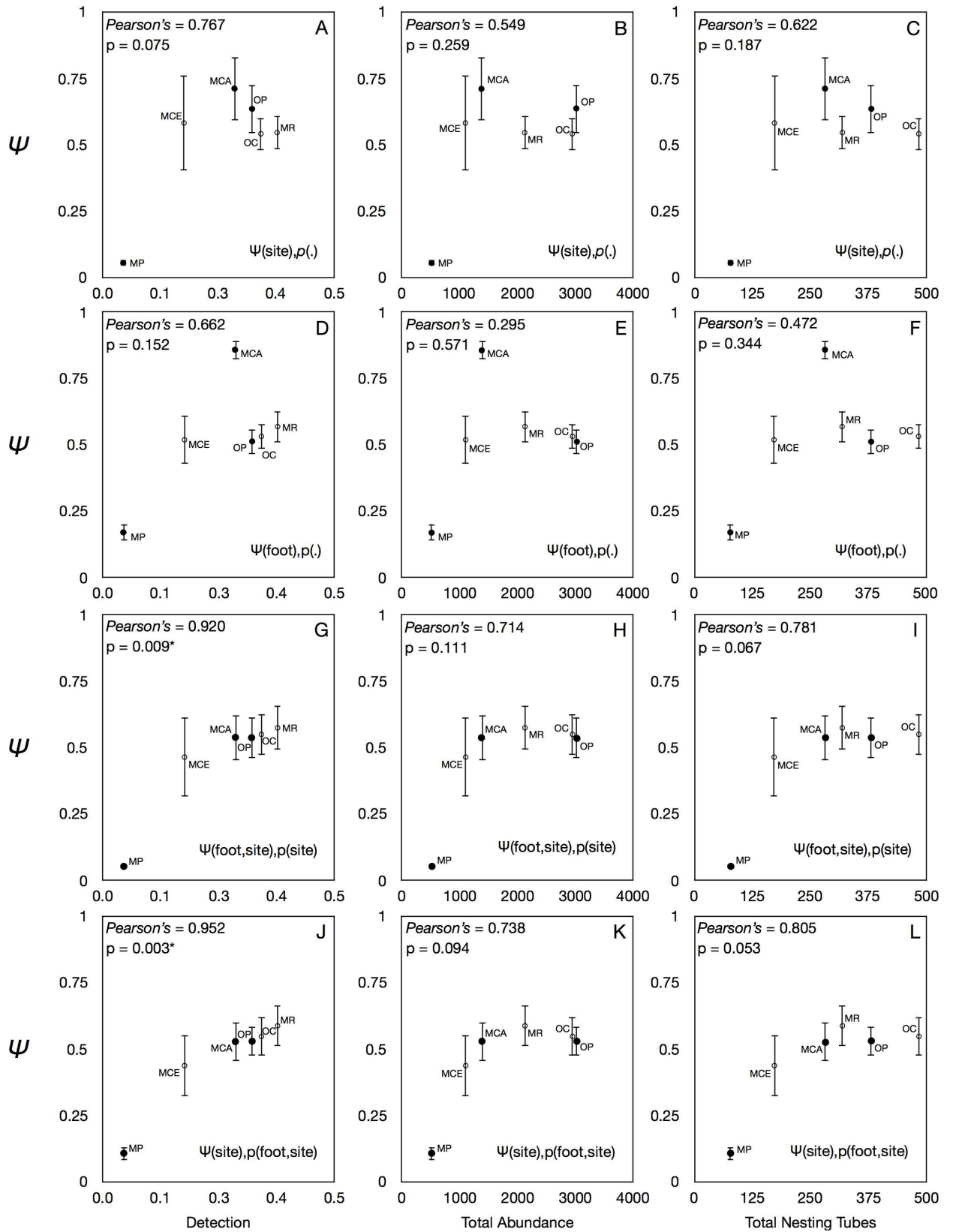
## Results

Among the six bee species examined, the ordering of species by predicted occupancy ( $\Psi$ ) differed from that based upon actual detection, total abundance, and the number of nesting tubes colonized (Fig 1). Introduced *O. caerulescens* and *M. rotundata* and the native *O. pumila* were all detected at more sites and were more abundant than *M. campanulae* (Fig 1A), even though the  $\Psi$  for *M. campanulae* was significantly greater than that of all other species except *O. pumila* (Fig 2). Variances in the model estimates of  $\Psi$  were lower for each of the introduced species than for the native ones (Fig 1).

The model equations of best fit for interpreting data as determined by AIC selection are shown in Table 1. The Gelman-Rubin convergence diagnostic tests indicated that all top models for all species converged appropriately (S1 File) as each PSRF value calculated was equal to 1. Species detection was positively correlated with occupancy in two of the four top models,  $\Psi(\text{site}), p(\text{foot}, \text{site})$  (Fig 1G) and  $\Psi(\text{foot}, \text{site}), p(\text{site})$  (Fig 1J). There was also a moderately positive relationship between occupancy and the number of nesting tubes completed (Fig 1L). Species abundance was not correlated with  $\Psi$  estimates using the models of best fit for any species or for any of the other top model equations (Fig 1).

The model equations of best fit indicated that only  $\Psi$  of the native *M. pugnata* was negatively correlated with the proportion of building footprint surrounding the nesting site within a 300m radius (S2 Table). Increasing building footprint also led to a significant decline in the detected abundance and number of nesting tubes colonized by *O. pumila* ( $F = 1.986$ ,  $p = 0.001$  and  $F = 1.841$ ,  $p = 0.003$ , respectively, S2 Table). No other significant differences were recorded for any other species, however two introduced bees (*M. rotundata* and *M. centuncularis*) and one native (*M. campanulae*) had occupancy values that increased with building footprint (S2 Table).

