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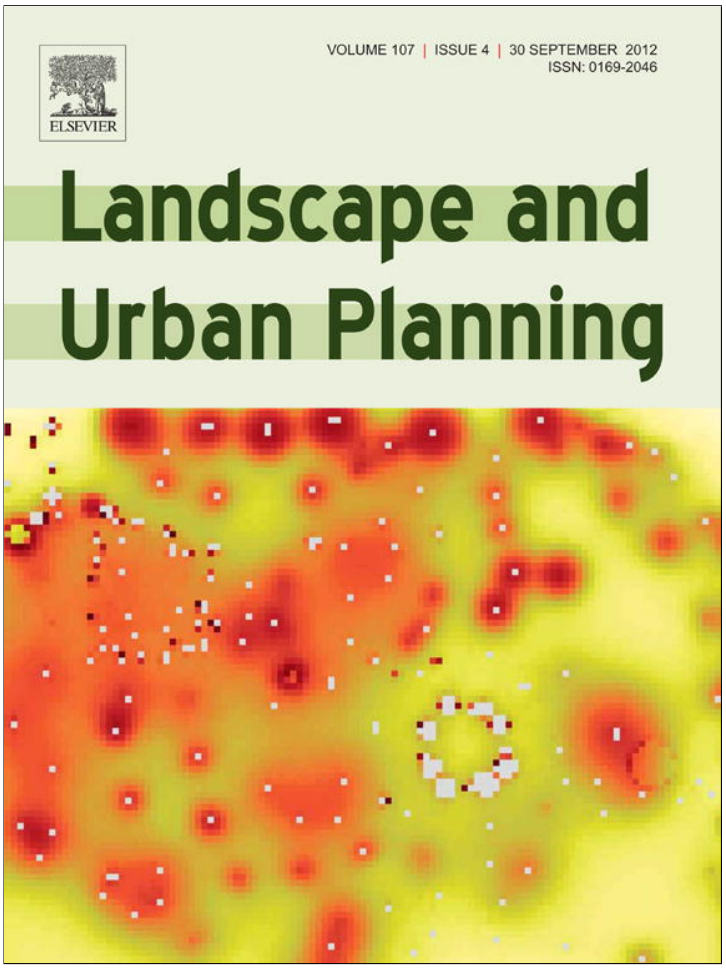

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An assessment of pollen limitation on Chicago green roofs

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HIGHLIGHTS

- We evaluated pollen limitation of nine native plant species on green roofs and ground-level sites through seed set studies and surveyed their associated pollinator communities.
- The percent of the maximum seed set on green roofs was significantly higher than that of nearby ground-level sites.
- Plants on green roofs were not pollen limited.
- Bee abundance on green roofs was lower than on the ground and bees found on green roofs had smaller overall body size.
- These results demonstrate that the ability of native plant species to produce seed is not hindered by being on a green roof, despite the lower number of pollinators.

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ABSTRACT

With increasing urbanization and creation of novel habitat types, green roofs can provide habitable space for many species. To date, most research on green roofs has focused on minimizing environmental impacts of buildings and little is known about the ecological services they may provide. Previous research has found a deficiency of pollinating bees on green roofs, which could result in pollen limitation, poor seed production and reproductive failure of many plant species requiring bee pollination. This study aims to determine whether pollination services on modern green roofs are sufficient for these novel habitats to function sustainably. Nine native Illinois prairie plant species and their pollinator communities were studied on green roofs and ground-level locations in the Chicago area. Pan traps were used to assess pollinator communities and supplemental pollination treatments were used to evaluate pollen limitation. All species showed significantly reduced seed set when pollinators were excluded but few significant differences were observed between supplemental and open pollination treatments. Seed set differed by habitat type in that green roofs had a higher overall mean percent maximum seed set compared to ground-level sites. Our results support previous studies, showing lower numbers and diversity of bees on green roofs compared to the ground level. Together, these data suggest that although green roofs contain a smaller and less diverse community of pollinators, the insects that are present provide sufficient pollinator services for many native plants. This study therefore supports the use of biotically pollinated native forbs in future green roof design.

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1. Introduction

As the global human population increases, urban landscapes are growing both in size and number, with over half of the current global population living in cities (UN-Habitat, 2010). Virtually all of the world's projected population increase over the next 30 years is expected to occur in urban areas (UN-Habitat, 2010). As this pattern continues, changes in habitat structure and function caused by habitat degradation, loss, and fragmentation will likely reduce the survival and reproductive ability of many plant communities (Aguilar, Ashworth, Galetto, & Aizen, 2006) as well as the species they support (Savard, Clergeau, & Mennechez, 2000; Winfree, Aguilar, Vazquez, LeBuhn, & Aizen, 2009).

