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Building height matters: nesting activity of bees and wasps on vegetated roofs

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Vegetated, “green” infrastructure, including terraces, balconies, and vegetated roofs and walls are increasingly common in urban landscapes, elevating habitat into novel contexts above ground. Highly mobile species, like bees and wasps, are often seen foraging on green infrastructure, but whether nesting opportunities are facilitated is not known. Cavity-nesting bees and wasps that provision brood in human-made trap nests were monitored over three years on 29 vegetated and non-vegetated roofs in Toronto, Canada. The study identified 27 species nesting on rooftops but found that building height was negatively correlated with the abundance of brood cells provisioned in trap nests, and positively correlated with the number of unfinished nests. A decline in green space area within a 600 m radius around each rooftop resulted in decreasing species richness and abundance. Although the introduced bee, *Megachile rotundata* (Fabricius) occupied more sites than any other bee or wasp (27.6%) and was the most abundant species, amounting to half (48.9%) of all brood reared, native bees were 73% of all bee species reared. The most abundant wasp was the native spider-collecting *Trypoxylon collinum* Smith (11.4%), but the introduced aphid-collecting *Psenulus pallipes* (Panzer) occurred at more sites (24.1%). For the pollination and pest controlling services they provide, bees and wasps should be considered in the design of vegetated roofs. Evidence here suggests that building height and surrounding green space at ground level impact bee and wasp diversity on vegetated roofs. Efforts supporting their populations using trap nests should target low- and mid-rise buildings (<5 building levels).

Keywords: urban; biodiversity; green roofs; cavity-nesting; trap nest; *Megachile*

Introduction

Studies investigating local and landscape impacts on insect populations are increasingly carried out in and around cities (Blair 1999; Hostetler & McIntyre 2001; Cane et al. 2006; Matteson et al. 2008; Sattler et al. 2010; Bates et al. 2012; Banaszak-Cibicka & Żmihorski 2012; Geslin et al. 2013; Braaker et al. 2014). City landscapes are usually more strongly three-dimensional and complex than surrounding natural landscapes (Allen 1998). In many cases, city buildings create even more complexity than that on cliff faces or other mountainous habitat (Larson et al. 2004). Studying how taxa interact with this complex environment may provide new insight into their ecology and conservation (Dearborn & Kark 2010).

Green infrastructure elevated above ground in three-dimensional space (including vegetated roof and walls, gardened terraces, balconies, and garages) increases green space vertically where space at ground is developed, providing new urban habitat opportunities (Pickett et al. 2013). The contribution of vegetated roofs is perhaps the best studied among them, with some suggesting they could aid in the conservation of rare species, or increase connectivity among fragmented habitat patches (reviewed in Williams et al. 2014). However, vegetated roofs like some ground level habitat might act as dispersal platforms for exotic or undesirable species that undermine native biodiversity conservation. It is important to consider habitat conditions in the design of green infrastructure to

facilitate – as well as study – both positive and negative novel responses of biodiversity to urban and environmental changes (McIntyre 2000; Felson & Pickett 2005; Goddard et al. 2010).

Many species in a wide range of taxonomic groups have been identified from surveys on vegetated roofs (e.g. Jones 2002; Millet 2004; Kadas 2006; Pearce & Walters 2012; Madre et al. 2013, MacIvor, Ruttan, & Salehi 2015; reviewed in MacIvor & Ksiazek 2015); however, adjacent or nearby ground level reference habitat yields higher diversity (Colla et al. 2009; MacIvor & Lundholm 2011; Tonietto et al. 2011). There is some quantitative data on the reproductive success of birds (Baumann 2006) but there is little data on whether vegetated roofs can act as a source or sink for species seeking nesting habitat (MacIvor & Ksiazek 2015). Cavity-nesting bees and wasps in particular may benefit from vegetated roofs as nesting habitat, as they regularly use cracks, crevices, nail- and drill holes in human-made infrastructure, and other cavities as nesting habitat in place of natural ones in wood and plant stems (Krombein 1967; Cane et al. 2007; MacIvor, Cabral, & Packer 2014). These include those that are accidentally or intentionally added to vegetated roofs and other forms of green infrastructure. Pollination by bees and predation on pest insects by solitary wasps are desirable ecosystem functions carried out by cavity-nesting species that should be encouraged in both natural and human-dominated landscapes

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(Tschamtko et al. 1998). However, it is not clear which, if any species of cavity-nesting bees and wasps will search for nesting habitat on roofs of buildings, especially when situated dozens of meters above ground.

