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Conservation in post-industrial cities: How does vacant land management and landscape configuration influence urban bees?

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Abstract

1. Rich pollinator assemblages are documented in some cities despite habitat fragmentation and degradation, suggesting that urban areas have potential as pollinator refuges. To inform urban bee conservation, we assessed local- and landscape-scale drivers of bee community composition and foraging within vacant lots of Cleveland, Ohio, USA. Cleveland is a shrinking city, a type of urban area that has an over-abundance of vacated greenspaces as a result of population loss and subsequent demolition of abandoned infrastructure. As such, Cleveland represents over 350 post-industrial cities worldwide that are all promising locations for bee conservation.

2. Across a network of 56 residential vacant lots (each ~30 m × 12 m), we established seven unique habitats, including seeded native prairies, to investigate how vegetation management and landscape context at a 1,500 m radius influenced urban bee communities. We assessed the distribution of several bee functional traits, diversity and abundance with pan and malaise traps. Foraging frequency was determined with plant–pollinator interaction networks derived from vacuum collections of bees at flowers.

3. We observed higher bee richness and increased abundance of smaller sized bees as the size of surrounding greenspace patches increased within a 1,500 m radius landscape buffer. Within habitats, seeded treatments had no effect on bees but greater plant biomass and shorter vegetation were correlated with increased bee richness and abundance. Plant–pollinator interaction networks were dominated by spontaneous non-native vegetation, illustrating that this forage supports urban bees.

4. *Synthesis and applications*. Our study indicates that proximity to larger greenspaces within an urban landscape promotes overall bee richness and increased occurrence of smaller bee species within residential vacant lots. While we did not observe our seeded native plants enhancing the bee community, native wildflowers were still establishing during the study and may have a greater influence when

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blooming at higher densities. Importantly, spontaneous non-native vegetation provided the majority of urban bee's forage. Thus, vacant land that is minimally managed and vegetated with what many consider undesirable 'weeds' provides valuable habitat for bee conservation in cities.

1 | INTRODUCTION

Urbanization poses strong constraints on species pools, often reducing biodiversity (Faeth et al., 2011). As landscapes are altered to accommodate growing cities, habitat loss and fragmentation can decrease species richness and abundance (Fahrig, 2013, 2017). For species that are able to overcome landscape-scale barriers, other pressures such as light, heat or heavy metal pollution can also impact population growth and fitness (Harrison & Winfree, 2015; Sivakoff et al., 2020). Typically, urban species pools are dominated by generalist, exotic and urban-adapted species (Faeth et al., 2011; Winfree et al., 2011). Some cities, however, have shown opposite patterns for urban taxa (Faeth et al., 2011). For example, high bee species richness and/or abundance has been documented in cities in Europe and Australia (Baldock et al., 2015; Threlfall et al., 2015), likely due to greater floral resources from human cultivation. If cities are to realize their conservation potential (Hall et al., 2017), it is critical to understand the drivers of these ecological patterns to establish guidelines for habitat management (Turo & Gardiner, 2019).

Ecological hypotheses suggest that those cities with an intermediate amount of greenspace may benefit the most from new conservation habitat (*see hypothesis 7 in* Tscharntke et al., 2012). For instance, agro-environmental schemes are more effective in agricultural landscapes with an intermediate amount (1%–20%) of semi-natural habitat as compared to more complex or simple landscapes (Scheper et al., 2013). Applying this pattern to urban ecosystems, we conjecture that large, highly urbanized cities may be less suited for investment in urban conservation initiatives as they often contain limited greenspace, especially at the scales necessary to support organisms with restricted dispersal capacities. However, there are an estimated 350 shrinking cities worldwide (Rieniets, 2009), which may represent opportune locations for urban conservation given their more intermediate greenspace holdings. In these post-industrial cities, economic decline has resulted in extensive demolition of urban infrastructure which is then transformed into large holdings of minimally managed vacant land. For example, Detroit, Michigan, USA contains 122,397 vacant lots (Data Driven Detroit pers. comm., 12 December 2019). This overabundance of vacant land offers a unique opportunity to experiment with both large-scale urban habitat restorations and optimal landscape placement of these habitats. Whereas greenspace is a fixed element within most growing cities, vacant land is arrayed in flexible landscape patterns. As restoration initiatives are more apt to succeed with optimal landscape placement (Gilby et al., 2018), shrinking cities represent key investments for urban conservation.

