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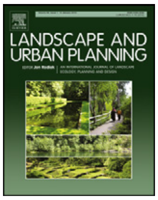

A comparison of bee communities of Chicago green roofs, parks and prairies

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ABSTRACT

Due to loss of natural habitats, human-dominated green spaces are likely to increase in importance for biodiversity support. We assessed the potential value of urban “green roofs” for native pollinator conservation in the Chicago region, comparing them with reference habitats of tallgrass prairie natural areas and traditional city-park green spaces. We found that native bees are present on green roofs, though at lower abundance and diversity than in reference habitats. Green-roof and prairie bee communities were distinct from each other, while those in parks were intermediate and similar to the other two habitat types. Bee-community patterns were related to habitat characteristics at both the site and landscape scales. Overall, bee abundance and species richness increased with greater proportions of green space in the surrounding landscape. However, this relationship disappeared in cases where green space was dominated by turf grass. At the site scale, bees benefited from greater plant diversity, and bee and plant-community composition were significantly correlated. Green roofs are potentially valuable sites for bee conservation in urban areas, particularly if planted with diverse native forbs to provide foraging resources, and designed to accommodate bees with different nesting habits.

1. Introduction

Certain pollinators have declined globally due to habitat loss and other land-use changes (Murray, Kuhlmann, & Potts, 2009; Winfree, Aguilar, Vasquez, LeBuhn, & Aizen, 2009). Long-term declines of honey bees and some wild bees, particularly bumble bees, have been documented in North America (Grixti, Wong, Cameron, & Favret, 2009; National Research Council, 2006). According to some, this decline has already reached a crisis stage (Klein, Steffan-Dewenter, Buchori, & Tscharntke, 2002; Kremen & Ricketts, 2000; Larsen, Williams, & Kremen, 2005; Steffan-Dewenter, Potts, & Packer, 2005; Williams & Kremen, 2007). However, studies in urban, agricultural, and natural systems have continued to find most wild bees in expected diversity and abundance according to historical records (Cane, 2001; Giles & Ascher, 2006; Marlin & LaBerge, 2001; Tuell, Ascher, & Issacs, 2009). To better understand, monitor and support native pollinators habitat needs, more pollinator research should be included within restoration ecology, especially within anthropogenically altered landscapes (Dixon, 2009).

There is an emerging recognition that properly designed and managed human-dominated landscapes can play an important role in biodiversity support, allowing native species to continue to colonize sites that have been altered from their natural state (Daily, 1997; Rosenzweig, 2003). The protection and restoration of natural areas are critical. Remnant habitats are often insufficient to conserve biodiversity in urban areas making these managed, or created habitats even more valuable (Daily, 2006; Rosenzweig, 2003). There is growing evidence that substantial components of native bee communities can persist in anthropogenic landscapes (Cane, 2001; Hernandez, Frankie, & Thorp, 2009; Matteson, Ascher, & Langellotto, 2008).

Worldwide, native bee abundance and diversity in agricultural systems are generally positively correlated with proximity to and proportion of natural areas in the surrounding landscape (Kremen, Williams, Bugg, Fay, & Thorp, 2004; Ricketts et al., 2008). However, anthropogenic habitats can also be of high value to native bees. For example, wild bee abundance and diversity were greater in agricultural and suburban areas of New Jersey than within forested areas, the dominant pre-settlement land cover (Winfree, Griswold, & Kremen, 2007). Other agricultural habitats, such as blueberry fields, are known to support very diverse communities of native bees (Tuell et al., 2009).

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While bee communities associated with agriculture are well-documented, few replicated studies have compared bee communities across multiple urban habitats (Cane, Minckley, Kervin, Roulston, & Williams, 2006; Hernandez et al., 2009). Urban bee studies have tended to focus on one habitat type, such as natural-area remnants (Cane et al., 2006; Hisamatsu & Yamane, 2006) or gardens or parks (Fetridge, Ascher, & Langellotto, 2008; Frankie et al., 2009; Hernandez et al., 2009; Matteson et al., 2008; McFrederick & LeBuhn, 2006) without detailed assessment of plant community composition or surrounding land uses (Hernandez et al., 2009; but see Winfree et al., 2007). One recent studies from the Neotropics found lower bee diversity at an urban site than a nearby ecological reserve (Dalmazzo, 2010) whereas another found the impact of the urban matrix to be minimal and that floral resource abundance and distribution were correlated with bee abundance in an urban landscape (Wojcik, 2011).