The type of urban green space had a significant impact on  $\Psi$  of two natives (*M. campanulae* and *O. pumila*) and one introduced bee (*O. caerulescens*) (Fig 3). Both natives had  $\Psi$  greatest



**Fig 1. Rank correlations of species detection, abundance, and number of nesting tubes colonized against occupancy estimates for all species derived from the top four model equations.** Top model equations were determined by AIC applied to each species individually (see Table 1). Plots A-C show results for  $\Psi$  estimates from model equation  $\Psi(\text{site}), p(\cdot)$ , D-F is  $\Psi(\text{foot}), p(\cdot)$ , G-I is  $\Psi(\text{site}), p(\text{foot}, \text{site})$ , J-L is  $\Psi(\text{foot}, \text{site}), p(\text{site})$ . An asterisk indicates significance at the  $\alpha = 0.05$  level. Native species are denoted with opaque circles and introduced species with open circles.

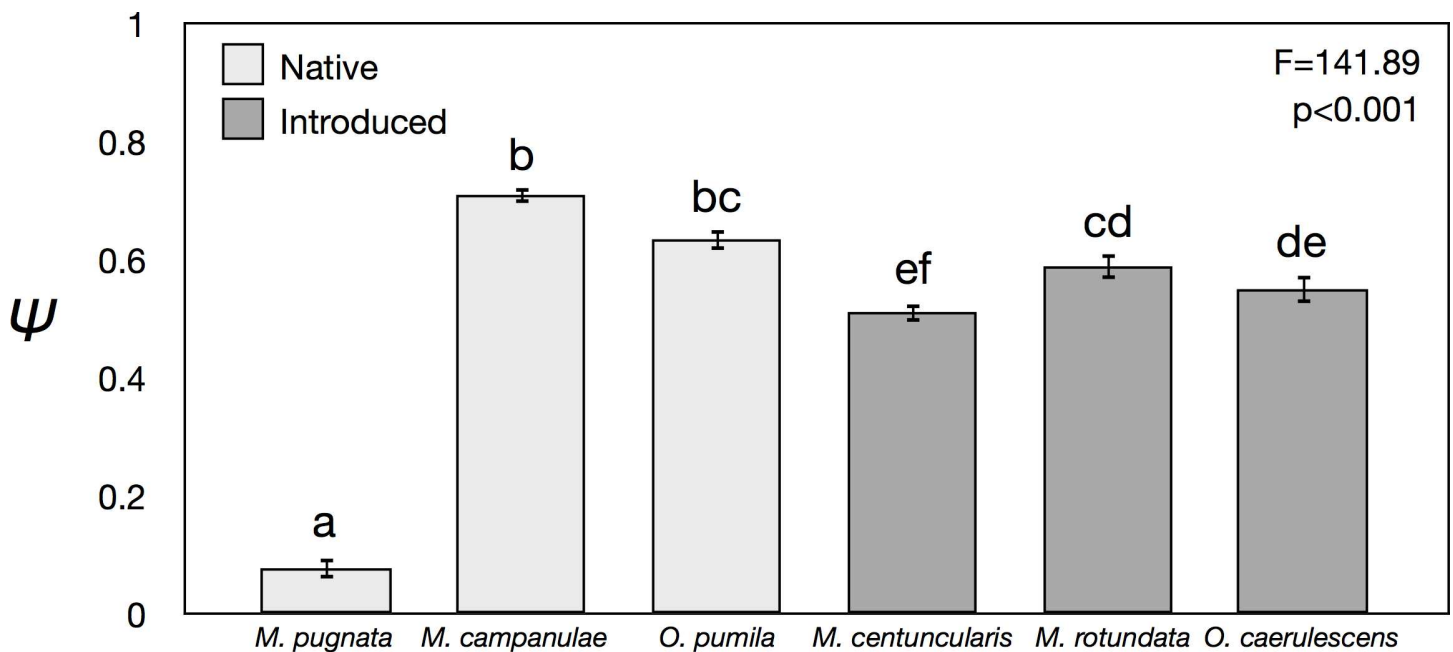
doi:10.1371/journal.pone.0164764.g001

in home gardens while *O. caerulescens* had greater  $\Psi$  in community gardens compared to roofs, but not when compared to parks or home gardens (Fig 3). Differences in  $\Psi$  among site types for introduced *M. rotundata* approached significance, with home gardens exhibiting the highest estimates.