Urban environments are particularly susceptible to the recently documented declines in pollinator diversity and richness (Potts et al., 2010). Increased fragmentation and infrastructure common to urban landscapes affect plant reproductive success due to changes in pollinator movement, diversity, and density (McIntyre & Hostetler, 2001; Tommasi, Miro, Higo, & Winston, 2004; Winfree et al., 2009). For example, isolated or fragmented patches are less accessible to pollinators than larger areas and require them to

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alter their foraging behavior to maximize floral resources (Andrieu, Dornier, Rouifed, Schatz, & Cheptou, 2009; Goverde, Schweizer, Baur, & Erhardt, 2002; Hadley & Betts, 2009). Plant species flowering in these urban patches may receive fewer successful pollinating visits resulting in pollen limitation; a reduction in plant reproductive success due to the deposition of low quality or a reduced quantity of pollen (Aguilar et al., 2006; Aizen & Harder, 2007). Further, smaller fragments in or near urban areas are often dominated by *Apis mellifera* (introduced European honey bee) and are characterized by a decrease in native (Aizen & Feinsinger, 1994; Gonzalez-Varo, Arroyo, & Aparicio, 2009), oligolectic, or pollen collecting specialists (Cane, Minckley, Kervin, Roulston, & Williams, 2006; Steffan-Dewenter, Klein, Gaebele, Alfert, & Tscharntke, 2006) and ground-nesting bee species (Cane et al., 2006). Visitation by non-specialist species and other ineffective pollinators experienced by plant species in urban environments can lead to decreased reproductive success (Cheptou & Avendano, 2006; Segal, Sapir, & Carmel, 2006; Liu & Koptur, 2003). If pollinator decline in highly disturbed urban landscapes continues (Winfree et al., 2009), pollen limitation could become increasingly common in fragmented urban plant populations (Knight et al., 2005). However, the complete array of community-wide effects of pollen limitation and long-term consequences are not completely well documented (Ashman et al., 2004; Steffan-Dewenter et al., 2006) and few empirical studies to date have demonstrated that perturbations in the pollinator community result in increased pollen limitation and reduced fitness in offspring (Cosacov, Nattero, & Cocucci, 2008; Gomez, Abdelaziz, Lorite, Munoz-Pajares, & Perfectti, 2010).

In contrast to the wake of urban expansion and the resulting fragmented habitat, the number of internationally reported green roof projects has increased from 93 in 2000 to over 1300 in 2012 (Greenroofs.com, 2012). Green roof installation on new and retrofitted buildings in North America has increased as a result of policies and technology standards employed by cities and municipalities that encourage their use (Carter & Fowler, 2008). Known environmental benefits include reduction in stormwater runoff (Carter & Butler, 2008; Dunnett, Nagase, Booth, & Grime, 2008; Oberndorfer et al., 2007), mitigation of the urban heat-island effect due to an increase in evapotranspiration (Getter & Rowe, 2006), pollution abatement (Rowe, 2011), and reduction in energy use by buildings for heating and cooling (Carter & Butler, 2008; Oberndorfer et al., 2007; Spala et al., 2008).

Despite the progress that has increased our understanding of how green roofs function, little research has focused on the ecosystem processes green roofs foster and how they compare to those in natural areas. Additionally, ecosystem functions, including the ability of these novel habitats to support communities of native plants and pollinators, have yet to be investigated in detail.

Native plants are increasingly being incorporated into green roof design and though they are often assumed to support native wildlife, few studies have shown that pollinating insects and birds use this available habitat (Baumann, 2006; Brenneisen, 2006; Colla, Willis, & Packer, 2009; Fernandez-Canero & Gonzalez-Redondo, 2010; Kadas, 2006; MacIvor & Lundholm, 2011; Tonietto, Fant, Ascher, Ellis, & Larkin, 2011). Furthermore, few published studies compare the abundance and diversity of pollinators on green roofs to nearby or similar habitats at the ground-level. Two recent investigations found marginal to no significant differences between pollinating species on green roofs and ground level (Colla et al., 2009; MacIvor & Lundholm, 2011). In Chicago, however, lower abundance and diversity of bees has been found on green roofs compared to nearby parks and natural areas (Tonietto et al., 2011). If the pollinator communities on green roofs are composed of fewer individuals and are less diverse, reductions in pollinator visitation and increases in pollen limitation could result in reduced seed set and reproductive success of plants on green roofs. The relationship between pollinator abundance and plant reproductive success has not previously been investigated in these urban habitats.

This study examines potential deficiencies in plant–pollinator interactions on green roofs in the Chicago area. We tested the following hypotheses focused on pollination on green roofs with pollen limitation and seed set studies: (1) plants on green roofs are pollen limited, and (2) seed set is lower in green roof plants than in nearby gardens or natural areas due to a reduction in pollinator diversity and abundance on green roofs.

2. Materials and methods

2.1. Site locations and characteristics

Chicago, IL, USA and its surrounding suburbs were chosen for the location of this study, as there are currently over 500 green roofs completed or in the process of being built in this area (Kamin, 2010). Experiments were conducted at four green roof locations and four ground level locations (Table 1); green roofs varied in size, distance from ground-level, time since establishment, sun exposure, irrigation regimes, and number of plant species. Three of the ground and green roof locations selected were paired, with ground sites adjacent to the buildings upon which the green roofs were located. All ground locations were landscaped with horticultural species and prairie species native to Illinois. The ground locations each contained a minimum of six of the species that were also found on the green roofs.