The conservation value of novel urban green spaces should be investigated further, as their value for biodiversity support is often unknown (Rosenzweig, 2003). This is especially true of green roofs, a rare example of an urban green space rapidly increasing in area in North America (Green Roofs for Healthy Cities, 2009). Green roofs are typically flat or slightly sloped rooftops with soil substrates to support vegetation. While green roofs often house honey-bee hives (Shevory, 2010), we know of only two published study that assessed green roofs as potential habitat for native bees in North America (Colla, Willis, & Packer, 2009; MacIvor & Lundholm, 2010). Bee species diversity was not statistically compared by Colla et al. (2009), and MacIvor and Lundholm (2010) focused on insect counts, and compared collections from green roofs and ground sites without species identification.

We chose the city of Chicago and surrounding metropolitan areas in northeastern Illinois to test whether green roofs support wild bee communities. In Illinois, loss of natural land cover has been severe. From 1972 to 1997, the proportion of developed land in the metropolitan region increased by 49% (Wang & Moskovits, 2001). Over 80% of the state's total land cover is agricultural, and only 0.001% of tallgrass prairie, the dominant pre-settlement ecosystem, remains (Illinois Department of Agriculture, 2009; National Research Council, 2006). However, Chicago has become the leading city in the United States for green roof implementation; as of 2010, over five hundred were extant or in development (Kamin, 2010).

We investigated green roofs as habitat for native bees by comparing them against a reference natural habitat (tallgrass prairie) and traditional urban green space (ecologically managed areas in city parks). Within these three habitat types, we assessed the abundance, diversity and bee community composition. We tested the extent to which bee community patterns could be explained by habitat characteristics at the site and landscape scales in the form of plant community composition and land-use cover, respectively.

2. Materials and methods

2.1. Site descriptions

We collected and observed bees at six green roofs, six city parks, and six prairies from June to October 2008. All sites were within the greater metropolitan Chicago (Cook, Lake, and Will counties; IL). Entire park area ranged from 6 to 485 ha, yet the natural area plantings were all less than 2 ha in area. The smallest prairie was also 6 ha, but the largest was slightly over 6000 ha.

The vegetation of two green roofs was dominated by plants native to Illinois. The other four were dominated by *Sedum* spp.; short-statured succulents that quickly produce dense mats of flowering vegetation. Planted areas of green roofs ranged from 0.01 to 0.23 ha, and were located on buildings ranging from 2 to 15 stories tall. All park sites had small, managed areas of native prairie plants. Prairie sites were located outside of Chicago in Cook, Lake, or Will Counties and have undergone active management and varying degrees of restoration.

We characterized the surrounding landscape and vegetation of each site. We imported Google Earth (Version 4.3.7204.0836, 2008 Google) images into ArcMap (ArcGIS version 9.2, 2006 ESRI) and quantified land cover categories (urban, suburban, water, and green space) within a 500-m radius of each site. Green space was further divided into turf grass and natural area.

To characterize foraging resources for pollinators, we recorded the identities of all blooming species within a 5-m radius surrounding focal plants. We also measured the density of all blooming species in 0.25-m^2 plots surrounding focal plants. We did not record grasses or non-blooming forbs, as they were not available foraging resources for bees.

2.2. Bee sampling

We performed bee observations using two bee-pollinated native forbs: an early summer-blooming foxglove (*Penstemon digitalis*), and a late summer-blooming Asteraceae; either *Echinacea* or *Rudbeckia* spp. We planted two *P. digitalis* or native coneflower (*Echinacea purpurea*) on the three green roofs lacking these flower types, and used existing plants on the other roofs.

We observed each focal plant for three non-consecutive, sunny, warm days at each site. Observations were performed for 15-min periods starting at 9:00 am, 10:30 am, 12:00 pm, and 1:30 pm. We recorded bees using size and color morphological criteria (e.g., small and dark). Bumble bees (*Bombus* spp.) and honey bees (*Apis mellifera*) were recorded to genus and species, respectively.

We employed two collection methods. At each site, we captured bees that landed on observed flowers with insect nets for 15 min at the end of one early-season (May–early July) and one late-season (late July–September) observation day. And we deployed bee bowls: 3-oz pan traps coated with UV-reflective paint and filled with a water/dish-detergent solution (LeBuhn et al., 2003). We haphazardly placed 15 bowls, 5 each of 3 different colors (blue, white, yellow), 1–5-m apart at each site. At sites with vegetation >1-m tall, we mounted bowls on a 1.5-m dowel. We placed bowls at each site for approximately 24 h, once in the early and once in the late bloom seasons.

Bees were identified to genus using Michener, McGinley, and Danforth (1994), and later verified and identified to species by J.S. Ascher and J. Gibbs (*Lasioglossum*). Specimens are housed at the Chicago Botanic Garden. Bees' nesting and foraging traits were obtained from Michener (2000) and Giles and Ascher (2006).

2.3. Statistics

Data were analyzed in R version 2.12.0 (R Development Core Team, 2010) except as noted.