Nest site locating behaviors of cavity-nesting bees and wasps often involve vertical movement as the insects search for holes in dead wood in trees (Wcislo 1996). Thus, cavity-nesting bees and wasps might have some pre-adapted traits for searching for nest sites at the heights of vegetated roofs. The use of trap nests (Krombein 1967) can provide such suitable nesting sites and many cavity-nesting species readily adopt them (Tschamtko et al. 1998). Trap nests have been used in many ecological and conservation studies (Gathmann et al. 1994; Steffan-Dewenter et al. 2002; Tylianakis et al. 2006; Praz et al. 2008; MacIvor, Cabral, & Packer 2014) and they have been shown to reflect overall bee diversity (Westphal et al. 2008). However, few studies have used trap nests to survey cavity-nesting bees and wasps in urban landscapes (Alves-dos-Santos, 2003; Gaston et al. 2005; Loyola & Martins 2006; Everaars et al. 2011; Pereira-Peixoto et al. 2014; MacIvor & Packer 2015).

In this study I assess the impact of building height, number of buildings, and the proportion of local ground level green space upon the species richness and abundance of bees and wasps colonizing trap nests. Horizontal landscape isolation from florally diverse habitats has been

correlated with reduced observations of wild bees on flowers (Jauker et al. 2009; Garibaldi et al. 2011). Moreover, increasing horizontal distance from floral resources has resulted in fewer offspring provisioned in cavity-nesting bees (Peterson & Roitberg 2006; Schüepp et al. 2011). In this study, I hypothesized building height, which reflects vertical isolation from ground level habitat opportunities, would result in decreasing colonization of trap nests by bees and wasps. Further, I hypothesized that as the proportion of green space at ground level increases there would be an increase in colonization of trap nests, as studies sampling bees on vegetated roofs have determined ground level green space to be a predictor of greater abundance and diversity (Tonietto et al. 2011; Braaker et al. 2014).

Methods

Bees and wasps were sampled from May to October over three years (2011–2013) using trap nests set up on 29 rooftops (one per roof) each separated by a minimum 250 m throughout the city of Toronto (Figure 1). The roofs were at varying heights from one (approximately 3.3 m from ground level) to nine building levels (approximately 29.7 m) and were classified into three types: (1) intensively planted vegetated roofs with numerous wild flowers, some shrubs and with growing media deeper than 15 cm; (2) extensive *Sedum*- or grass-dominant vegetated