2.2. Species selection

Nine species were selected for analysis in the pollen limitation study: *Allium cernuum* Roth (nodding onion), *Amorpha canescens* Pursh (lead plant), *Aquilegia canadensis* L. (red columbine), *Baptisia alba* (L) Vent. (also known as *Baptisia leucantha* (L.) Vent. or wild white indigo), *Baptisia australis* (L.) R. Br. (blue wild indigo), *Dalea purpurea* Vent. (purple prairie clover), *Monarda fistulosa* L. (wild bergamot/bee balm), *Penstemon digitalis* Nutt. Ex. Sims (foxglove penstemon), and *Zizia aurea* (L.) W.D.J. Koch (golden Alexander). Species were chosen based on the following criteria: present at a minimum of three study sites, native to Illinois, animal-pollinated flowers, and production of seeds large enough to be contained within pollinator/seed predator exclusion bags. All species are perennials, reproduce by seed, and are primarily pollinated by bees (Cane, 2006; Cruden, Hermanutz, & Shuttleworth, 1984; Davis & Hendrix, 2008; Dieringer & Cabrera, 2002; Eckert & Schaefer, 1998; Haddock & Chaplin, 1982; Zorn-Arnold & Howe, 2007). Species were only used if there were more than ten individuals present at each site so as not to disrupt future persistence of the population by over-collection of fruits and seeds. The green roof at the Center for Green Technology lacked large populations of our selected species and therefore was not included in the pollen limitation experiment.

2.3. Autogamy

To determine the rate of spontaneous autogamy (self-fertilization), six individuals per species were haphazardly chosen at each location and a pollinator exclusion bag (Delnet® Pollinator Bags, Delstar Technologies, Inc.; 0.5 mm diameter pore size) was placed over a single flower bud or buds on a single inflorescence per plant. All pollinator exclusion bags were cut and sewn to the appropriate size based on flower/inflorescence length and secured with wire. Bags were left on the plant for the duration of the flowering period to exclude pollinators and seed predators. The proportion of the seed set attributable to autogamy was calculated for each location and species by dividing the average seed set of the closed

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Table 1
Research site information. Height of green roofs indicates the floor of the building on which the roof is accessible. Site area approximations were made using Google Earth and plant species estimates combine species lists provided by green roof owners with visual estimates of self-colonizing species.

Site name	Site type	Height above ground (stories)	Approx. site area (m^2)	Plant species estimate	Irrigation available?	Latitude	Longitude
Chicago Botanic Garden	Roof	2	1480	130–150	Yes	42.14443	−87.78591
	Ground	–	31,300	>300	No	42.14443	−87.78591
Chicago City Hall	Roof	12	2380	180–220	Yes	41.88385	−87.63240
Chicago Center for Green Technology	Roof	3	230	20–40	No	41.88916	−87.70072
	Ground	–	2500	>200	No	41.88916	−87.70072
Peggy Notebaert Nature Museum	Roof	3	200	70–100	Yes	41.92662	−87.63490
	Ground	–	2320	>200	No	41.92662	−87.63490
Waters School Community Garden	Ground	–	2500	150–200	No	41.96338	−87.69181

(bagged and autogamous pollination) treatment by that of the open treatment.

2.4. Pollen limitation

To test for pollen limitation, twenty-four healthy flowering individuals per species were haphazardly selected at each site and assigned to one of two treatments; open or supplemental pollination. One flower or inflorescence per plant was selected for each treatment and colored wires were attached to the focal flower or inflorescences to track treatment assignment and to correctly identify flowers involved in the treatment once fruit had matured. Both treatments were applied simultaneously to eliminate effects of light availability, precipitation, and variations in pollinator community (Kearns & Inouye, 1993). Flowers in the open pollination treatment received no additional pollen. For the supplemental treatment, plants were hand-pollinated (Bierzychudek, 1981). Pollen was collected from at least six unmarked individuals of the same species at the same time and combined to make species-specific pollen mixtures. Pollen that was stored in 1.5 ml Eppendorf tubes was used on the same day as collection or was stored in an air-tight box filled with silica. All pollen was applied within 48 h to ensure its viability. To facilitate the release of pollen from *P. digitalis*, anthers were placed in 1.5-ml Eppendorf tubes and left open in air-tight boxes with silica overnight.

When stigmas were visible and sticky (receptive), the pollen mixture was applied using one small sterile brush per population, the size and texture of which varied by species. Pollen was applied to stigmas until the receptive portion was completely coated to ensure maximum coverage. All brushes were washed, soaked in ethanol for 30 min, rinsed, and allowed to dry overnight between uses to prevent interspecific or nonviable pollen from inadvertently clogging the stigmas of the supplemented individuals. Flowers of each species were hand-pollinated once a week during the time of day when stigmas appeared most receptive. Flowers were accessible to pollinators for the remainder of the flowering period.