### Discussion

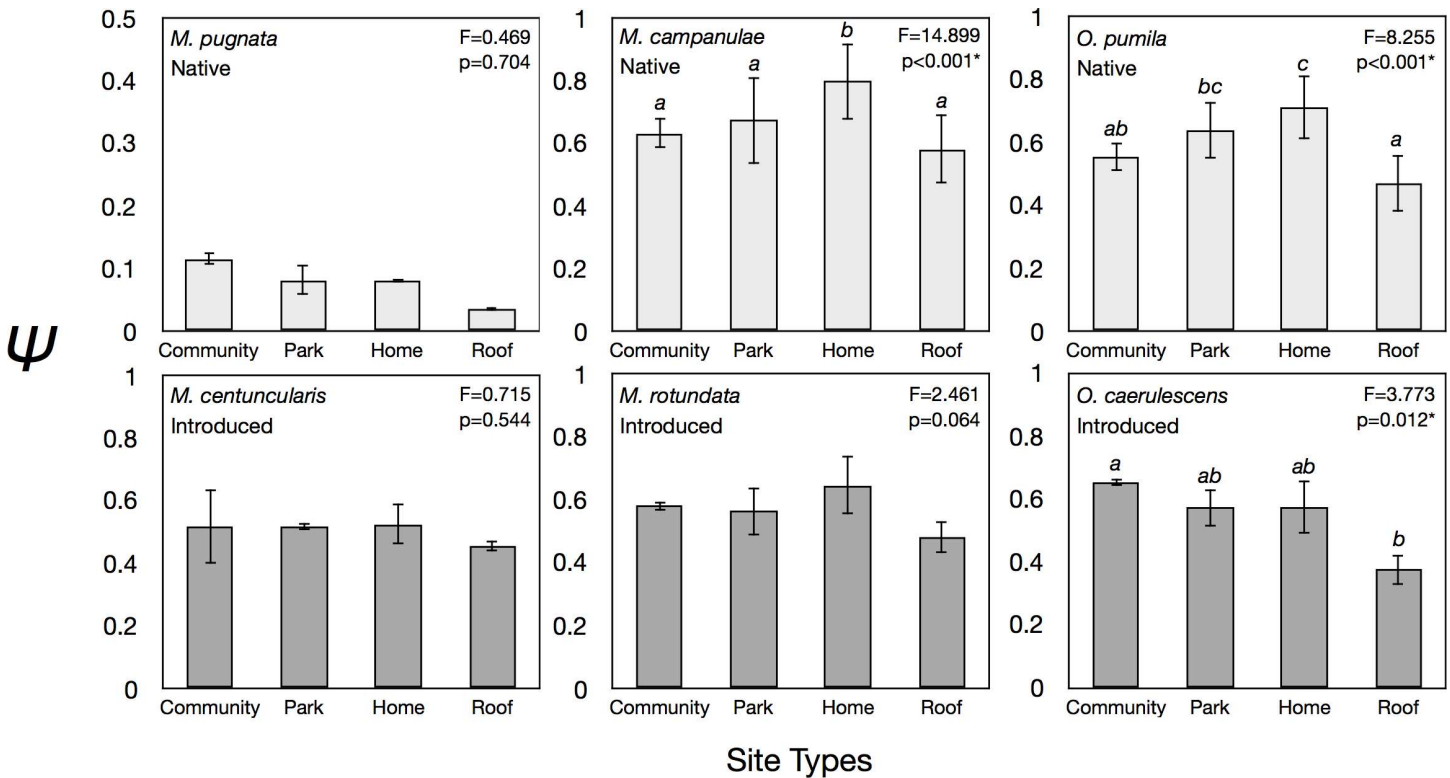
This study is the first to employ occupancy modelling as a tool to estimate patterns in bee detection and false absences. We found that estimates of occupancy probabilities provided additional details for each species that were not evident from interpretation of detection or abundance data alone (Fig 1). For example, the native *M. campanulae* had the greatest  $\Psi$  recorded among all six bees, i.e. it was predicted to be present at the most sites whether it was found in the nest boxes or not. However, *M. campanulae* ranked 4<sup>th</sup> in detection, abundance, and the number of nesting tubes colonized. This illustrates the value of the additional data provided through occupancy modelling: even though *M. campanulae* was less abundant overall, it was predicted to be the most ubiquitous when non-detection was incorporated using occupancy modelling.

Occupancy probability estimates were more variable among native bees and more consistently high among introduced species (Fig 2). However, there was no indication that introduced bees exhibited higher  $\Psi$  than native bees overall, leading to rejection of our first hypothesis: that introduced bees would have higher occupancy than native bees. The two



**Fig 2. Occupancy probability scores for each of the six species using the model equation  $\Psi(\text{site}), p(\cdot)$ .** Significant differences ( $\alpha = 0.05$ ) are indicated alphabetically. Native species in pale grey and introduced species in darker grey.

doi:10.1371/journal.pone.0164764.g002



**Fig 3. Mean occupancy probabilities of native and introduced bee species when grouped by site using the model equation  $\Psi(\text{site}), p(\cdot)$ .** Community gardens (N = 14), building rooftops (N = 20), city parks (N = 43), and home gardens (N = 72).

doi:10.1371/journal.pone.0164764.g003

native bees (*M. campanulae* and *O. pumila*) exhibited the greatest occupancy probabilities among all those tested (Fig 2) despite two introduced species (*M. rotundata* and *O. caerulescens*) having higher site detection and total abundance (Fig 1). This example provides evidence that native bees may occur more broadly in urban environments [45,49,76] than is evident from abundance-based studies that find the most common species to be introduced ones [51,77,78].

### Gradient of urbanization

Overall, increasing urbanization, as determined by surrounding building footprint, was not correlated with  $\Psi$  for five of the six bee species. Increased building density had a strong negative impact on  $\Psi$  of one native (*M. pugnata*) which declined to 0 occupancy at sites with >30% building footprint (S1 File). Moreover, although the native *O. pumila* was the most abundant species and had high  $\Psi$  indicating it is widespread, its occupancy estimates declined with increasing building footprint. Nonetheless, based upon our data *in toto*, we reject the second hypothesis that  $\Psi$  by native species would decline more with building footprint than that of introduced bees.