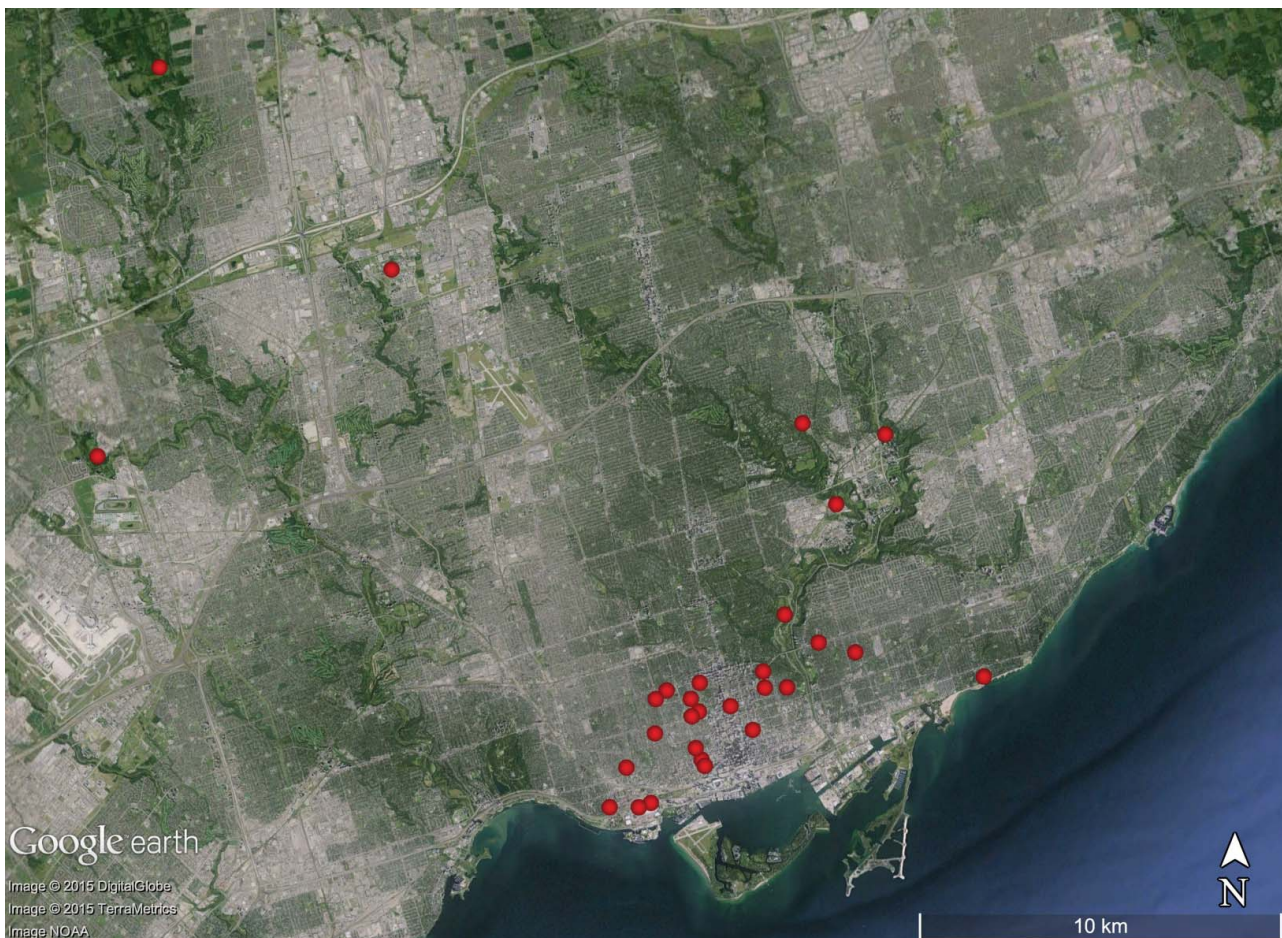


Figure 1. A map of trap nests set up on rooftops in the city of Toronto.

roofs having growing media depths of less than 15 cm (Oberndorfer et al. 2007), and (3) non-vegetated conventional roofs having no vegetation and comprising of rock ballast, asphalt, or bituminous roofing shingles (Table 1). Since rooftop sites in this study were located at different distances from one another, a Moran's I test for spatial autocorrelation and a spatial correlogram in SAM v4.0 (Rangel et al. 2010) were used to examine whether trap nest colonizers from more proximal sites were more similar than what would be expected in a random spatial pattern (Legendre 1993). It was determined that the trap nests on rooftops in this study were not spatially autocorrelated ($I/I_{\max} = 0.075$).

Each trap nest was constructed from a 30 cm piece of recyclable PVC pipe of 10 cm diameter with one end fitted with a pipe cap, the other with a faceplate with 30 cardboard tubes inserted, 10 of each of three widths (3.4, 5.5, and 7.6 mm) plugged at the capped end of the pipe (MacIvor, Cabral, & Packer 2014). Trap nests were set up facing southeast and attached using zip-ties to fixed features on the roof in April of each year. Trap nests were not visited again until collection in October, and once recovered the cardboard tubes were opened and the contents analyzed. Species richness and abundance (the number of brood cells reared per trap nest) for bees, wasps, and their parasites were determined once removed from the cardboard tubes. Nest loss was also recorded as the proportion of cell series that were initiated, in which pollen or prey and/or nesting material had been provisioned, but no offspring developed, representing an energetic cost for a surviving female or mortality. Either way, this results in no reproductive success despite reproductive effort and was used as a qualitative means of assessing net negative impacts on the local population.

Local and landscape variables for analysis were calculated using both ground-truthing and geospatial software. Local variables included the number of building levels ("height") at which the trap nest was set up, and roof vegetation categorization ("planting"). Three categories were identified: intensive, extensive, or none. Intensive referred to vegetated roofs having greater than 15 cm of substrate depth and a more diverse planting than extensive vegetated roofs, which are more shallow (<15 cm) and support less diverse plantings. Geospatial tools in ArcGIS v.10 (ESRI, Toronto, Canada) using city of Toronto municipal spatial reference data shape files (accessed from the York University Map Library) were used to determine landscape variables: building footprints ("footprint"), number

of buildings ("build"), and the proportion of green space within buffered regions surrounding the trap nest sites at 150 m ("X150m") and 600 m ("X600m") radii. These radii are of similar dimension to other studies examining landscape factors on bee populations (Steffan-Dewenter et al. 2002; Schüepp et al. 2011; Williams & Winfree 2013). The area within each buffer occupied by building footprint (m^2) was calculated because it is applicable city wide across different land use zones, and the total building density (number of buildings within an area) was counted because it is correlated with an increasing number of managed gardens (Davies et al. 2008). The proportion of green space surrounding each nest site was calculated using land use shape files from the Toronto and Region Conservation Authority by summing "Open Area" (e.g. open meadows and non-residential lawns) and "Parks and Recreation Area" (e.g. urban parks and forests) land use types.