Once stigmas were no longer receptive and pistils had withered, exclusion bags (described above) were placed over the developing fruits to prevent fruit and seed predation. Once fruits were ripe, they were taken to the Reproductive Biology Lab at the Chicago Botanic Garden, where seeds were extracted and counted using a dissecting microscope and seed counter (Seedburo™ 801 Count-A-Pak®, Seedburo Equipment Company). When inflorescence was the focal unit, flower number was counted or estimated (via inflorescence length) before seeds were removed, depending on inflorescence structure (Table 2). Seeds were dried and stored in paper envelopes at 15 °C. Ten to twenty seeds from each individual were weighed and the total mass was divided by the number of measured seeds to calculate mean seed weight. To insure accuracy of measurements for all species including those with very low individual seed mass (for example, *M. fistulosa*), individuals with fewer than ten seeds were excluded from the analysis.

Pollen limitation value (PLV) as defined by Zorn-Arnold and Howe (2007) was used to quantify pollen limitation within a location for each species. Pollen limitation value per species (PLV_s) was calculated as $PLV_s = ((\bar{S}_s - \bar{O}_s)/\bar{S}_s) \times 100$, where $\bar{O}_s$ is the mean seed set in the open treatment and $\bar{S}_s$ is the mean seed set in the supplemental pollination treatment. For species for which inflorescence was the focal unit, the number of seeds per inflorescence or length of inflorescence (a proxy for flower number in species with indeterminate racemes) was used (Table 2).

Additionally, percent of the maximum seed set (PMSS) was used to assess differences at the plant community level. PMSS was used rather than measures of seed set across all species because the average number of seeds produced per focal unit varied based on species biology. For each species, $PMSS_s = (I_{si}/L_s) \times 100$, where I_{si} is the seed set of each individual and L_s is the largest seed set for a given species across all sites. The mean $PMSS_s$ was calculated for each site type (ground and roof) by dividing the sum of all roof or ground $PMSS_s$ values by the total number of individuals present at that site type.

Mean seed weight at each site type was calculated to assess seed quality for each species. The percent of the maximum seed weight (PMW_s) for each species was calculated as $PMW_s = (P_{si}/H_s) \times 100$, where P_{si} is the mean seed weight of each individual within a species and H_s is the highest mean seed weight observed for the species across all sites.

2.5. Insect collection and processing

Pan traps were used to assess the insect pollinator community as per Tonietto et al. (2011) on days with no precipitation and less than 60% cloud cover. Traps were set out before 0800 h and removed after 1600 h or left for a period of 24 h (LeBuhn et al., 2003). Insects were collected approximately every 4 weeks (LeBuhn et al., 2003) for 3 months to coincide with the full flowering period of all nine study species. Trapped insects were rinsed with water and stored in Whirl-Pak® bags with 70% ethanol within 24 h of being collected (Davis & Hendrix, 2008). All insects were identified to order using Bland and Jaques (1978). Bees were grouped by body length (small < 8 mm, medium 8–12 mm, and large > 12 mm) to separate the collected genera a posteriori, based on classifications from previous studies (Dieringer & Cabrera, 2002; Tonietto, 2009).

2.6. Statistical analyses

2.6.1. Pollen limitation

Statistical analyses were performed in R, version 2.10.1 (R Development Core Team, 2009) and JMP, version 5.1.2 (JMP, 1989). We used the plot (lm.model) function in R to test for non-normality and heteroskedacity of the data. Seed set and seed weight data for all nine species except *B. alba* were normally distributed. Data for *B. alba* were therefore log-transformed before analyses. Best fit linear models (using the (lm) function in R) were used to test for significance between pollination treatments (supplemented versus open)

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Table 2
Species-specific collection information and percent of seed set that can be explained by autogamy. Autogamy measurements were derived by comparing mean seed set in the bagged control to the open treatment. Significance and adjusted R^2 values were obtained from the least square model analysis of seed set between the bagged control and open treatment.

Species	Focal unit	Number of sites (ground/roof)	Bloom period	Seed set attributed to autogamy (%)	p	Adjusted R^2
Allium cernuum	Flower	3/3	August	11	<0.0001	0.65
Amorpha canescens	Raceme length (mm)	1/2	June–July	2	<0.0001	0.87
Aquilegia canadensis	Flower	3/3	May–June	49	<0.001	0.10
Baptisia alba	Flower	3/1	June–July	6	<0.01	0.19
Baptisia australis	Flower	2/1	May–June	4	<0.001	0.19
Dalea purpurea	Spike length (mm)	1/3	July	45	<0.001	0.17
Monarda fistulosa	Head	3/2	July–August	7	<0.0001	0.57
Penstemon digitalis	Flower	4/2	June–July	12	<0.0001	0.18
Zizia aurea	Umbel	3/2	May–June	40	<0.01	0.11

for each species at both site types (roof and ground) and to determine effect of site type and treatment on pollen limitation and seed weight. A standard least square model was used in JMP to evaluate the effect of treatment and site on seed set.