Bees are appropriate targets for urban conservation as their global populations are in decline (Potts et al., 2010) and over 800 million urban farmers (Smit et al., 2001) benefit from pollination services. Distributions of urban bees are influenced by several landscape- and patch-scale factors. At a landscape scale, greenspace abundance (Tonietto et al., 2011), increased patch size (Beninde et al., 2015; Quistberg et al., 2016; Stewart et al., 2018) and patch connectivity (Banaszak-Cibicka et al., 2016; Beninde et al., 2015; Marini et al., 2014) are drivers of bee abundance, richness and evenness. Moving forward, these patterns should be assessed through city-wide manipulations of pollinator habitat to evaluate the relative importance of patch area and fragmentation for urban bee communities (*see hypothesis 2 in* Tscharntke et al., 2012). At a patch scale, increased floral abundance correlates with greater numbers and/or richness of urban bees (Hülsmann et al., 2015; Quistberg et al., 2016; Shwartz et al., 2013; Stewart et al., 2018), but no consistent patterns have been identified in regard to floral identity. In many cases, native plants attract a rich and abundant urban bee community (Salisbury et al., 2015; Threlfall et al., 2015); however, non-natives are also documented as important urban forage (Larson et al., 2014; Salisbury et al., 2015; Sivakoff et al., 2018). Thus, assessments of recommended native bee forage versus spontaneous non-native vegetation are needed to inform future conservation initiatives.

We established the Cleveland Pocket Prairie Project in Cleveland, Ohio, USA to investigate how urban greenspace design and landscape context influence bee community composition and foraging patterns. Cleveland, which has lost over half of its peak population, is a shrinking city that contains 27,000+ vacant lots covering 1,600 acres (Western Reserve Land Conservancy, 2015). Both greenspace availability and governmental interest in sustainability (e.g. Cleveland Climate Action Plan, Green City Blue Lake Program, Cleveland's Neighborhood Progress) facilitated our city-wide manipulated field experiment. We hypothesized that residential vacant lots seeded with native Ohio wildflowers, exhibiting an increased bloom abundance, would support a more abundant and diverse bee community relative to the existing urban spontaneous vegetation found within vacant lots. Furthermore, we expected

that habitats seeded for increased floral diversity would feature more specialized foraging networks as specialist bees are more likely to recruit to a diverse habitat. Likewise, we predicted that landscape fragmentation would negatively affect bee richness and abundance and restrict the incidence of specialist foragers by impairing dispersal to greenspaces.

2 | MATERIALS AND METHODS

2.1 | Study sites

From June 2015 to August 2016, we studied 56 residential vacant lots across eight neighbourhoods in Cleveland, Ohio, USA. Within each neighbourhood, seven vacant lots were randomly assigned to habitat treatments. *Control* and *Meadow* treatments contained pre-existing vegetation; all other treatments were seeded. Treatments were as follows: (a) *Control*: non-native turf grasses and spontaneous vegetation, mown monthly, (b) *Meadow*: non-native turf grasses and spontaneous vegetation, mown annually, (c) *Fine-fescue Lawn*: low-growing, non-native fine-fescue grasses, (d) *Flowering Lawn*: low growing, non-native fine-fescue grasses with four non-native forbs, (e) *Grass Prairie*: three tall, native grass species, (f) *Low Diversity Prairie*: a tall, flowering habitat with three native grasses and six forbs and (g) *High Diversity Prairie*: a tall, flowering habitat with three native grasses and 22 species of forbs (see Table S1). During 2015, all treatments, except *Meadow*, were mown monthly to facilitate establishment of seeded species. In 2016, *Control* and *Lawn* habitats were mown monthly while *Meadow* and *Prairie* sites were mown annually in October. One *Meadow* replicate was not included in 2016 due to reoccurring vandalism.

2.2 | Vegetative community assessment

Plant assessments occurred in early and late season 2015 (*early*: 16 June–17 July, *late*: 22 July–13 August), and early, middle and late season 2016 (*early*: 13–24 June, *middle*: 11–22 July, *late*: 4–16 August). In the centre of each vacant lot, we created a 7 × 15 m grid and randomly sampled this grid to monitor vegetation height, bloom area, dominant species diversity and plant biomass.