Including all local and landscape variables, step-wise model selection following Akaike information criterion (AIC) (Burnham & Anderson 2004) was used to determine the best model for interpreting trap nest species richness, abundance, the number of lost cell series (those initiated but incomplete), and parasitism rates. These models of best fit were then analyzed using linear models in R v. 3.0.1 (R Core Team 2013). A canonical correspondence analysis (CCA) in the R Vegan statistical package (Oksanen 2013) was implemented to explore correlations between the explanatory local and landscape variables and the abundances of bee, wasp, and parasite species at colonized sites.

Results

Twenty-seven species in 16 genera of bee and wasp were recorded from 21 of 29 trap nests colonized over the three-year period (eight trap nests were never colonized over the duration of the study) (Table 2). The 11 bee species (including one cleptoparasite) combined were three times more abundant in trap nests on rooftops than wasps despite 16 species of wasps recorded (including 5 parasites) (Table 2). More native bee and wasp species were recorded than introduced ones; however, the most abundant bee was the introduced *Megachile rotundata*. The bee was collected at 27.6% of sites and accounted for 48.9% of all brood reared in the study. Due to the dominance of *M. rotundata*, the abundance of introduced bee species outnumbered native bee species in trap nests (Table 2). Among wasps, the most abundant species recorded was the native spider-collecting *Trypoxylon collinum* at 11.4% of the total sample, and 20.9% of sites. The introduced aphid-collecting *Psenulus pallipes* occurred at more site (24.1%), but only 6.6% of the total sample (Table 2). Overall, the most species-rich site included 10 species (in eight genera) and was located on an extensive vegetated roof on the third floor of a private home in a dense residential neighborhood. The most densely occupied trap nests were located on an intensive vegetated roof at the York University Campus where 580 individuals were reared over the three years investigated.

Table 1. The height in building levels, and planting type of each rooftop surveyed in the study.

	Building levels								
	1	2	3	4	5	6	7	8	9
Extensive	1	2	5	4	3				1
Intensive		2	1	1		2	1		
None			4		1	1			
Total	1	4	10	5	4	3	1		1

Table 2. The number of sites colonized and the abundances of each bee, wasp, and parasite species identified from trap nests set up on rooftops in the study.

Group	Family	Genus	Species	Code	Nest choice (mm)	Sites colonized (%)	Relative abundance	Total abundance
Bees	Megachilidae	<i>Megachile</i>	<i>rotundata</i> Fabricius	M.rot	5.5	0.276	0.489	1058
			<i>campanulae</i> (Roberston)	M.camp	5.5	0.172	0.026	57
			<i>centuncularis</i> (Linneaus)	M.cent	5.5	0.138	0.022	47
			<i>pugnata</i> Say	M.pug	7.6	0.034	0.002	4
	<i>Osmia</i>	<i>caerulescens</i> (Linneaus)	O.cae	3.4, 5.5	0.207	0.120	257	
		<i>lignaria</i> Say	O.lig	5.5	0.034	0.003	7	
		<i>pumila</i> Cresson	O.pum	3.4	0.103	0.009	20	
	<i>Heriades</i>	<i>carinata</i> Cresson	Her.car	3.4,5.5	0.172	0.021	46	
		<i>Coelioxys</i>	<i>sayi</i> Robertson ^{*1}	C.say	5.5	0.034	0.0005	1
	Colletidae	<i>Hylaenus</i>	<i>affinis/modestus</i>	Hyl.sp	3.4	0.103	0.015	33
Wasps	Sphecidae	<i>Isodonia</i>	<i>mexicana</i> (Saussure)	I.mex	7.6	0.172	0.028	61
	Crabronidae	<i>Trypoxylon</i>	<i>frigidum</i> Smith	T.fri	3.4, 5.5	0.138	0.016	35
			<i>collinum</i> Smith	T.col	3.4, 5.5	0.209	0.114	248
			<i>lactitarse</i> Saussure	T.lac	7.6	0.034	0.002	5
	Vespidae	<i>Passaloecus</i>	<i>gracilis</i> (Curtis)	Pas.gra	3.4	0.172	0.012	25
		<i>Psenulus</i>	<i>pallipes</i> (Panzer)	Pse.pal	3.4	0.241	0.068	147
		<i>Ancistrocerus</i>	<i>antilope</i> (Panzer)	A.ant	7.6	0.069	0.026	57
			<i>gazella</i> (Panzer)	A.gaz	5.5	0.034	0.004	9
		<i>Euodynerus</i>	<i>foraminatus</i> (Saussure)	E.for	5.5, 7.6	0.034	0.005	10
		<i>Symmorphus</i>	<i>canadensis</i> (Saussure)	S.can	3.4, 5.5	0.034	0.001	3
	Sapygidae	<i>Sapyga</i>	<i>louisii</i> Krombein ^{*2}	Sap.lou	3.4	0.069	0.004	9
		Chrysididae	<i>Caenochrysis</i>	<i>doriae</i> (Gribodo) ^{*3}	C.dor	3.4, 5.5	0.103	0.004
	<i>tridens</i> (Lepelletier) ^{*4}			C.tri	5.5	0.034	0.001	3
	<i>Perithous</i>			<i>divinator</i> (Rossi) ^{*5}	P.div	3.4	0.034	0.0005
	Chalcididae	<i>Monodontomerus</i>	<i>obscurus</i> Westwood ^{*6}	Mon.obs	—	0.034	0.002	4