To assess relationships between land-cover and bee-community attributes, we used linear models and multiple regressions for each habitat type with proportion of land cover as the independent variable and bee abundance or species richness as the dependent variable. We used analysis of covariance (ANCOVA) to test whether relationships differed by habitat type.

Floral species richness and bloom density were analyzed using Wilcoxon rank-sum tests with continuity correction for non-normal variance. Correlations between landscape-scale factors and habitat types were calculated using linear regression.

Generalized linear models (assigned a Poisson distribution to account for zero-inflated data) were used to test for effects of habitat type on visitation rates. We used a priori contrasts to compare visitation rates between habitat types.

Non-metric multidimensional scaling (NMDS) ordinations were used to compare species composition of bees and plants across habitat types using the vegan package in R (Oksanen et al., 2010). Bee species only collected once during the study were removed from the analysis. Data were relativized by samples and species due to high coefficients of variation and the NMS was constructed using three axes.

We performed permutational multivariate analysis of variance (PERMANOVA) to test for differences among habitat types in bee and plant–species composition and bee nesting habits (soil-dwelling, cavity-dwelling, or cleptoparasitic) using the program PERMANOVA (Anderson, 2005). Analyses were based on Bray–Curtis dissimilarity with 1000 permutations for each test and pair-wise comparisons between habitat types.

Having found significant differences by PERMANOVA, we evaluated which species were most responsible for differentiating communities using similarity percentage (SIMPER) analysis. SIMPER evaluates the contributions of each species to the Bray-Curtis dissimilarity of all pairs of samples between groups (Clarke & Warwick, 2001) and was implemented in PRIMER v6 (Clarke & Gorley, 2006).

We conducted a Mantel test to determine if there was a significant relationship between bee and plant community composition by habitat type using the vegan package in R (Oksanen et al., 2010).

3. Results

3.1. Landscape-level characteristics

Overall, habitat type was a predictor for the proportion of green space in the surrounding landscape ($p = 0.002$). There was more green space surrounding prairies than green roofs ($p = 0.003$) or parks ($p = 0.06$). There was also a greater proportion of green space around parks than green roofs ($p = 0.07$). The proportion of green space categorized as natural area differed by habitat type ($p = 0.001$) and was greater around prairies than parks ($p = 0.02$) or green roofs ($p = 0.02$), which were similar to each other ($p = 0.95$). Although the proportion of green space composed of turf grass was not related to habitat type ($p = 0.15$), it was greater surrounding parks than green roofs ($p = 0.07$). There were no differences between prairies and parks ($p = 0.17$) or green roofs ($p = 0.60$).

Across habitat types, bee richness and abundance were positively correlated with surrounding green space (species richness: $p = 0.0004$, $R = 0.55$; abundance: $p = 0.04$, $R = 0.65$). However, relationships differed by habitat type: richness and green space were positively correlated for prairies ($p = 0.02$, $R = 0.7$) and the trend was positive, but not significant for green roofs ($p = 0.12$, $R = 0.45$). There was a negative, but not significant, trend for parks ($p = 0.13$, $R = 0.46$). The trend for parks was significantly different from that of green roofs or prairies ($p = 0.009$ and 0.002, respectively; Fig. 1a). Bee abundance was not correlated with green space at prairies ($p = 0.12$, $R = 0.45$), parks ($p = 0.33$, $R = 0.23$) or green roofs ($p = 0.27$, $R = 0.29$).

For all habitats, there was a positive trend between bee species richness and proportion of natural area in the surrounding landscape, which was significant only at prairies (prairies: $p = 0.06$, $R = 0.61$, parks: $p = 0.23$, $R = 0.32$, green roofs: $p = 0.22$, $R = 0.34$; Fig. 1b). Bee abundance was not correlated with natural area in the surrounding landscape for green roofs ($p = 0.10$, $R = 0.54$), parks ($p = 0.20$, $R = 0.36$) or prairies ($p = 0.18$, $R = 0.38$).