2.6.2. Insect collections

We used a generalized linear model (using the (glm) function in R) to evaluate the relationship between the numbers of bees from different size categories and site type. A contingency table of site type by bee size was created and a Pearson's chi-square analysis was performed to determine significant variations from expected values in bee communities between green roofs and ground-level sites. Expected values for this analysis were generated for each cell by multiplying the row total by the column total and dividing by the grand total. To view the pollen limitation data in light of the pollinator collections, the relationship between the mean PMSS of all species combined was plotted against the total number of bees caught at each location. The bee data from the green roof at the Chicago Center for Green Technology was excluded due to the lack of PMSS data at this location.

3. Results

3.1. Autogamy

When data from all sites were combined, seed set in the closed treatment was 18.76% of that of the open treatment. Autogamy explained less than 12% of seed set in six of the nine species, but seed set was substantial in the absence of pollinators for three species: *A. canadensis* (49%), *D. purpurea* (45%), and *Z. aurea* (40%). Although the proportion of the seed set attributable to autogamy was high for some species and site combinations, the closed treatment had significantly fewer seeds than the open treatments in all cases ($p < 0.01$, Table 2). As the closed treatment revealed significantly lower seed set for all species, the data from the bagged treatment were not included in the remainder of the analyses.

3.2. Pollen limitation

Using t-tests, we found no significant support for pollen limitation (comparing open versus supplemental pollination) for any of the species, except for *A. cernuum* ($p = 0.001$) which had higher mean seed set with supplemental pollination at both green roofs (1.50 ± 0.11 seeds/flower) and at ground level sites (1.10 ± 0.10 seeds/flower) compared to the open pollination treatment (1.04 ± 0.07 seeds/flower at green roofs; 0.98 ± 0.06 seeds/flower at ground level). There was a significant difference in seed set ($p < 0.05$) by location (individual sites) for all species except *A. canescens* ($p > 0.05$). There was no significant interaction for seed set between location and treatment except for *A. canadensis* ($p = 0.004$) and *P. digitalis* ($p = 0.025$), which was driven by a single but different location in each case according to a pair-wise Student's t-test. Controlling for family wise error using a Bonferroni–Holm correction allowed the null hypothesis to be accepted for *P. digitalis* but not *A. canadensis*. Specifically, supplemental pollination significantly decreased mean seed set for *A. canadensis* at the Chicago Botanic Garden green roof (102.83 ± 10.63 seeds/flower in open treatment, $N = 12$ compared with 48.17 ± 24.66 seeds/flower in supplemented treatment, $N = 6$).

The majority of species (six of nine) exhibited a small degree of pollen limitation at only one site type, as determined by the PLV_S metric; *A. cernuum* and *B. australis* were the only species with substantial pollen limitation at both site types (Table 3). Overall, mean PLV_S was low for most species with many showing no evidence of pollen limitation (Table 3). No significant difference was found between mean ground PLV and mean roof PLV when data from all species were combined by site type (mean ground PLV = 9.04 ± 4.07; mean roof PLV = 13.65 ± 9.17).

No significant effect of treatment or treatment by site type interaction on $PMSS_S$ was found. As no significant effects of pollen supplementation on seed set was found, the data from the open and supplemented treatment were pooled. Site type was significant (ANOVA, $F_{1,741} = 12.5$, $p < 0.001$) with plants on the ground having a significantly lower mean PMSS ($28.96\% \pm 1.01$, $N = 400$) than those on the green roofs ($36.58\% \pm 1.30$, $N = 343$; Fig. 1). There was a significant interaction between site type and species on mean PMSS (ANOVA, $F_{8,781} = 10.79$, $p < 0.001$). For six species, $PMSS_S$ was higher on the roofs than at the ground-level, although the difference was statistically significant for only two species (Fig. 1): *B. australis* ($p < 0.001$) had a lower mean $PMSS_S$ on the roof, while *D. purpurea* ($p = 0.015$) had a lower mean $PMSS_S$ on the ground. Data from *B. alba* were excluded from the comparative PMSS analysis due to the necessary log-transformation correction.

No effect of treatment or its interaction with site type was found on seed weight. Site type had a significant effect on seed weight (ANOVA, $F_{1,770} = 21.7$, $p < 0.001$); plants on the green roofs had higher overall mean PMW values (65.84 ± 2.38, $N = 353$) than plants on the ground (54.74 ± 1.61, $N = 419$).

3.3. Insect collections

The number of insects collected at each site type and in each body size category per trapping period was low and no significant effect of bowl color or the interaction of bowl color with site type was found on the total number of bees captured. Data from pan traps were therefore pooled for sites within each site type category (Table 4). Green roofs had fewer bees ($N = 133$) than ground level sites ($N = 281$). There was a significant negative correlation between mean PMSS and overall bee abundance ($R^2 = 0.708$, $p < 0.01$; Fig. 2). Pollinator community composition also differed by site type; ground and roof communities were dominated by small bees (*Augochlorella*, *Caliopsis*, *Halictus*, *Hylaeus*,

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Table 3
The mean pollen limitation value (PLV_s) and percent of the maximum seed weight (PMW_s) for each species by ground level and green roofs sites. Negative values of PLV_s were converted to zeros, indicating lack of pollen limitation. See Section 2 for, PLV_s and PMW_s equations.