Note: Bolded species indicate they are introduced to the study region. An asterisk indicates the species is a parasite and superscripted numeration refers to the host from which the parasite was collected: ¹*M. rotundata*, ²*H. carinata*, ³*T. collinum*, ⁴*E. foraminatus*, ⁵*P. pallipes*, ⁶*M. campanulae*.

AIC model selection yielded top models for abundance (“height” + “footprint” + “X150m” + “X600m” + “planting”), species richness (“height” + “footprint” + “build” + “X600m” + “planting”), parasitism (“planting”), and the number of incomplete cells (“height” + “planting”) that were used for analysis. Relative abundance of bees and wasps declined significantly with increasing building height ($t = 3.240$, $p = 0.004$) (Figure 2) and with decreasing proportion of green space surrounding the building within a 600 m radius ($t = 3.035$, $p = 0.006$) (Figure 3). Species richness did not decline with building height ($t = 1.336$, $p = 0.195$). Species richness was however significantly less on vegetated roofs surrounded by declining proportions of ground level green space within 600 m ($t = 2.341$, $p = 0.029$) (Figure 3). Roof planting type (intensive, extensive, none) had no effect on species richness or abundance but parasitism was highest on intensively planted vegetated roofs ($t = 2.086$, $p = 0.05$). The number of incomplete cell series among all species within a trap nest significantly increased with increasing building height ($t = 3.432$, $p = 0.003$) (Figure 4). There was no effect of the amount of green space at ground level within 150 m of the vegetated roof site.

Some variation in the response of bees, wasps, and parasites to local and landscape variables was evident. The first axis in the CCA captured 36.9% of the variation present in the data, 22.3% was captured in the second axis, and permutation testing ($N = 10,000$) demonstrated that the CCA model was a good fit ($df = 6$, $F = 1.27$, $p = 0.05$) (Figure 5). The vectors indicated the amount of green space at 150 and 600 m radii was very similar, each accounting for the proportion of green space in the region around the building. The vectors for building height and the rooftop planting type were different from all ground level landscape variables. Three of the exotic species in the study *Megachile rotundata*, *Osmia caerulescens*, *Passaloecus gracilis* did not respond to any of the variables identified in the biplot and were found on vegetated roofs of all plantings, heights, and landscape conditions.

Discussion

Although an increasing number of studies examine which local and landscape factors limit nesting activity of bees and wasps in urban green spaces (Loyola & Martins 2006; McFrederick & LeBuhn 2006; Schüepp et al. 2011; Pereira-Peixoto et al. 2014), none address the role of

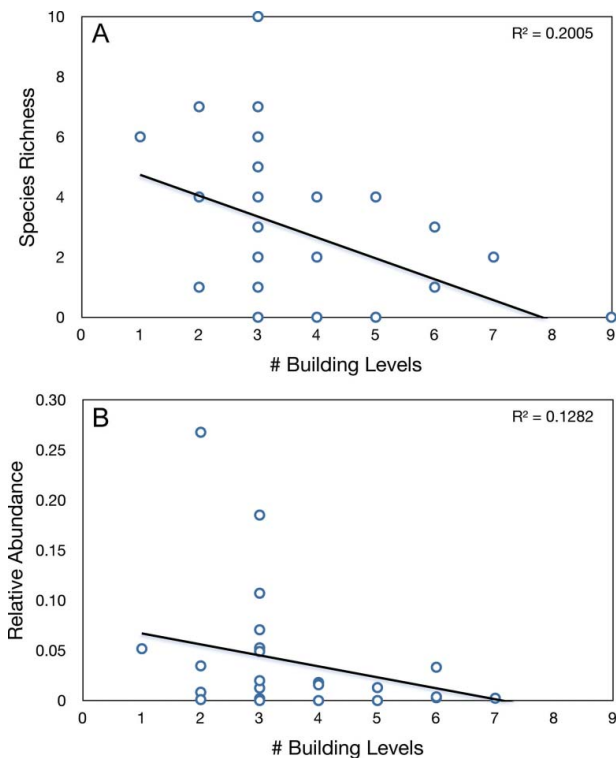


Figure 2. Scatterplots that demonstrate the relationships between increasing building height and: (A) species richness ($p = 0.195$) and (B) declining relative abundance ($p = 0.004$) in trap nest.

vegetated roofs. Here I demonstrate associations between local (building height) and landscape (surrounding green space at ground level) factors that are implicated in the contribution of vegetated roofs to nesting of cavity-nesting bees and wasps.