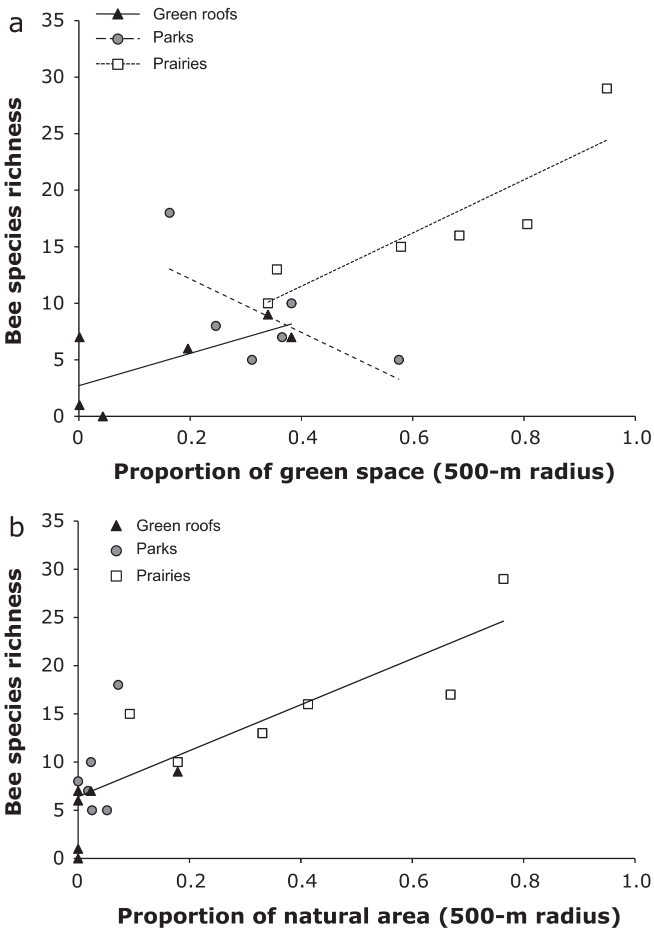

Fig. 1. Multiple regressions of (a) bee species richness against the proportion of green space in the surrounding landscape at green roofs ($p = 0.12$, $R = 0.45$), parks ($p = 0.13$, $R = 0.46$), and prairies ($p = 0.02$, $R = 0.76$), and (b) bee species richness against the proportion of natural area in the surrounding landscape at green roofs ($p = 0.22$, $R = 0.34$), parks ($p = 0.23$, $R = 0.32$), and prairies ($p = 0.06$, $R = 0.61$).

3.2. Site-level characteristics

Blooming-plant species richness differed by habitat type ($p = 0.002$). Green roofs had fewer species in bloom than parks ($p < 0.001$) or prairies ($p < 0.001$). Richness of blooming plants was marginally greater at prairies than parks ($p = 0.09$). Habitat type was a significant predictor of blooming-plant species composition (Fig. 2a, PERMANOVA: $p = 0.002$).

3.3. Bee surveys

We performed 114 h of pollinator observations over 59 days from 9 June to 6 October, 2008. We observed fewer bees visiting flowers on green roofs ($n = 111$) than in parks ($n = 668$) or prairies ($n = 746$) ($p = 0.024$). Visitation rate at parks was slightly lower than at prairies ($p = 0.08$) and was much lower at green roofs compared to parks ($p = 0.03$) or prairies ($p = 0.0001$).

Aggregating bee-bowl and net samples, we collected 677 bees belonging to 5 families, 23 genera, and 63 species; 30% of species were represented by a single individual (see Appendix 1). We collected more bees in prairies ($n = 329$) than in parks ($n = 225$) or green roofs ($n = 123$). Bee species richness was significantly different between habitat type ($p = 0.006$). We collected marginally more bee species from prairies ($n = 46$) than parks ($n = 30$), but the difference was not significant ($p = 0.07$). We collected significantly more species from prairies than green roofs ($n = 19$, $p = 0.005$). There was