	Ground		Roof	
	PLV_s (*N*)	Mean $PMW_s \pm$ SE (*N*)	PLV_s (*N*)	Mean $PMW_s \pm$ SE (*N*)
Allium cernuum	11.36 (70)	59.29 ± 1.62 (70)	30.77 (63)	70.68 ± 1.62 (67)
Amorpha canescens	0.00 (22)	47.19 ± 1.70 (23)	2.24 (47)	64.78 ± 1.95 (50)
Aquilegia canadensis	0.00 (55)	70.72 ± 1.48 (58)	0.00 (44)	60.23 ± 2.04 (48)
Baptisia alba[a]	0.00 (49)	57.98 ± 3.31 (34)	0.00 (7)	41.12 ± 29.45 (3)
Baptisia australis	30.92 (34)	79.21 ± 1.91 (33)	81.96 (22)	86.03 ± 4.30 (9)
Dalea purpurea	0.00 (22)	57.62 ± 2.53 (24)	0.00 (64)	70.58 ± 1.38 (75)
Monarda fistulosa	0.00 (70)	44.74 ± 1.31 (77)	7.87 (46)	57.72 ± 2.06 (50)
Penstemon digitalis	13.32 (68)	41.32 ± 2.17 (51)	0.00 (44)	46.07 ± 3.41 (33)
Zizia aurea	25.76 (59)	41.81 ± 1.45 (49)	0.00 (13)	55.79 ± 4.93 (18)
All species combined	9.04 ± 4.07 (449)	54.74 ± 2.38 (419)	13.65 ± 9.17 (350)	65.84 ± 2.38 (353)

[a] Seed set data for *B. alba* were log-transformed to calculate PLV_s.

Table 4
Number and proportion of bee from each size category captured at ground level and on green roofs. For body size categories: small <8 mm, medium 8–12 mm, large >12 mm.

Body size category	Total	Ground		Total	Roof	
		Mean ± SE	Community proportion (%)		Mean ± SE	Community proportion (%)
Small	175	40 ± 7	62.28	77	19 ± 9	57.89
Medium	16	4 ± 2	5.70	28	7 ± 3	21.05
Large	90	22 ± 2	32.03	28	7 ± 3	21.05
Total	281			133		

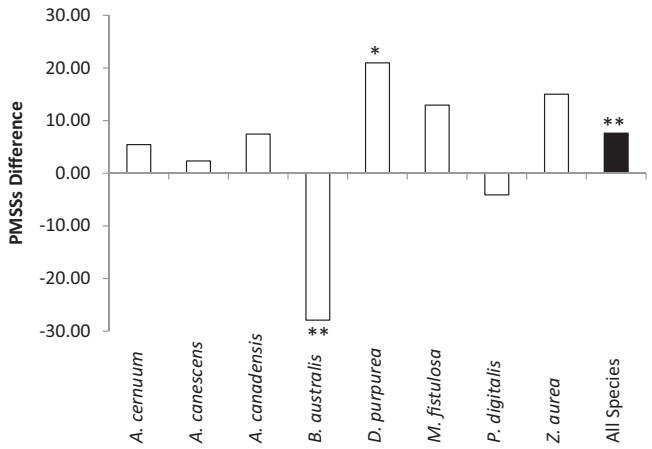

Fig. 1. Difference between mean percent of the maximum seed set ($PMSS_s$) at green roofs and the ground level for combined treatments (open and supplemental pollen). Asterisks indicate a significant difference between treatments at the $p < 0.05$ (*) and $p < 0.001$ (**) levels.

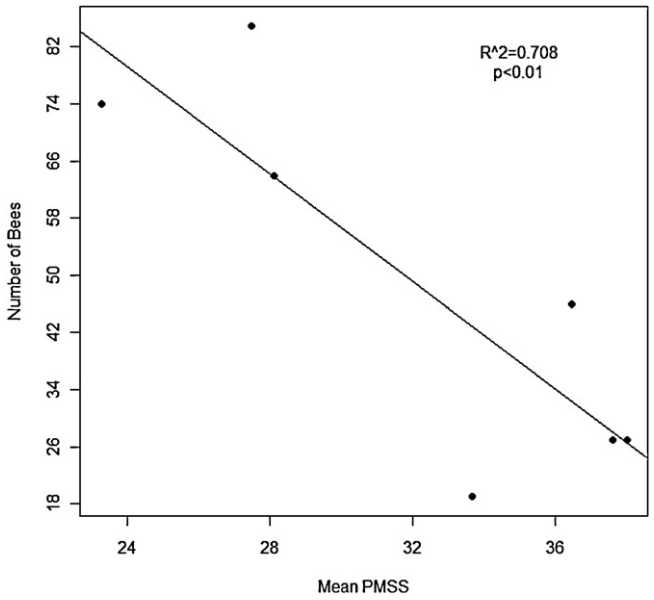

Fig. 2. Relationship between the total number of bees captured and the mean percent of the maximum seed set (PMSS) for all species combined at each site. Information from the green roof at the Chicago Center for Green Technology has not been included due to lack of seed set data.

and Lasioglossum; 62.28% and 57.89% of the total community, respectively) while large bees (*Agapostemon*, *Bombus*, *Melissodes*, *and Xylocopa*) represented 32.03% of the community on the ground. Only a few medium bees were found on the ground (5.70% of the community, genera including *Apis*, *Megachile*, *and Anthidium*; Table 4). On green roofs, medium and large bees were found in equal proportions (21.05%; Table 4).