Other studies of urban bee communities have found high bee diversity in areas of low to medium urbanization [50,79] and fewer species in the dense urban core [80] where the proportion of impervious surface is highest [81]. However, occupancy of three bee species, the native *M. campanulae* and the introduced *M. rotundata* and *M. centuncularis*, increased with building footprint.



## Urban green space type

Occupancy probabilities for native *M. campanulae* and *O. pumila* were significantly greater in home gardens compared to other urban green space types surveyed (except for no difference between home gardens and parks for *O. pumila*) (Fig 3). *Megachile campanulae* uses resins for nesting materials, obtaining them from a variety of trees including white pine [82], which are widely planted in home landscapes and other nearby urban green spaces. *Osmia pumila* also has its nesting material requirements (mud and masticated leaves) [83] widely distributed among our urban study sites. Our data support the view that home gardens are suitable for many native bees and may be critical in maintaining wild bee populations in urban landscapes [84,85].

Among introduced bees, *O. caerulea* had  $\Psi$  that was higher in community gardens than elsewhere (Fig 3). Not surprisingly, community gardens have also been identified as hotspots for urban bee activity [86,87], as well as pollination services [88]. Occupancy probabilities for the other two introduced bees, *M. rotundata* and *M. centuncularis*, did not differ among site types, indicative of their flexibility to persist in a wide variety of urban green spaces, including vegetated rooftops. Although introduced bees can be effective pollinators of cultivated crops [89–91], they disproportionately visit introduced flowers and this could facilitate the outcompetition of native plants [92,93]. Nest boxes can contribute to the monitoring of introduced species that left unchecked could outcompete native bees with negative consequences for plant communities and pollination networks [19,59].

## Conclusion

This study illustrates the importance of including  $\Psi$  as a variable in biodiversity survey work: it yielded patterns that were biologically meaningful and different from those based upon detection and abundance data alone (Fig 1). Inclusion of environmental variables in more complex occupancy models could improve the precision of resulting estimates and provide a deeper explanation of patterns that increase the accuracy of monitoring or management of introduced species [94]. For example, the combination of nest box sampling with occupancy modelling will allow us to predict where introduced species exist but were not found during sampling. This may be particularly useful for determining areas of occupancy of aggressively spreading introduced species, such as *Megachile sculpturalis* [95,96].

Our data indicate that different bee species, even within the same nesting guild, thrive best in different urban green space types. This suggests that complementary and collaborative planning of such space could be specifically designed to foster native species. More research is required on the impacts of different management plans and conservation actions to ensure that ‘scaled up’ urban habitat alteration has positive outcomes [97,98]. We have found that occupancy modelling provides additional details that are not discovered with detection and abundance-based sampling and conclude that this approach should be incorporated into urban habitat management planning.

## Supporting Information

**S1 Fig. A map of the study area identifying the location of each site sampled.** The type of urban green space is identified in the figure legend.  
(PDF)

**S1 File. Occupancy estimates and standard error for the top four models for each species and site.**

As well as the proportion of impervious surface surrounding each site and the urban green space type (community gardens = 1, green roofs = 2, urban parks = 3, home gardens = 4). (XLSX)

**S1 Table. Summary of model selection processes for each of the six bee species using Akaike's Information Criterion (AIC).**  $\Psi$  denotes the probability of a bee occupying a site when not detected, and  $p$  denotes the probability of being detected using a nest box when present at the site. The terms in parentheses indicate what factors are affecting each probability with a '.' indicating the probability is constant across all states.  $\Delta$ AIC is the relative difference in AIC values,  $w$  is the AIC model weight,  $-2l$  is twice the negative log-likelihood and  $K$  is the number of parameters in the model. For all models the same structure was maintained for the detection-related component of the model.

(DOCX)

**S2 Table. Statistical output from comparisons of occupancy probability per bee and the proportion of building footprint within a 300m radius around each site.** Significant differences calculated using the Z-score of building footprint. Asterisk indicates significant difference within species.

(DOCX)

## Acknowledgments

We thank the participants of the study that permitted access to their properties to monitor nest boxes and the bees therein. Thanks to Dr. Alana Pindar, three anonymous reviewers and the editor for comments on the manuscript. As well, to Baharak Salehi, Jen Albert, Jennifer Cabral, Veronica Ladico, and Armando Ponte for help organizing, sorting, and rearing nest box contents and to the PCYU team for discussion. The first author was funded by a scholarship awarded by the Natural Sciences and Engineering Research Council of Canada (CGS D 408565) and both were supported by an NSERC discovery grant awarded to the second author.