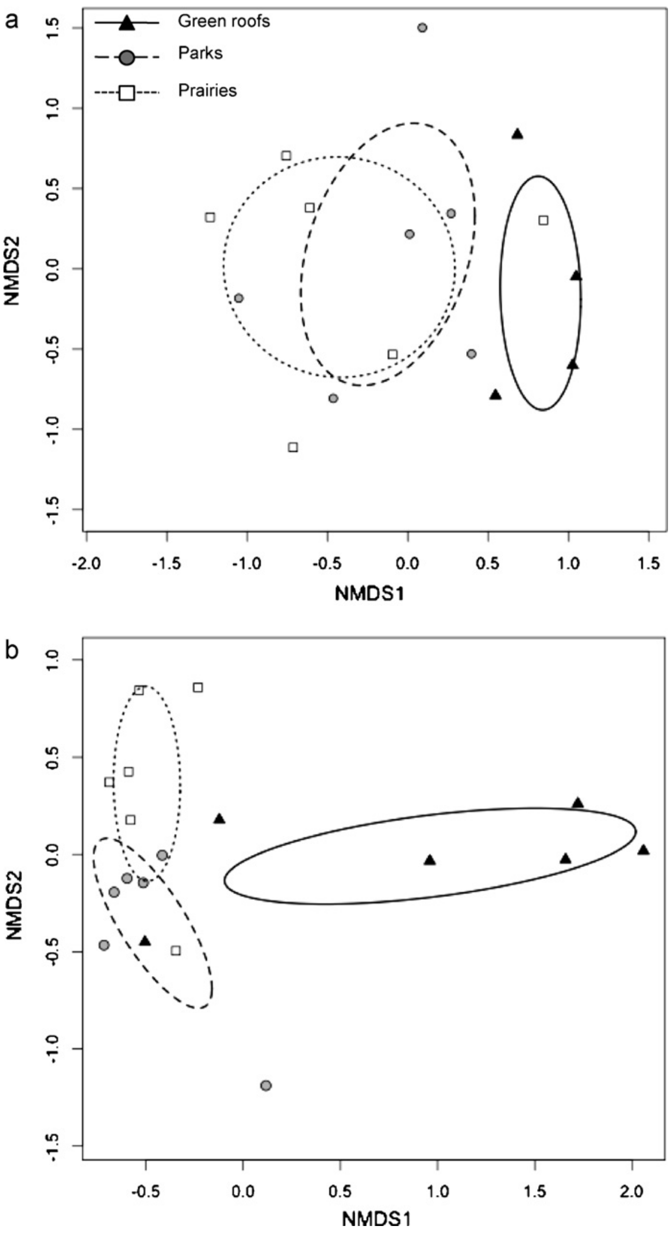

Fig. 2. Bee species abundance curves at green roofs, parks, and prairies.

not a significant difference between bee species richness at parks and green roofs ($p = 0.4$). Green roofs had a greater proportion of bee species represented by a single individual than parks or prairies (Fig. 3).

Bee species composition differed by habitat type (Fig. 2b, PERMANOVA: $p = 0.008$). There was a significant relationship between bee species and blooming-plant species composition by habitat type (Mantel: $p = 0.032$, $R = 0.17$).

Based on SIMPER analysis, four halictine bee species (*Agapostemon virescens*, *Halictus ligatus*, *Lasioglossum anomalum* and *H. ligatus*) made particularly strong contributions to differentiating communities by habitat type (Table 1).

Most bee species collected (87%) are native to Illinois. Prairies had the greatest proportion and number of native species (91%, $n = 42$), followed by parks (83%, $n = 25$), and green roofs (73%, $n = 14$). Native species represented 97% of individuals collected from prairies and 94% from parks, but only 74% from green roofs.

Nesting habitat distribution did not differ by habitat (PERMANOVA: $p = 0.86$). Over 60% of bee species collected from each habitat were ground nesters (green roofs: 13 spp., $n = 200$, parks: 20 spp. $n = 270$, prairies: 29 spp. $n = 90$). Of those, more than half of species and individuals were soil-dwelling solitary bees. Almost 30% of individuals collected from green roofs were cavity nesters but these made up only 8% of individuals collected from parks and 11% from prairies. Wood- and pith-nesting bees were collected in prairies and parks, but not green roofs. Soft- or rotting-wood nesting bees were found only in prairie sites. We collected only three individual cleptoparasitic bees, one from each habitat, each a different species.

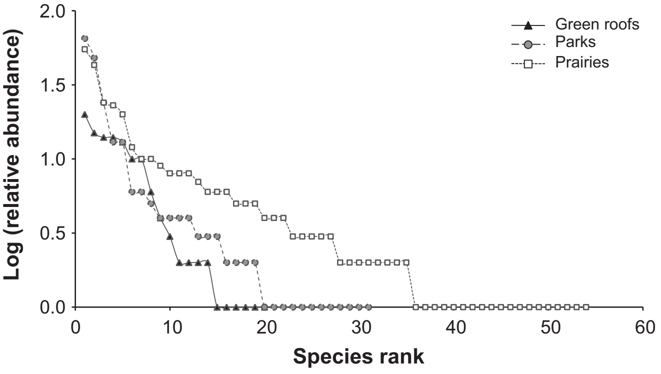

Fig. 3. Nonmetric multidimensional scaling ordination of study sites according to (a) plant species composition (stress of 9.31) and (b) bee species composition (stress of 15.2), points represent sites, and ellipses represent habitat types.

Only 3 of the 63 bee species collected are oligolectic (pollen specialists on a particular plant species or group). All specimens of these three species (*Colletes latitarsis* [$n = 1$], *Melissodes desponsa* [$n = 4$], and *Peponapis pruinosa* [$n = 1$]) were collected from prairies. All other species collected are generalist foragers without a strict dietary preference for pollen.

Table 1
Bee species most responsible for differentiating bee communities by habitat type (SIMPER analysis).