The numbers of large and medium bees for green roof and ground level sites deviated significantly from expected values ($\chi^2 = 24$, df = 2, $p < 0.001$; Table 4) with the green roof sites having more medium and fewer large bees than the ground-level sites.

4. Discussion

All nine of the plant species we examined rely on pollinators for maximum reproductive output and we found no evidence that native plants on green roofs are more pollen limited than when planted at ground-level locations. Further, green roofs supported a lower abundance of bees (particularly large bees) than nearby urban green space, consistent with previous research in the Chicago area (Tonietto et al., 2011). Our data suggest that pollen limitation is not common in the metropolitan Chicago region, as our sites were located in areas of moderate to dense urban development. These data highlight the importance of viable pollinator communities in sustaining pollinator-dependent native plant species used in green roof design (Butler, Butler, & Orians, 2012).

The fact that supplemental pollination did not increase seed set suggests that plant reproductive success at both site types is not affected by low pollen quality or quantity. In addition, while the

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contribution of autogamy varies among the species studied here, all nine species have the potential to benefit from the reproductive assurance afforded by self compatibility in situations where pollinators are rare or when nonviable or interspecific pollen is deposited on stigmas. Though pollen limitation can occur in species with self-compatible breeding systems (DeMauro, 1993), as are all of the species in our study, pollen limitation may be more pronounced in species with self-incompatible breeding systems (Knight et al., 2005), where reproductive assurance via selfing does not occur. Future studies investigating the patterns of pollen limitation on green roofs in self-incompatible plant species would provide useful information to this field.

Of the nine species studied, *A. cernuum* was the only species with significantly greater seed set when provided with supplemental pollen. However, this effect was observed at both ground and green roof sites, indicating that pollen limitation in this species was not confined to green roofs. Schuett and Vamosi (2010) found that *A. cernuum* is usually pollinated by *Bombus* and *Andrena* species. *Bombus* have experienced population declines in the Chicago area (Grixti, Wong, Cameron, & Favret, 2009) and *Andrena* were not found in large numbers at any of the study sites, which suggests that the effective pollinators of this species may be lacking in these urban sites and may therefore explain pollen limitation in *A. cernuum* in our study. Although there was no significant difference in seed set in the remaining eight species, *B. australis* exhibited pollen limitation at both site types, indicating that supplemental pollination may contribute (albeit not significantly) to increased seed set.

A surprising exception to the observed trend in the supplemental pollination treatment was the decreased seed set in one green roof population of *A. canadensis*. This species is highly self-compatible and capable of spontaneous autogamy (Eckert & Schaefer, 1998). Supplemental pollination would still be expected to increase seed set unless the hand pollination procedure itself interfered with reproductive success by inadvertently damaging reproductive structures, which has been documented by Young and Young (1992).

While few studies have investigated the relationship between urban fragmentation and pollen and pollinator limitation, our results are similar to those of fragmented agricultural landscapes (Steffan-Dewenter et al., 2006), where habitat area and population size do not affect seed set. Habitat patch size may not affect pollinator diversity or fruit set of prairie plant species growing in fragmented landscapes (Slage & Hendrix, 2009); even small patches of habitat such as that provided by green roofs, have the potential to provide the floral resources necessary to support pollinators. However, caution must be taken when applying the observed trends too broadly, as pollen limitation of a small number of individuals does not necessarily imply pollen limitation at larger population-level scales (Ashman et al., 2004).

At both site types, small bee genera were more dominant than medium and large-sized bees. Although the pan trap sampling method may have excluded larger bees (Roulston, Smith, & Brewster, 2007), the lack of large bees captured on green roofs in our study is consistent with the pattern documented in a previous study in the same region in which a combination of pan traps, netting, and pollinator observations were used (Tonietto et al., 2011). As body size is positively correlated to homing and foraging distance (Gathmann & Tscharntke, 2002; Greenleaf, Williams, Winfree, & Kremen, 2007), the large number of small genera found in this study suggests these bees live within or in close proximity to these locations. For green roofs surrounded by limited green space, this may imply that communities of small-bodied bees are able to effectively use green roofs as habitat. While the combined use of pan traps, netting and pollinator observations was beyond the scope of the present study, future research should employ these methods to confirm that medium- and large-bodied bees are not more abundant and do not contribute significantly to the pollinator communities and plant reproductive success on green roofs.