## Author Contributions

**Conceptualization:** JSM LP.

**Data curation:** JSM.

**Formal analysis:** JSM.

**Funding acquisition:** JSM LP.

**Investigation:** JSM.

**Methodology:** JSM.

**Project administration:** JSM LP.

**Resources:** LP.

**Software:** JSM.

**Supervision:** LP.

**Validation:** JSM.

**Visualization:** JSM.

**Writing – original draft:** JSM LP.

**Writing – review & editing:** JSM LP.

## References

1. MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, Langtimm CA. Estimating site occupancy rates when detection probabilities are less than one. *Ecology*. 2002; 83: 2248–2255.
2. Bailey LL, Simons TR, Pollock KH. Estimating site occupancy and species detection probability parameters for terrestrial salamanders. *Ecological Applications*. 2004; 14: 692–702.
3. MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE. *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Massachusetts: Academic Press; 2006.
4. MacKenzie DI, Royle JA. Designing occupancy studies: General advice and allocating survey effort. *Journal of Applied Ecology*. 2005; 42: 1105–1114.
5. Tyre AJ, Tenhumberg B, Field SA, Niejalke D, Parris K, Possingham HP. Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications*. 2003; 13: 1790–1801.
6. Field SA, Tyre AJ, Possingham HP. Optimizing allocation of monitoring effort under economic and observational constraints. *Journal of Wildlife Management*. 2005; 69: 473–482.
7. Lobo JM, Jiménez-Valverde A, Hortal J. The uncertain nature of absences and their importance in species distribution modelling. *Ecography*. 2010; 33: 103–114.
8. Tanadini LG, Schmidt BR. Population size influences amphibian detection probability: Implications for biodiversity monitoring programs. *PLoS One*. 2011; 6: e28244. doi: [10.1371/journal.pone.0028244](https://doi.org/10.1371/journal.pone.0028244) PMID: [22164250](https://pubmed.ncbi.nlm.nih.gov/22164250/)
9. Welsh AH, Lindenmayer DB, Donnelly CF. Fitting and interpreting occupancy models. *PLoS One*. 2013; 8: e52015. doi: [10.1371/journal.pone.0052015](https://doi.org/10.1371/journal.pone.0052015) PMID: [23326323](https://pubmed.ncbi.nlm.nih.gov/23326323/)
10. Pollock KH, Nichols JD, Simons TR, Farnsworth GL, Bailey LL, Sauer JR. Large scale wildlife monitoring studies: Statistical methods for design and analysis. *Environmetrics*. 2002; 13: 105–119.
11. Guillera-Aroita G, Ridout MS, Morgan BJ. Design of occupancy studies with imperfect detection. *Methods in Ecology and Evolution*. 2010; 1: 131–139.
12. Olea PP, Mateo-Tomás P. Spatially explicit estimation of occupancy, detection probability and survey effort needed to inform conservation planning. *Diversity and Distributions*. 2011; 17: 714–724.
13. Gu W, Swihart RK. Absent or undetected? Effects of non-detection of species occurrence on wildlife-habitat models. *Biological Conservation*. 2004; 116: 195–203.
14. MacKenzie DI, Nichols JD, Seamans ME, Gutiérrez RJ. Modeling species occurrence dynamics with multiple states and imperfect detection. *Ecology*. 2009; 90: 823–835. PMID: [19341151](https://pubmed.ncbi.nlm.nih.gov/19341151/)
15. Bradford DF, Neale AC, Nash MS, Sada DW, Jaeger JR. Habitat patch occupancy by toads (*Bufo punctatus*) in a naturally fragmented desert landscape. *Ecology*. 2003; 84: 1012–1023.
16. Kawanishi K, Sunquist ME. Conservation status of tigers in a primary rainforest of peninsular Malaysia. *Biological Conservation*. 2004; 120: 329–344.
17. Studds CE, Marra PP. Nonbreeding habitat occupancy and population processes: an upgrade experiment with a migratory bird. *Ecology*. 2005; 86: 2380–2385.
18. Guillera-Aroita G, Lahoz-Monfort JJ, MacKenzie DI, Wintle BA, McCarthy MA. Ignoring imperfect detection in biological surveys is dangerous: a response to ‘Fitting and interpreting occupancy models’. *PLoS One*. 2014; 9: e99571. doi: [10.1371/journal.pone.0099571](https://doi.org/10.1371/journal.pone.0099571) PMID: [25075615](https://pubmed.ncbi.nlm.nih.gov/25075615/)
19. MacIvor JS, Packer L. ‘Bee hotels’ as tools for native pollinator conservation: A premature verdict? *PLoS One*. 2015; 10: e0122126. doi: [10.1371/journal.pone.0122126](https://doi.org/10.1371/journal.pone.0122126) PMID: [25785609](https://pubmed.ncbi.nlm.nih.gov/25785609/)
20. Klein AM, Vaissiere BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, et al. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society B: Biological Science*. 2007; 274: 303–313.
21. Kennedy CM, Lonsdorf E, Neel MC, Williams NM, Ricketts TH, Winfree R, et al. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology Letters*. 2013; 16: 584–599. doi: [10.1111/ele.12082](https://doi.org/10.1111/ele.12082) PMID: [23489285](https://pubmed.ncbi.nlm.nih.gov/23489285/)
22. Klatt BK, Holzschuh A, Westphal C, Clough Y, Smit I, Pawelzik E, et al. Bee pollination improves crop quality, shelf life and commercial value. *Proceedings of the Royal Society B: Biological Sciences*. 2014; 281: 20132440. doi: [10.1098/rspb.2013.2440](https://doi.org/10.1098/rspb.2013.2440) PMID: [24307669](https://pubmed.ncbi.nlm.nih.gov/24307669/)