Bee species	Average	Abundance	Contribution %[a]
Prairies vs. parks			
Lasioglossum anomalum	1.17	11.5	12.42
Halictus ligatus	7.17	4	11.96
Melissodes bimaculata	4	0.67	5.95
Lasioglossum mitchelli	2.67	1.5	5.70
Bombus impatiens	2	1	5.69
Agapostemon virescens	9.17	2.17	5.19
Lasioglossum pilosum	0	8	4.73
Halictus confusus	1.33	0.67	3.86
Apis mellifera	0.17	0.83	3.68
Ceratina calcarata or *dupla*	1.67	0.17	3.34
Prairies vs. green roofs			
Megachile rotundata	0	2	12.16
Agapostemon virescens	9.17	4	11.01
Halictus ligatus	7.17	0.6	6.57
Lasioglossum ellisiae	0.83	2	6.40
Lasioglossum mitchelli	2.67	2.8	6.19
Melissodes bimaculata	4	0.4	5.01
Anthidium oblongatum	0.83	3	4.82
Lasioglossum illinoense	1	2.8	4.81
Lasioglossum zephyrum	0	2.6	4.58
Parks vs. green roofs			
Megachile rotundata	0.17	2	11.95
Lasioglossum anomalum	11.5	1.2	11.51
Halictus ligatus	4	0.6	10.28
Agapostemon virescens	2.17	4	9.48
Lasioglossum ellisiae	0.5	2	6.43
Lasioglossum mitchelli	1.5	2.8	6.30
Bombus impatiens	1	0.2	4.80

[a] Proportion of the bee community difference attributed to each species cumulatively responsible for the first 60% of dissimilarity between habitat types.

Five of the species collected were new records for the state of Illinois, four of which were reported by Tonietto and Ascher (2009). We collected one specimen each of two rarely collected native bees: *Coelioxys banksi* (a cleptoparasite of *Megachile* spp.) from a prairie, and *Lasioglossum michiganense*, a presumed social parasite of eusocial, metallic *L.* (*Dialictus*), at a park. Other new records for Illinois were two exotic cavity-nesting megachilids introduced from the Palearctic to the eastern United States and are now widely distributed: *Anthidium manicatum* and *Anthidium oblongatum*. All four specimens of *A. manicatum* were collected from park sites, whereas *A. oblongatum* was collected from all habitats. Subsequent to publication of Tonietto and Ascher (2009), we identified one male of another new species for Illinois, *Megachile inermis*. This northern species, well known in Wisconsin, was found at our northernmost prairie site.

4. Discussion and conclusions

Native bees were present on green roofs in Chicago but were represented by fewer species and individuals than in prairies or park natural areas. In all habitat types, >70% of collected species were native to Illinois, and soil-dwelling species were most common. Over 30% of species were represented by a single individual, consistent with proportions of singletons found in other studies (Cane, 2001). Composition of bees was significantly different across habitat types. Compared to parks and prairies, green roofs had fewer species of blooming plants and distinct plant community composition. At the landscape scale, bee richness was positively correlated with the proportion of natural area within a 500-m radius. At the site scale, bee diversity increased with the diversity of blooming plants.

North American urban bee studies typically report the proportion of green space in the surrounding landscape without differentiating its composition, or report only local floral components of sites (Fetridge et al., 2008; Frankie et al., 2005; reviewed by Hernandez et al., 2009). We agree with Hernandez et al. (2009) that urban bee studies should include landscape-scale analyses, with categories derived with bees' habitat and foraging needs in mind. Had we used undifferentiated green space as our land-cover category, we would have concluded that there was a negative trend between green space and bee diversity in parks. This was an artifact of most green space around park sites being turf grass, which is maintained to eliminate bare patches and weeds (including common flowering lawn weeds such as dandelions and clover that would support bees), is frequently mowed, and has compacted soil. As a result, park turf grass at our sites has fewer foraging resources and its maintenance discourages soil nesting.

For many of the landscape and vegetation characteristics measured, parks and prairies were similar, while green roofs differed. Park sites in this study included managed areas of native prairie plants. Such vegetation differs from that in most urban parks, which are typically managed for recreational or aesthetic considerations that do not favor native status (Gobster, 2001; Loeb, 2006). Wild bees have been shown to prefer native plant species over exotic ornamentals (Frankie et al., 2005; Hinners, 2003), so these sites may draw more native bees than typical parks. These natural areas fulfilled restoration goals (sensu Rosenzweig, 2003), as anthropogenic habitats supporting wild bee communities similar in diversity and abundance to natural areas.

Our findings are consistent with others' that sites with greater plant diversity generally have greater bee diversity (Hendrix, Kwaiser, & Heard, 2010; Potts, Vulliamy, & al, 2003; Wojcik, 2011). The green roof with the greatest number of bee species and individuals collected was planted with native prairie species, and had the highest plant diversity of all green-roof sites. The two sites most similar in bee community composition, a park and a prairie, had the greatest diversity of blooming plants and bees within their respective habitat types. Planting of green roofs with diverse native species, rather than monotypes of *Sedum*, would increase their value for bee conservation. This approach would provide a greater variety of foraging resources to attract a wider variety of native bees, and would also provide foraging resources for more of the blooming season. Ideally, green roofs in temperate regions should have diverse native forbs in bloom from May to October. Bees typically live in habitats where foraging resources are patchily distributed and spatially dissociated (Cane, 2001), so planted rooftops need not be contiguous or have similar plant composition, but maintaining temporal contiguity of blooms is important (The Xerces Society, 2011).