To assess plant height, bloom abundance and bloom area, we selected six 1 m^2 grid quadrats and placed a 0.5 m^2 PVC pipe square in each quadrat's centre, wherein data were collected. We measured plant height (cm) at the centre and at two opposite corners of the quadrat. Then, we calculated a *mean plant height* for each site by averaging all height measurements. Bloom abundance and area were estimated from the same six quadrats. For each flowering species, we counted all floral units to determine *bloom abundance* (see Table S5). We then took five random measurements (mm^2) of individual floral units per species. Average bloom size per species was calculated and then multiplied by bloom abundance to quantify total *bloom area* at a site.

Plant biomass and diversity were estimated from 20 separate quadrats in our plot grid. We recorded the three most dominant plant species. Grasses were pooled into one general category. *Dominant species diversity* was calculated from a total of 60 plant records per site with a Shannon–Wiener Index. To estimate vegetation biomass, we used a comparative yield method (Haydock & Shaw, 1975). We identified five quadrats within the grid that represented a subjective scale of least (1.0) to most (5.0) plant biomass. We then compared the biomass from our 20 random quadrats to this scale (1.0–5.0) and estimated, in quarter increments, the relative density of plants within. We harvested vegetation from a representative 0.5 m^2 portion of each standard, dried it and measured dry plant weight. Linear regression equations were created for each site from these five dry weights, and *plant biomass* per site was averaged from the 20 dry weight estimates.

2.3 | Landscape features

Landscape data were obtained through the Cleveland City Planning Commission and described landscape cover at 1 m^2 resolution from 2011 aerial imagery for a 1,500 m radius surrounding each site (Galvin & O'Neil-Dunne, 2013). We classified landscapes in a binary land cover system as either 'greenspace' (*shrubs and grass*, *tree canopy over shrubs and grass*) or 'other' (*impervious surface*, *buildings*, *tree canopy over impervious surface and buildings*). We then examined landscape configuration, as patch area and connectivity are important biodiversity drivers (Tscharntke et al., 2012) identified in previous bee studies (Banaszak-Cibicka et al., 2016; Marini et al., 2014). We used FRAGSTATs software (McGarigal et al., 2012) to measure four class level indices: (a) total area (m^2) of greenspace within a landscape (*total.gs*), (b) mean patch size (m^2) of greenspace (*gs.size*), (c) percentage of a landscape composed by the largest patch of greenspace (*LPI.gs*) and (d) mean isolation (m) between greenspaces (*ENN*).

2.4 | Urban bee communities and foraging preferences

We conducted a bee community assessment with pan traps and SLAM Malaise traps (Bugdorm© MegaView Science Co.) in a subset of treatments (*Control*, *Fine-fescue Lawn*, *Flowering Lawn*, *Grass Prairie*, *Low Diversity Prairie*, n = 40) in 2015 and all treatments (n = 55) in 2016. Sampling took place once per sampling period from 10 a.m. to 2 p.m. on non-rainy days in early, middle and late season in 2015 (*early*: 16–26 June, *middle*: 16–27 July, *late*: 11–21 August) and 2016 (*early*: 9–21 June, *middle*: 5–20 July, *late*: 2–12 August). Bees were sampled with one malaise trap and seven bright yellow plastic bowls (12 oz; Solo© Dart Container Corporation) filled 2/3 with a 1% dish soap solution (Blue Dawn© Proctor and Gamble). Pan traps were placed on the ground in

randomly selected quadrats while malaise traps were deployed at the lot's centre.

Foraging bees were actively sampled once per month on non-rainy days within all flowering treatments (*Control, Meadow, Flowering Lawn, Low Diversity Prairie, High Diversity Prairie*) in early and late summer in 2015 (*early*: 8–15 July, *late*: 12–19 August, 13–25 September) and in 2016 (*early*: 9–21 June, 5–8 July, *late*: 2–8 August). Bees were collected with hand vacuums (© Bioquip) at each lot for 4.5 min per floral species between the times of 10 a.m. and 4 p.m.