23. Ollerton J, Winfree R, Tarrant S. How many flowering plants are pollinated by animals? *Oikos*. 2011; 120: 321–326.
24. Frankie GW, Thorp RW, Newstrom-Lloyd LE, Rizzardi MA, Barthell JF, Griswold TL, et al. Monitoring solitary bees in modified wildland habitats: implications for bee ecology and conservation. *Environmental Entomology*. 1998; 27: 1137–1148.
25. Williams NM, Minckley RL, Silveira FA. Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology*. 2001; 5: 1–7.
26. Grixti JC, Packer L. Changes in the bee fauna (Hymenoptera: Apoidea) of an old field site in southern Ontario, revisited after 34 years. *Canadian Entomologist*. 2006; 138: 147–164.
27. Westphal C, Bommarco R, Carré G, Lamborn E, Morison N, Petanidou T, et al. Measuring bee diversity in different European habitats and biogeographical regions. *Ecological Monographs*. 2008; 78: 653–671.
28. Leonhardt SD, Gallai N, Garibaldi LA, Kuhlmann M, Klein AM. Economic gain, stability of pollination and bee diversity decrease from southern to northern Europe. *Basic and Applied Ecology*. 2013; 14: 461–471.
29. Kearns CA, Inouye DW, Waser NM. Endangered mutualisms: the conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics*. 1998; 29: 83–112.
30. Biesmeijer JC, Roberts SPM, Reemer M, Ohlemüller R, Edwards M, Peeters T, et al. Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*. 2006; 313: 351–354. doi: [10.1126/science.1127863](https://doi.org/10.1126/science.1127863) PMID: [16857940](https://pubmed.ncbi.nlm.nih.gov/16857940/)
31. Colla SR, Packer L. Evidence for decline in eastern North American bumblebees (Hymenoptera: Apidae), with special focus on *Bombus affinis* Cresson. *Biodiversity and Conservation*. 2008; 17: 1379–1391.
32. Osborne JL, Martin AP, Shortall CR, Todd AD, Goulson D, Knight ME, et al. (2008) Quantifying and comparing bumblebee nest densities in gardens and countryside habitats. *Journal of Applied Ecology*. 2008; 45: 784–792.
33. Byrne A, Fitzpatrick Ú. Bee conservation policy at the global, regional and national levels. *Apidologie*. 2009; 40: 194–210.
34. Williams NM, Crone EE, Minckley RL, Packer L, Potts SG. Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*. 2010; 143: 2280–2291.
35. Garbuzov M, Ratnieks FL. Listmania: the strengths and weaknesses of lists of garden plants to help pollinators. *BioScience*. 2014; 64: 1019–1026.
36. Kerr JT, Pindar A, Galpern P, Packer L, Potts SG, Roberts SM, et al. Climate change impacts on bumblebees converge across continents. *Science*. 2015; 349: 177–180. doi: [10.1126/science.aaa7031](https://doi.org/10.1126/science.aaa7031) PMID: [26160945](https://pubmed.ncbi.nlm.nih.gov/26160945/)
37. Oertli S, Müller A, Dorn S. Ecological and seasonal patterns in the diversity of a species-rich bee assemblage (Hymenoptera: Apoidea: Apiformes). *European Journal of Entomology*. 2005; 102: 53–63.
38. Sheffield CS, Pindar A, Packer L, Kevan PG. The potential of cleptoparasitic bees as indicator taxa for assessing bee communities. *Apidologie*. 2013; 44: 501–510.
39. Gathmann A, Tschamtko T. Foraging ranges of solitary bees. *Journal of Animal Ecology*. 2002; 71: 757–764.
40. Greenleaf SS, Williams NM, Winfree R, Kremen C. Bee foraging ranges and their relationship to body size. *Oecologia*. 2007; 153: 589–596. doi: [10.1007/s00442-007-0752-9](https://doi.org/10.1007/s00442-007-0752-9) PMID: [17483965](https://pubmed.ncbi.nlm.nih.gov/17483965/)
41. Zurbuchen A, Landert L, Klaiber J, Müller A, Hein S, Dorn S. Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*. 2010; 143: 669–676.
42. Gibb H, Hochuli DF. Habitat fragmentation in an urban environment: large and small fragments support different arthropod assemblages. *Biological Conservation*. 2002; 106: 91–100.
43. Cane JH, Minckley RL, Kervin LJ, Roulston TAH, Williams NM. Complex responses within a desert bee guild (Hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications*. 2006; 16: 632–644. PMID: [16711050](https://pubmed.ncbi.nlm.nih.gov/16711050/)
44. Matteson KC, Langellotto GA. Determinates of inner city butterfly and bee species richness. *Urban Ecosystems*. 2010; 13: 333–347.
45. Lowenstein DM, Matteson KC, Xiao I, Silva AM, Minor ES. Humans, bees, and pollination services in the city: the case of Chicago, IL (USA). *Biodiversity and Conservation*. 2014; 23: 2857–2874.
46. Salisbury A, Armitage J, Bostock H, Perry J, Tatchell M, Thompson K. Enhancing gardens as habitats for flower-visiting aerial insects (pollinators): should we plant native or exotic species?. *Journal of Applied Ecology*. 2015; 52: 1156–1164.