Oligolectic bees were only represented by three species in our study, all collected from prairies. Other urban bee studies have also found few floral specialists, presumably due to a lack of appropriate host plants (Dalmazzo, 2010; Hernandez et al., 2009). Oligolectic bees made up only 2–9% of bees collected from urban and suburban gardens in the New York City region (Fetridge et al., 2008; Matteson et al., 2008), although a considerable diversity of oligolectic species occur in larger parks, botanical gardens, and cemeteries. The oligoleges we collected in prairies all specialize on plant species we never found on green roofs: *Physalis pruinosa* (ground cherry), the host of *Colletes latitarsis*; *Cirsium* spp. (thistle), the host of *Melissodes desponsa*; and *Curcurbita* spp. (squash), the host of *Peponapis pruinosa*. Frankie et al. (2005) attributed encountering very few pollen specialists in California gardens to a lack of host plants. If green roofs were intentionally planted with bee-friendly and specialist-attracting forbs, it is likely that more specialist bees would use these habitats.

In a recent review of urban bee ecology, one of the main patterns was an increase in abundance of cavity nesters over other nesting types (Hernandez et al., 2009; see also Dalmazzo, 2010), and a study of bee diversity in New York City urban gardens recorded nearly twice as many cavity-nesting as soil-dwelling individuals (Matteson et al., 2008). It was therefore surprising that most of the bees collected in our study from parks and roofs were ground nesters and that the proportions of ground-nesting species and individuals were similar to those found in prairies. Over 70% of bees collected from green roofs were soil dwellers, as were 80% at parks, compared with 66% at prairies. However, this may be an artifact of our collection methods, as certain ground-nesting taxa such as *Lasioglossum* (*Dialictus*) are more often trapped in bowls than cavity-nesters such as *Megachile*.

The presence of many soil-dwelling bees on green roofs is encouraging, as it shows that these sites are within their foraging range (including height above ground level) or that bees utilize green-roof substrates for nesting. It is possible that ground-dwelling bees, especially larger species, have nests on the ground nearby and fly up to rooftops to forage. Although data on bee foraging distances are available, there is a lack of data on typical foraging heights (Greenleaf, Williams, Winfree, & Kremen, 2007). Detailed observations of bees and nest excavations on green roofs are necessary to determine where soil-dwelling bees may be nesting. On typical green roofs used in this study, under a top layer of very small slate pebbles there are one to several layers of well-draining soils, many with a high proportion of sand, that may provide a suitable nesting substrate. Potential sites could also include small flower pots, as *Lasioglossum* (*Dialictus*) are well known to nest in these. In order to attract and support cavity-nesting bees, site managers or landscaping companies could install "bee condos" (wood blocks drilled with numerous small holes). In addition, paper/straw nests could be deployed for mason bees and dead branches could be added to provide habitat for small carpenter bees (*Ceratina*). Providing appropriate nesting substrates has already been shown to attract many bird species to green roofs (Fernandez-Canero & Gonzalez-Redondo, 2010).

Of the 15 bee species that collectively contributed over 60% of the bee-community differences among habitat types; four had their highest relative abundance on green roofs. The alfalfa leaf-cutter bee *Megachile rotundata*, was the greatest overall contributor to community differences across habitat types, and was the only species collected from one green roof site. This exotic species was also found to be common in California urban gardens (Frankie et al., 2009) and was collected widely in New York City (Matteson et al., 2008). Two additional exotic species of subgenus *Eutricharaea* are also locally numerous in urban North America. Other species that made up a large proportion of green-roof bee communities were *Lasioglossum tegulare*, *Lasioglossum mitchelli*, and *Lasioglossum illinoense*, all of which are native, eusocial soil dwellers, and small even for species of subgenus *Dialictus*. *Lasioglossum* (*Dialictus*) frequently occur in urban bee surveys (Frankie et al., 2009; Matteson et al., 2008) and made up 45% of individuals in a survey of two green roofs in Toronto, Ontario (Colla et al., 2009). Their relatively small size predicts short flight ranges (Greenleaf et al., 2007) and small habitat ranges so they would seem less likely than larger species to visit green roofs from distant ground-level nests. For some *Dialictus*, green roofs may serve as self-contained “islands” of suitable habitat.

Green roofs are functioning as novel habitat islands in urban settings, providing resources for native bees and other volant fauna. Vertical green corridors using trellises to hold plants against the sides of buildings or green steps along the outside of buildings have been proposed (Fernandez-Canero & Gonzalez-Redondo, 2010), and horizontal corridors already exist (e.g., the High Line in New York City) that enable access by non-flying animals. The addition of more green roofs, and especially those with diverse plant communities and ranges in height would help to support native bees, other insects, and birds (Fernandez-Canero & Gonzalez-Redondo, 2010).