All collected bees were identified to species where possible (Ascher & Pickering, 2018; Gibbs, 2011; Gibbs et al., 2013). We categorized bees by functional traits, including nesting guild, status in North America (*native* or *exotic*), known foraging specialization (*generalist* or *specialist*) and the community-weighted mean of bee body size (*CWM*; Ascher & Pickering, 2018; S. Droege pers. comm., 2 April 2019; Sivakoff et al., 2018). *CWM* was calculated using $\sum_{i=1}^{S} p_i x_i$, where p_i is the relative abundance of the *i*th species and x_i is the trait value (body size) of the *i*th species (Garnier et al., 2004). Nesting guilds included the following: *human cultivated* (*Apis mellifera* L.), *ground nesting*, *cavity nesting* (non-pith), *pith nesting*, and parasitic bees with *no-nests*. *Pith* (3.16%), *human* (0.34%) and *no-nest* (1.75%) guilds were further excluded from statistical analyses due to their low abundance in pan traps.

2.5 | Statistical analysis

2.5.1 | Plant community composition

This study was completed during the first 2 years of seeded plant establishment; thus, we tested whether plant communities significantly differed among our treatments in late and early season of 2015 and 2016. We performed a non-metric multidimensional scaling (NMDS) analysis in R (R Development Core Team, 2019) using the VEGAN package (Oksanen et al., 2019), and a pairwise permutational multivariate analysis of variation using the PAIRWISEADONIS package (Martinez Arbizu, 2019).

2.5.2 | Bee community structure

To assess local and landscape drivers of the pan-trapped bee community (*bee abundance, bee diversity, bee richness, CWM bee size, cavity nesting guild abundance, ground nesting guild abundance and Lasioglossum abundance*), we fitted generalized linear mixed-effects models. We examined five explanatory vegetation variables (*bloom area, bloom abundance, dominant species diversity, plant height* and *biomass*), and four landscape variables (*total.gs, gs. size, LPI.gs* and *ENN*) for this analysis. Prior to model selection, we checked all predictors for multicollinearity (VIF > 3) and removed the variable *total.gs* from our analysis. Two fixed categorical variables (*year, season*), and a random term, *neighbourhood*, were also

included. Pan trap data collected from June and July 2015 were pooled into one 'early season' collection to match vegetation sampling in 2015. To account for this and sporadic instances of unequal sample size, we included a sampling effort term, 'number of pans used', as an offset.

Count data from *bee abundance, bee richness, Lasioglossum abundance, ground nesting* and *cavity nesting* guilds were over dispersed and analysed with a negative binomial distribution from package LME4 package (Bates et al., 2015). Continuous data from *bee diversity* and *CWM bee size* were normally distributed and modelled using the LME4 package (Bates et al., 2015). Models for *CWM bee size* did not include sites where no bees were collected. For all response variables, we conducted a stepwise backwards model selection analysis, removing the least significant variable from the model and then comparing the full and reduced model with the 'ANOVA' function from the CAR package (Fox & Weisberg, 2019).

2.5.3 | Network analysis of plant–pollinator interactions

We examined bee foraging patterns by constructing plant–pollinator interaction networks at each flowering site (*Control, Flowering Lawn, Low Diversity Prairie* and *High Diversity Prairie*) based on vacuumed bee samples using the BIPARTITE package (Dormann et al., 2008). We created separate networks for early (from June to July) and late season (August–September) in 2015 and 2016. This resulted in up to four networks per site, for a total of 62 networks in 2015 and 66 networks in 2016. All networks that were identified by the bipartite function as too small to evaluate (only one bee or plant recorded) were eliminated (2015: *n* = 13; 2016: *n* = 12). We then used two indices in 'grouplevel' function to evaluate the structure of the remaining networks: (a) *generality*: mean number of plant species visited by a bee and (b) *niche overlap*: similarity among bee resource use. After calculating these indices for our observed networks, we generated 1,000 null models for each of these networks using the 'nullmodel' function with the 'r2dtable' method (Dormann et al., 2008) and calculated the same two indices for each null model. Finally, for both *generality* and *niche overlap*, we calculated the mean index score from the null models and divided that by the standard deviation of the null model scores. That value was then used to correct the raw index values as *z*-scores to ensure that these descriptions of ecological networks are not an artefact of sampling intensity or web dimension (Dormann et al., 2009).