47. McFrederick QS, LeBuhn G. Are urban parks refuges for bumble bees *Bombus* spp. (Hymenoptera: Apidae)? *Biological Conservation*. 2006; 129: 372–382.
48. Hernandez JL, Frankie GW, Thorp RW. Ecology of urban bees: a review of current knowledge and directions for future study. *Cities and the Environment*. 2009; 2: <http://digitalcommons.lmu.edu/cate/vol2/iss1/3/>.
49. Fortel L, Henry M, Guilbaud L, Guirao AL, Kuhlmann M, Mouret H, et al. Decreasing abundance, increasing diversity and changing structure of the wild bee community (Hymenoptera: Anthophila) along an urbanization gradient. *PLoS One*. 2014; 9: e104679. doi: [10.1371/journal.pone.0104679](https://doi.org/10.1371/journal.pone.0104679) PMID: [25118722](https://pubmed.ncbi.nlm.nih.gov/25118722/)
50. Baldock KC, Goddard MA, Hicks DM, Kunin WE, Mitchunas N, Osgathorpe LM, et al. Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society of London B: Biological Sciences*. 2015; 282: 20142849.
51. Matteson KC, Ascher JS, Langellotto GA. Bee richness and abundance in New York City urban gardens. *Annals of the Entomological Society of America*. 2008; 101: 140–150.
52. MacIvor JS. Cavity-nest boxes for solitary bees: a century of design and research. *Apidologie*. doi: [10.1007/s13592-016-0477-z](https://doi.org/10.1007/s13592-016-0477-z)
53. Tschamtko T, Gathmann A, Steffan-Dewenter I. Bioindication using trap-nesting bees and wasps and their natural enemies: community structure and interactions. *Journal of Applied Ecology*. 1998; 35: 708–719.
54. Goulson D. Effects of introduced bees on native ecosystems. *Annual Review of Ecology, Evolution, and Systematics*. 2003; 34: 1–26.
55. Madjidian JA, Morales CL, Smith HG. Displacement of a native by an alien bumblebee: lower pollinator efficiency overcome by overwhelmingly higher visitation frequency. *Oecologia*. 2008; 156: 835–845. doi: [10.1007/s00442-008-1039-5](https://doi.org/10.1007/s00442-008-1039-5) PMID: [18443825](https://pubmed.ncbi.nlm.nih.gov/18443825/)
56. Hudewenz A, Klein AM. Competition between honey bees and wild bees and the role of nesting resources in a nature reserve. *Journal of Insect Conservation*. 2013; 17: 1275–1283.
57. Morales CL, Arbetman MP, Cameron SA, Aizen MA. Rapid ecological replacement of a native bumble bee by invasive species. *Frontiers in Ecology and the Environment*. 2013; 11: 529–534.
58. Aizen MA, Morales CL, Morales JM. Invasive mutualists erode native pollination webs. *PloS Biology*. 2008; 6: e31. doi: [10.1371/journal.pbio.0060031](https://doi.org/10.1371/journal.pbio.0060031) PMID: [18271628](https://pubmed.ncbi.nlm.nih.gov/18271628/)
59. Barthell JF, Frankie GW, Thorp RW. Invader effects in a community of cavity nesting megachilid bees (Hymenoptera: Megachilidae). *Environmental Entomology*. 1998; 27: 240–247.
60. Bartomeus I, Ascher JS, Gibbs J, Danforth BN, Wagner DL, Hedtke SM, et al. Historical changes in northeastern US bee pollinators related to shared ecological traits. *Proceedings of the National Academy of Science*. 2013; 110: 4656–4660.
61. MacIvor JS, Ruttan A, Salehi B. Exotics on exotics: pollen analysis of urban bees visiting *Sedum* on a green roof. *Urban Ecosystems*. 2014; 18: 419–430.
62. Lizée MH, Mauffrey JF, Tatoni T, Deschamps-Cottin M. Monitoring urban environments on the basis of biological traits. *Ecological Indicators*. 2011; 11: 353–361.
63. Francis RA, Chadwick MA. What makes a species synurbic? *Applied Geography*. 2012; 32: 514–521.
64. Gilbert OL. *The Ecology of Urban Habitats*. New York City; Chapman and Hall: 1989.
65. Dunnett N, Kingsbury N. *Planting green roofs and living walls: 2<sup>nd</sup> edition*. Portland: Timber Press; 2010.
66. Torrance S, Bass B, MacIvor JS, McGlade T. 2013. City of Toronto guidelines for biodiverse green roofs. Toronto: City of Toronto; 2013. Available: [https://www1.toronto.ca/staticfiles/City%20of%20Toronto/City%20Planning/Zoning%20&%20Environment/Files/pdf/B/biodiversegreenroofs\\_2013.pdf](https://www1.toronto.ca/staticfiles/City%20of%20Toronto/City%20Planning/Zoning%20&%20Environment/Files/pdf/B/biodiversegreenroofs_2013.pdf).
67. Cane JH. Exotic nonsocial bees (Hymenoptera: Apiformes) in North America: ecological implications. In Strickler K., and Cane J. (eds.). *For nonnative crops, whence pollinators for the future?* Lanham, Maryland: Thomas Say Foundation, Entomological Society of America; 2003.
68. Giles V, Ascher JS. A survey of the bees of the Black Rock Forest Preserve, New York. *Journal of Hymenoptera Research*. 2006; 15: 208–231.
69. Gonzalez VH. Phylogeny and classification of the bee tribe Megachilini (Hymenoptera: Apoidea, Megachilidae), with emphasis on the genus *Megachile*. Ph.D. Dissertation, Lawrence, Kansas: University of Kansas; 2008.
70. Whitney GG. A quantitative analysis of the flora and plant communities of a representative midwestern US town. *Urban Ecology*. 1985; 9: 143–160.