Honey bees (*A. mellifera*) are known to be poor pollinators of many plant species due to idiosyncrasies of their behavior (Westerkamp, 1991) and a mismatch between their morphology and that of many flowers (Westerkamp & Gottsberger, 2000). Plants at sites where the bee community is dominated by honey bees rather than native solitary bees of various morphologies would be expected to experience an increase in magnitude of pollen limitation (Knight et al., 2005). Two green roofs sites (City Hall and Notebaert) had managed honey bee hives present for a portion of the study period and, as such, we expected the bee communities to be dominated by *A. mellifera*. However, while more *A. mellifera* individuals were present at these roofs than at the ground sites, they were not the most prevalent bee type. The lack of pollen limitation at these sites suggests that *A. mellifera* may increase the magnitude of pollen limitation, possibly due to the mismatch between body shape and flower morphology.

Although seed set was expected to increase with pollinator abundance, we observed a strong negative relationship between seed set and the number of bees captured at each site. This suggests that although there were fewer bees on green roofs relative to the ground level, those present occurred in numbers sufficient to successfully pollinate these plant species. Other studies have found that frequent pollinator visitation can lead to high amounts of pollen limitation (Hegland & Totland, 2008); if generalist bees visit flowers but do not transfer pollen, the observed presence of pollinators may not coincide with plant reproduction. Clearly, the role that pollinator abundance and visitation rate have on pollen limitation is very complex and warrants further investigation in which pollen transfer is explicitly measured through studies of single-visit effectiveness.

Many factors could account for the unexpected relationship between pollinator abundance and seed set observed in this study. Reproductive output is influenced by many factors other than pollination, including seed herbivory and maternal effects, or the availability of resources for the maturation of fertilized ovules (Knight et al., 2005). Differences in microclimate variables such as solar radiation, precipitation, temperature and relative humidity could also affect seed production in important ways (Jones, 1992). Many species planted on typical extensive green roofs do not thrive over multiple growing seasons due to the stressful growing environment (Monterusso, Rowe, & Rugh, 2005; Rowe, Getter, & Durhman, 2012), which could also contribute to seed set. Although the green roofs used for the pollen limitation portion of this study were all considered to be semi-intensive or extensive green roofs (study species were grown in no more than 6 in. of planting media), they were all display roofs with irrigation systems that could be used in times of limited precipitation or intense. Precise supplemental watering records were not available for these sites, though we believe it is unlikely that the plants growing on these green roofs would have produced more seeds than those on the ground in response to drought-induced stress.

Overall, this study provides support that native plant species on green roofs do not experience pollen limitation in the Chicago region. As green roofs technology expands globally, this unique study supports the use of green roofs to provide habitat for native plant and insect species in urban environments. With increasing urbanization, native pollinators with limited ranges face the threat of extinction in fragmented environments unless appropriate habitat corridors are available (Townsend & Levey, 2005). When planned appropriately, urban green areas can provide continuously abundant sources of pollen, nectar and seeds for birds, bees (Tommasi et al., 2004) and other insect guilds. Many buildings in urban areas could be retrofitted to include green roofs that

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offer such resources. As the loss of pollinators has been documented globally (Potts et al., 2010), further research in this field could contribute to their conservation (McIntyre & Hostetler, 2001). Many pollinators are currently found in urban green spaces such as parks, but their diversity depends on the quality of the surrounding vegetation (McFrederick & LeBuhn, 2006; Tonietto et al., 2011). Ensuring species-appropriate foraging and nesting habitats are available would help support long-term urban insect populations (Kearns, Inouye, & Waser, 1998). If native plant species can persist on green roofs, urban planners would be wise to incorporate these species along with high pollen- and nectar-yielding non-native species into city-wide biodiversity conservation and improvement projects.

As pollen limitation has been found to fluctuate across growing seasons (Aizen & Harder, 2007), additional long-term studies would provide independent validation of our conclusions which are derived from data collected during a single field season. Urban gardens are known to contribute to city-wide biodiversity and it has been suggested that they should be studied from the perspective of the entire matrix in which they exist, rather than as individual habitats (Goddard, Dougill, & Benton, 2009). Because it is difficult to speculate about broad-reaching trends from limited observational sites, data obtained from green roof studies such as ours should be incorporated into larger, comprehensive studies of urban habitat connectivity. Green roof technology continues to provide an increasing amount of habitable space for many native species (Butler et al., 2012) and has the potential to make even greater contributions to urban ecosystems as the ecological relationships that occur in these novel habitats is understood, fostered and protected. As this industry grows and interest in green roof ecology deepens, similar studies have the potential to contribute greatly to our understanding of the multi-functionality of green roofs.

Native species on green roofs have the potential to play an important role in reconciliation ecology practices, in which management techniques allowing humans and native wild species to occupy the same geographic ranges are used (Rosenzweig, 2001). At a time when urbanization is causing biotic homogenization (McKinney, 2006), the preservation of local native species is critical. While green roofs are certainly not the only technique needed in urban areas for preservation of future biodiversity, particularly due to their currently limited coverage, they represent a new piece of the conservation puzzle that extends ecosystems into the vertical dimension and has the potential to make important contributions to biodiversity in urban landscapes (Francis & Lorimer, 2011).

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