Our study and that of Colla et al. (2009) demonstrate that green roofs provide suitable habitats for North American wild bees including foraging resources and possibly to, an unknown extent, nesting substrates. Although native-bee communities on Chicago green roofs had fewer species and significantly lower abundance than ground-level urban natural areas, their overall bee-community composition did not significantly differ. Green roofs are a potentially important offset to habitat loss. By providing habitat for native species and thus supporting urban biodiversity, green roofs function as novel habitats valuable for conservation from a *reconciliation ecology* perspective (Rosenzweig, 2003). Urban green roofs are not suitable for all native bees, but a subset of them are supported by the foraging and (presumably) nesting resources green roofs provide. Relative to a surrounding, inhospitable matrix of buildings, streets, and traditional non-vegetated rooftops, green roofs are of high habitat value. In the face of land-use change and other anthropogenic disturbances, green roofs and other novel habitats are likely to play increasing roles in pollinator conservation.

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Appendix 1. Bee species abundance, nesting types, and foraging preferences collected from green roofs, parks, and prairies

Bee family genus	Species	Status[a]	Nest[b]	Green roofs	Parks	Prairies
Andrenidae						
Pseudopanurgus	albitarsis	N	S	0	0	2
Apidae						
Anthophora	terminalis	N	SW	0	0	1
Apis	mellifera	E	H	0	5	1
Bombus	auricomus	N	H	0	0	8
	fervidus	N	H	0	2	3
	griseocollis	N	H	0	1	9
	impatiens	N	H	1	6	12
Ceratina	calcarata or dupla	N	P	0	1	10
	dupla	N	P	0	0	7
Eucera	hamata	N	S	0	0	23
Melissodes	agilis	N	S	0	2	0
	agilis?	N	S	0	1	8
	agilis or trinodis	N	S	0	0	3
	bimaculata	N	S	2	4	24
	comptoides	N	S	0	0	1
	denticulata	N	S	0	1	0
	desponsa	N	S	0	0	4
	trinodis	N	S	0	0	2
	trinodis?	N	S	0	1	10
Peponapis	pruinosa	N	S	0	0	1
Svastra	obliqua	N	S	0	0	2
Xylocopa	virginica	N	W	0	1	1
Colletidae						
Colleies	latitarsis	N	S	0	0	2
Hylaeus	affinis	N	C	0	0	1
	affinis or modestus	N	C	0	0	7
	hyalinatus	E	C	4	3	3
	leptocephalus	E	C	2	0	0
	mesillae	N	C	0	6	4
Halictidae						
	virescens	N	S	20	13	55
Agapostemon						
Augochlora	pura	N	Sw	0	0	2
	aurata	N	S	0	0	5
Augochlorella						
Halictus	confusus	N	S	1	4	8
	ligatus	N	S	3	24	43
	parallelus	N	S	0	0	1
Lasioglossum	(Dialictus) unknown	N	S or SW	3	2	0
	albipenne	N	S	0	3	2
	anomalum	N	S	6	65	3
	cf callidum	N	S	0	0	1
	cinctipes	N	S	0	0	1
	coriaceum	N	S	0	0	2
	ellisiae	N	S	10	3	5
	illinoense	N	S	14	0	6
	leucozonium	E	S	0	0	1
	michiganense	N	CP	0	1	0
	mitchelli	N	S	14	13	20
	pectorale	N	S	2	4	0
	perpunctatum	N	S	0	0	3
	pilosum	N	S	0	48	0
	pruinosum	N	S	0	2	0
	zephyrum	N	S	13	1	0
	zophops	N	S	1	0	0
Sphecodes	unknown	N	CP	1	0	0
Megachilidae						
Anthidium	manicatum	E	C	0	4	0
	oblongatum	E	C	15	1	5
Coelioxys	banksi	N	CP	0	0	1
Hoplitis	pilosifrons	N	C	0	0	6
	producta	N	C	0	0	1
Megachilie	centuncularis	E?	C	1	0	0
	inermis	N	C	0	0	1
	latimanus	N	C	0	1	0

Bee family genus	Species	Status[a]	Nest[b]	Green roofs	Parks	Prairies
Osmia	mendica	N	C	0	1	0
	montivaga	N	C	0	0	5
	rotundata	E	C	10	1	0
	[Chenosmia] albiventris	N	C	0	0	1
		N	C	0	0	2
		Total bees collected		123	225	329

[a] Status in Illinois: N, native; E, exotic; E?, exotic status uncertain, treated as exotic for purposes of analyses.

[b] Nest location: S, soil; C, cavity; SW, soft wood; CP, cleptoparasitic.

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