Our findings indicate that we can accept our first hypothesis that increasing building height results in decreasing numbers of bees and wasps using in trap nests. Further, of the eight rooftops not colonized over the three-year study, six were extensive and two were conventional and not vegetated; all were over three building levels in height. This is an important detail for those involved in vegetated roof policy and application. For example, the city of Toronto has a vegetated roof by-law and construction standard mandating vegetated roofs on certain new buildings, including residential buildings greater than six building levels (City of Toronto 2014). Simultaneously, the city encourages best practices for providing wildlife habitat on vegetated roofs (Torrance et al. 2013), without any acknowledgment of site conditions such as building height on the impact wildlife enhancements may have on local biodiversity. Presumably, even installers of vegetated roofs on condominium buildings, some dozens of meters from ground level, are encouraged to include plans for wildlife on these elevated habitats. This study suggests that plans for encouraging cavity-nesting bees and wasps using trap nests on vegetated roofs need to take into account the height of the building; that is, efforts supporting their populations using trap nests should target

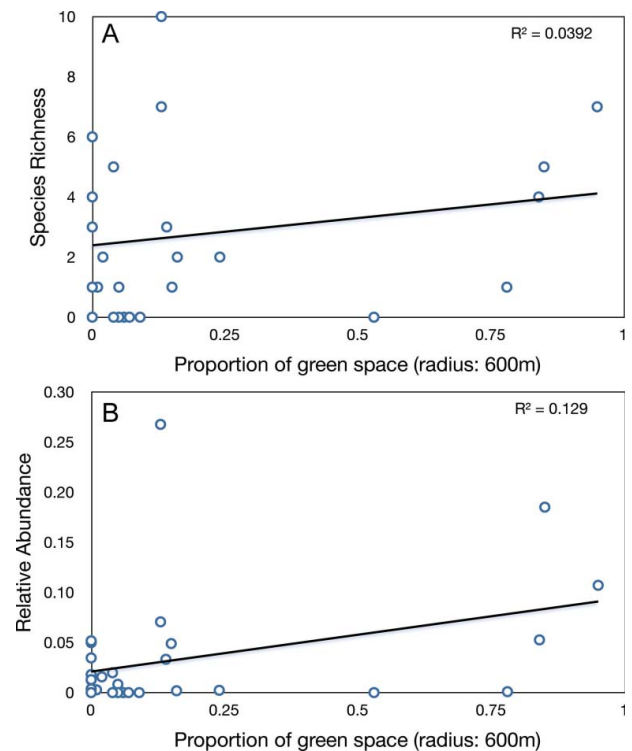


Figure 3. Scatterplots that show that an increasing proportion of green space within a 600 m radius surrounding the rooftop led to increasing (A) species richness and (B) relative abundance ($p = 0.006$).

low- and mid-rise buildings (<5 building levels). Our second hypothesis that increasing proportions of surrounding ground level green space contributes to an increase in colonization of bees and wasps in trap nests on rooftops was accepted; however, the R^2 values supporting this significant relationship for species richness and abundance were low (Figure 3) and altogether warrants further study. The proportion of green space surrounding surveyed vegetated roofs was also a significant predictor of bee diversity on six roofs in Chicago (Tonietto et al. 2011).

Despite some bees maintaining a level of constancy in flower foraging height (Waddington & Holden 1979), when no suitable forage is available, bees may search vertically (Osborne et al. 1999) and thus might have an easier time flying down to ground level. Pollen and nectar are light and can be compacted using hairs and appendages adapted for efficient storage capacity during flight (Schmid-Hempel et al. 1985). This adaptation permits bees to not have to nest too close to foraging resources (Zurbuchen et al. 2010). Since the impact of wind on buildings increases with height (Irwin 2009), bees and wasps might find it increasingly difficult to travel to and from nests that are higher up and choose to colonize lower roofs instead. Foraging between nearby vegetated roofs might also be possible for bees. Braaker et al. (2014) recently showed that bee diversity collected from 40 vegetated roofs was highly dependent on the connectivity of surrounding vegetated roofs in a dense urban environment.