To assess how flowering greenspace designs and season influenced *niche overlap* and *generality*, we created linear mixed-effects models with package LME4 (Bates et al., 2015). Included in these models were two predictor variables, treatment (*Control, Flowering Lawn, Low Diversity Prairie* and *High Diversity Prairie*) and season (*early* and *late*), as well as the interaction between *treatment* and *season*, and a random term, *neighbourhood*. We also conducted a

separate linear mixed-effects model analysis, incorporating the same vegetation and landscape structure predictors as in our bee community analysis, to quantify how *niche overlap* and *generality* changed within different landscapes and vegetative communities. Backwards model selection was used to evaluate the relative significance of these predictors for foraging. Finally, we investigated if bloom area drove foraging frequency for the three most visited plants. For each plant species, we created a regression model with package GLMMADMB (Skaug et al., 2013) that included two sampling terms (*year* and *season*), a random term (*neighbourhood*), and used a negative binomial distribution to account for overdispersion.

3 | RESULTS

We collected 3,806 bees, of which 1,751 were vacuumed and 2,055 were pan trapped. Our collection comprised 107 species, 74 from the vacuums and 91 from the pan traps (see Table S2). In the pan traps, most individuals were from *ground nesting* (55.4%) or *cavity nesting* (35.5%) guilds, whereas vacuumed samples were predominately *cavity nesting* (48.1%), *ground nesting* (21.7%) and *human cultivated* (*A. mellifera*, 14.1%). In general, larger species were underrepresented in pan traps, whereas smaller bees were underrepresented in vacuum samples. For example, *Bombus* spp.

composed 22% of all vacuumed bees but only 1% of pan trapped bees. Likewise, *Lasioglossum* spp. composed only 9% of vacuumed bees but 40% of pan trapped specimens. While species assemblages did vary by sampling method, this variation primarily affected rarer species. In total, 93% of the bee abundance was represented by 58 species collected by both sampling methods (see Table S2).

3.1 | Plant community composition

Non-native spontaneous vegetation dominated all sites, including seeded treatments, throughout all time periods. *Trifolium pratense* L., *Cichorium intybus* L. and *Plantago lanceolata* L. were often the most abundant species present (see Table S3). Only seven of our 22 seeded forbs were recorded from *High Diversity* prairies throughout our study, and only one species, *Ratibida pinnata* (Vent.) Barnhart, consistently occurred. Despite this, permutational multivariate analysis of variance revealed that the vegetation composition of all seeded treatments significantly differed from *Control* vegetation throughout 2016 and most of 2015 (Figure 1; see Table S4). In 2015, vegetation in *Control* habitats did not differ from (a) *High Diversity* prairies in early ($R^2 = 0.09$, $F = 1.34$, $p = 0.117$) and late season ($R^2 = 0.09$, $F = 1.33$, $p = 0.167$), or (b) *Low Diversity* prairies in late season ($R^2 = 0.08$, $F = 1.28$, $p = 0.161$). Importantly, significant
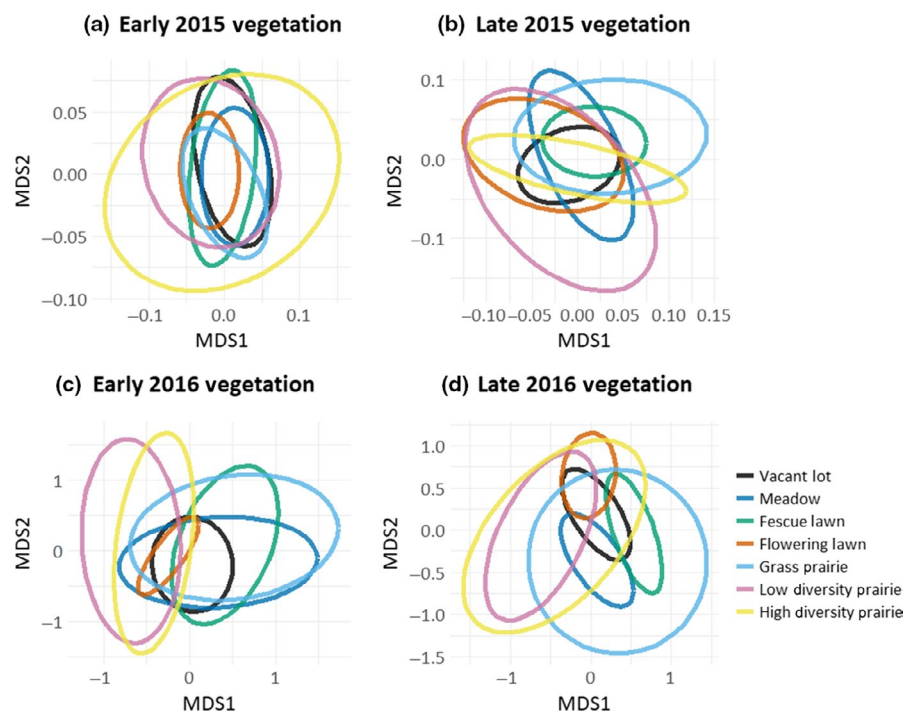