71. Davies RG, Barbosa O, Fuller RA, Tratalos J, Burke N, Lewis D, et al. City-wide relationships between green spaces, urban land use and topography. *Urban Ecosystems*. 2008; 11: 269–287.
72. Burnham KP, Anderson DR. Multimodel inference understanding AIC and BIC in model selection. *Sociological Methods & Research*. 2004; 33: 261–304.
73. Plummer, M. (2013). *rjags: Bayesian graphical models using MCMC*. R package version, 3.
74. R Core Team. R: A language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; 2013. ISBN 3-900051-07-0. Available: <http://www.R-project.org/>
75. Gelman A., & Rubin D. B. (1992). Inference from iterative simulation using multiple sequences. *Statistical science*, 457–472.
76. Banaszak-Cibicka W, Zmihorski M. Wild bees along an urban gradient: winners and losers. *Journal of Insect Conservation*. 2012; 16: 331–343.
77. Blair RB. Land use and avian species diversity along an urban gradient. *Ecological Applications*. 1996; 6: 506–519.
78. Suarez AV, Bolger DT, Case TJ. Effects of fragmentation and invasion on native ant communities in coastal southern California. *Ecology*. 1998; 79: 2041–2056.
79. Fetridge ED, Ascher JS, Langellotto GA. The bee fauna of residential gardens in a suburb of New York City (Hymenoptera: Apoidea). *Annals of the Entomological Society of America*. 2008; 101: 1067–1077.
80. Hostetler NE, McIntyre ME. Effects of urban land use on pollinator (Hymenoptera: Apoidea) communities in a desert metropolis. *Basic and Applied Ecology*. 2001; 2: 209–218.
81. McDonnell MJ, Pickett ST, Groffman P, Bohlen P, Pouyat RV, Zipperer WC, et al. Ecosystem processes along an urban-to-rural gradient. *Urban Ecosystems*. 1997; 1: 21–36.
82. Maclvor JS, Salehi B. Bee species-specific nesting material attracts a generalist parasitoid: implications for co-occurring bees in nest box enhancements. *Environmental Entomology*. 2014; 43: 1027–1033. doi: [10.1603/EN13241](https://doi.org/10.1603/EN13241) PMID: [24959997](https://pubmed.ncbi.nlm.nih.gov/24959997/)
83. Goodell K. Food availability affects *Osmia pumila* (Hymenoptera: Megachilidae) foraging, reproduction, and brood parasitism. *Oecologia*. 2003; 134: 518–527. doi: [10.1007/s00442-002-1159-2](https://doi.org/10.1007/s00442-002-1159-2) PMID: [12647124](https://pubmed.ncbi.nlm.nih.gov/12647124/)
84. Frankie G, Thorp RW, Hernandez J, Rizzardi M, Ertter B, Pawelek JC, et al. Native bees are a rich natural resource in urban California gardens. *California Agriculture*. 2009; 63: 113–120.
85. Pardee GL, Philpott SM. Native plants are the bee's knees: local and landscape predictors of bee richness and abundance in backyard gardens. *Urban Ecosystems*. 2014; 17: 641–659.
86. Matteson KC, Langellotto GA. Bumble bee abundance in New York City community gardens: implications for urban agriculture. *Cities and the Environment*. 2009; 2: <http://digitalcommons.lmu.edu/cate/vol2/iss1/5/>.
87. Ahm k K, Bengtsson J, Elmqvist T. Bumble bees (*Bombus* spp) along a gradient of increasing urbanization. *PLoS One*. 2009; 4: e5574. doi: [10.1371/journal.pone.0005574](https://doi.org/10.1371/journal.pone.0005574) PMID: [19440367](https://pubmed.ncbi.nlm.nih.gov/19440367/)
88. Potter A, LeBuhn G. Pollination service to urban agriculture in San Francisco, CA. *Urban Ecosystems*. 2015; 18: 885–893.
89. Bohart GE. Management of wild bees for the pollination of crops. *Annual Review of Entomology*. 1972; 17: 287–312.
90. Stephen WP. Solitary bees in North American agriculture: a perspective. In Strickler K., and Cane J.H. (Eds). *For nonnative crops, whence pollinators of the future?* Lanham, MD; Thomas Say Publications: 2003.
91. Pitts-Singer TL, Cane JH. The alfalfa leafcutting bee, *Megachile rotundata*: the world's most intensively managed solitary bee. *Annual Review of Entomology*. 2011; 56: 221–237. doi: [10.1146/annurev-ento-120709-144836](https://doi.org/10.1146/annurev-ento-120709-144836) PMID: [20809804](https://pubmed.ncbi.nlm.nih.gov/20809804/)
92. Morales CL, Aizen MA. Does invasion of exotic plants promote invasion of exotic flower visitors? A case study from the temperate forests of the southern Andes. *Biological Invasions*. 2002; 4: 87–100.
93. Stout JC, Kells AR, Goulson D. Pollination of the invasive exotic shrub *Lupinus arboreus* (Fabaceae) by introduced bees in Tasmania. *Biological Conservation*. 2002; 106: 425–434.
94. Jim nez-Valverde A, Peterson AT, Sober n J, Overton JM, Arag n P, Lobo JM. Use of niche models in invasive species risk assessments. *Biological Invasions*. 2011; 13: 2785–2797.
95. Mangum WA, Sumner S. A survey of the North American range of *Megachile* (Callomegachile) *sculpturalis*, an adventive species in North America. *Journal of the Kansas Entomological Society*. 2003; 76: 658–662.

96. Roulston TA, Malfi R. Aggressive eviction of the eastern carpenter bee (*Xylocopa virginica* (Linnaeus)) from its nest by the giant resin bee (*Megachile sculpturalis* Smith). *Journal of the Kansas Entomological Society*. 2012; 85: 387–388.
97. Goddard MA, Dougill AJ, Benton TG. Scaling up from gardens: biodiversity conservation in urban environments. *Trends in Ecology and Evolution*. 2010; 25: 90–98. doi: [10.1016/j.tree.2009.07.016](https://doi.org/10.1016/j.tree.2009.07.016) PMID: [19758724](https://pubmed.ncbi.nlm.nih.gov/19758724/)
98. Colding J. 'Ecological land-use complementation' for building resilience in urban ecosystems. *Landscape and Urban Planning*. 2007; 81: 46–55.