Wasps that carry relatively large prey such as *Isodontia mexicana* (collects katydids) or *Ancistrocerus antilope*

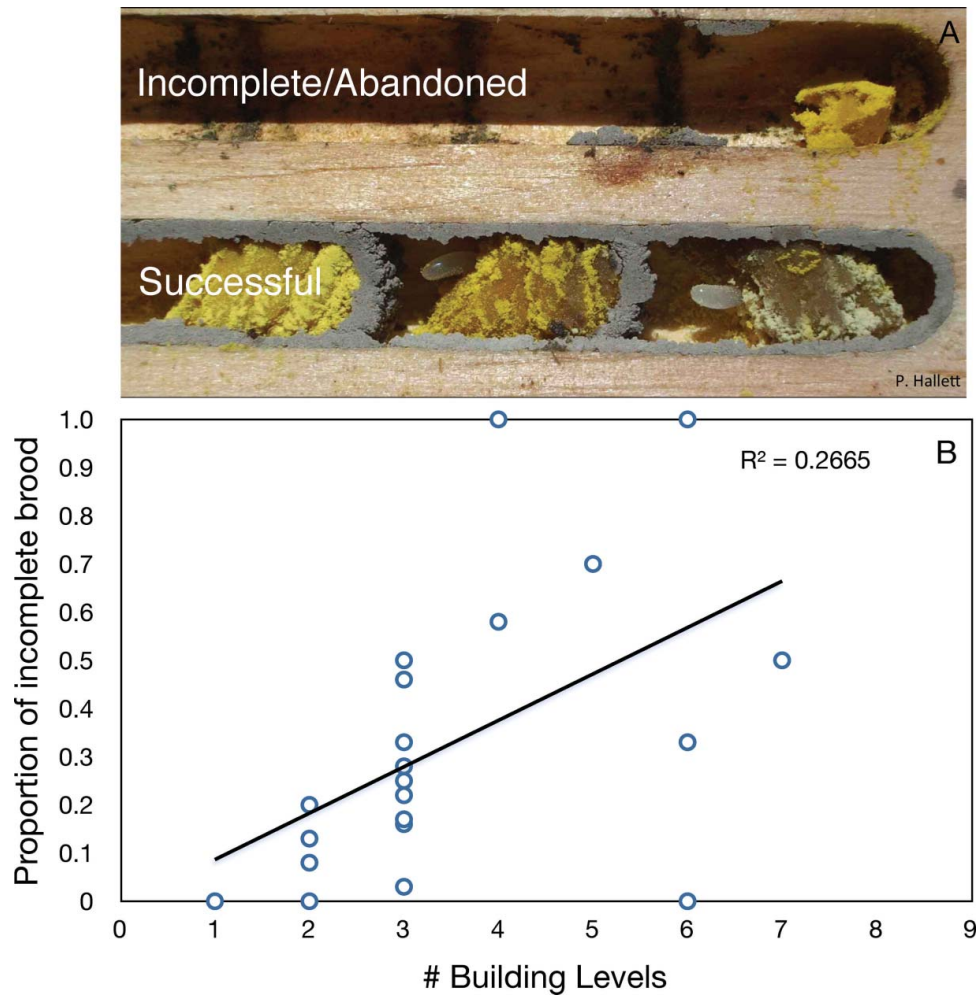


Figure 4. (A) Image of a complete nest and an incomplete nest (or abandoned) of a cavity-nesting bee nest (photo taken by: Peter Hallett) and (B) a scatterplot demonstrating the significant increase ($p = 0.003$) in nest loss by cavity-nesting species with increasing building height.

(collects caterpillars) would have a more difficult time flying back up to the nest than would wasps carrying lighter prey such as *Passaloecus cuspidatus* (collects aphids) or *Trypoxylon collinum* and *Trypoxylon frigidum* (collects spiders) (Hastings 1986; Coelho 2011). Although not analyzed, in trap nests on rooftops, smaller wasps were more abundant than larger wasps. For cavity-nesting wasps, the energy expended carrying a large prey item up from ground level might be too great and this could limit some species in vertically isolated trap nests on vegetated roofs. Further support is evident in the CCA biplot (Figure 5). The large wasps (e.g. *Ancistrocerus antilope*, *Euodynerus foraminatus*, and *Isodontia mexicana*) were found in the quadrant where vectors representing the proportion of green space surrounding the site were also found, presumably because their prey would be more abundant in green spaces containing their host trees and large shrubs (Krombein 1967; Ercit 2014) rather than on or near green infrastructure which is dominated by low growing perennials and grasses.

In this study, there was no difference in richness or abundance of bee and wasp species between the different roof vegetation types (intensive, extensive, none) but

parasitism rates were highest on intensive vegetated roofs. Schindler et al. (2011) found no effect of vegetation type on insect diversity on extensive vegetated roofs, but did not examine non-vegetated roofs. These findings do not correspond entirely with other recent studies linking intensively planted vegetated roofs to greater diversity and abundance of insects (Madre et al. 2013). Kadas (2006) also noted a greater diversity of bees on “biodiverse” roofs, and Brenneisen (2006) noted collecting twice as many bees on vegetated roofs with “diverse vegetation” compared to *Sedum*-only ones. At ground level, urban green spaces having more diverse plantings can lead to a greater diversity in bees (Gaston et al. 2005; Cane et al. 2006; Matteson & Langellotto 2010; Lowenstein et al. 2014). Different from the sampling methods used in the aforementioned studies, I deployed trap nests that when analyzed are indicative of the nesting environment of bees and wasps, and not necessarily the foraging environment. Thus, conditions for foraging created by dense or diverse flowering vegetated roof plantings might not correspond to suitable nesting habitats, and each need to be addressed together when planning for urban wildlife conservation (Colding 2007; Williams et al. 2014).

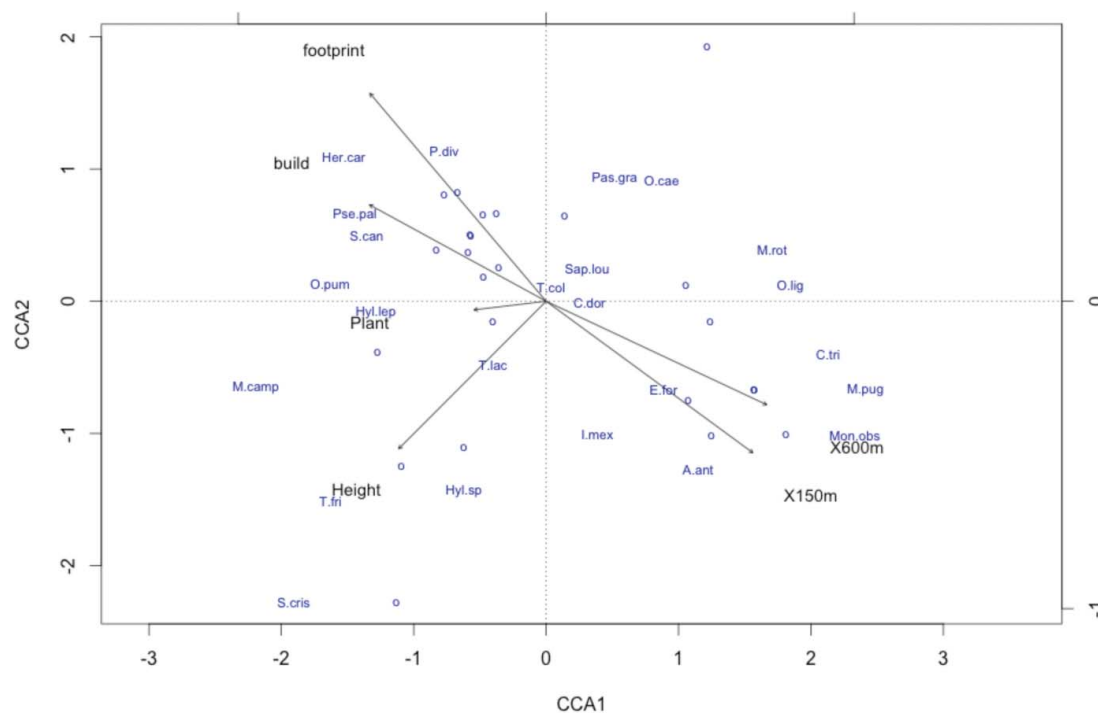


Figure 5. A CCA ordination biplot with local and landscape vectors plotted with bee and wasp species recorded. Vectors are detailed in the methods section and vector acronyms include “footprint” = building footprint within buffer radius, “build” = a count of the number of buildings contained within the buffer radius, “Plant” = the type of roof vegetation (extensive, intensive, none), “Height” = the number of building levels, “X150m” and “X600m” = the proportion of green space within 150 and 600 m buffer radii, respectively. Acronyms for each bee and wasp species are given in Table 2.

Despite many resources for enhancing cavity-nesting bee and wasp nesting opportunities, more research is needed to elucidate the ecology and diversity of species that successfully inhabit human-dominated environments. Although not examined here, identifying behavioral flexibility that allows a species to thrive in urban landscapes can increase capacity to discern between urban adapting and urban avoiding species (Müller et al. 2013). Data-driven ecological research can assist urban planners and designers in enhancement strategies to ensure they effectively include nesting material elements and nest analogues for bees and wasps in building integrated habitat (MacIvor & Packer 2015). These actions could buffer against change in urban landscapes having de-stabilizing effects on bee and wasp species assemblages, regional pollination and pest controlling services, as well as other urban ecosystem services (Tzoulas et al. 2007; Andersson et al. 2014). These activities can serve doubly in public outreach and pollinator stewardship initiatives, as trap nests require little maintenance or cost.

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