FIGURE 1 Establishment of vegetative communities in urban greenspaces. Non-metric multidimensional scaling (NMDS) plots of the vegetative community sampled from all seven greenspace treatments in early (a) and late 2015 (b) and early (c) and late 2016 (d). All seeded treatments significantly differed from control vacant lots, except for *High Diversity* prairies in early and late 2015, and *Low Diversity* prairies in late 2015. Establishment progressed further in 2016, however, and all seeded treatments were significantly different from our control. Importantly, prairie treatments showed increased variance among sites as microsite conditions heavily influenced establishment. Ellipses represent 95% confidence intervals for vegetation communities in a habitat treatment

TABLE 1 Regression models for bee community predictors

Predictors	Bee richness				Bee diversity				Bee size (CWM)				Foraging niche overlap			
	Coef	SE	z-value	p-value	Coef	SE	t-value	p-value	Coef	SE	t-value	p-value	Coef	SE	t-value	p-value
Intercept	−0.39	0.10	−4.02	<0.001	−1.71	0.14	−12.56	<0.001	4.12	0.17	24.21	<0.001	−1.09	0.11	−9.96	<0.001
Year	−0.28	0.09	−3.18	0.001	−0.62	0.12	−5.05	<0.001	0.95	0.20	4.79	<0.001				
Season (mid)	0.23	0.09	2.63	0.009	0.24	0.12	1.99	0.048								
Season (late)	−0.21	0.13	−1.66	0.097	−0.16	0.15	−1.03	0.305								
Lpi.gs	0.09	0.05	1.98	0.048	0.12	0.06	1.91	0.058	−0.30	0.10	−3.17	0.002				
Biomass	0.09	0.05	1.99	0.047												
Plant height	−0.11	0.05	−2.19	0.029					0.20	0.10	2.08	0.038	−0.23	0.11	−2.00	0.048
Bloom area									0.20	0.10	2.07	0.040				

Predictors	Bee abundance				Lasioglossum abundance				Ground nesters abundance				Cavity nesters abundance			
	Coef	SE	z-value	p-value	Coef	SE	z-value	p-value	Coef	SE	z-value	p-value	Coef	SE	z-value	p-value
Intercept	0.21	0.13	1.66	0.096	−0.50	0.14	−3.57	<0.001	−0.20	0.15	−1.29	0.198	−1.26	0.20	−6.45	<0.001
Year	−0.38	0.11	−3.39	<0.001	−0.84	0.14	−6.18	<0.001	−0.64	0.12	−5.31	<0.001	0.44	0.15	2.91	0.004
Season (mid)	0.09	0.11	0.81	0.416	−0.02	0.13	−0.16	0.875	−0.11	0.12	−0.96	0.337	−0.19	0.19	−1.02	0.306
Season (late)	−0.39	0.15	−2.59	0.010	−0.53	0.20	−2.62	0.009	−0.57	0.17	−3.35	<0.001				
Biomass	0.11	0.06	1.99	0.047	0.14	0.07	2.18	0.029								
Plant height	−0.14	0.06	−2.18	0.029	−0.23	0.08	−2.85	0.004								

Note: CWM = community-weighted mean of bee size, Year = 2015 versus 2016, Season (mid) = collection period (early vs. mid-summer), Season (late) = collection period (early vs. late summer), LPI.gs = largest patch size of greenspace within the landscape, Biomass = mean plant biomass (g/0.5 m²), Plant height = mean height of vegetation (cm), Bloom area = average bloom area (mm²) at a site
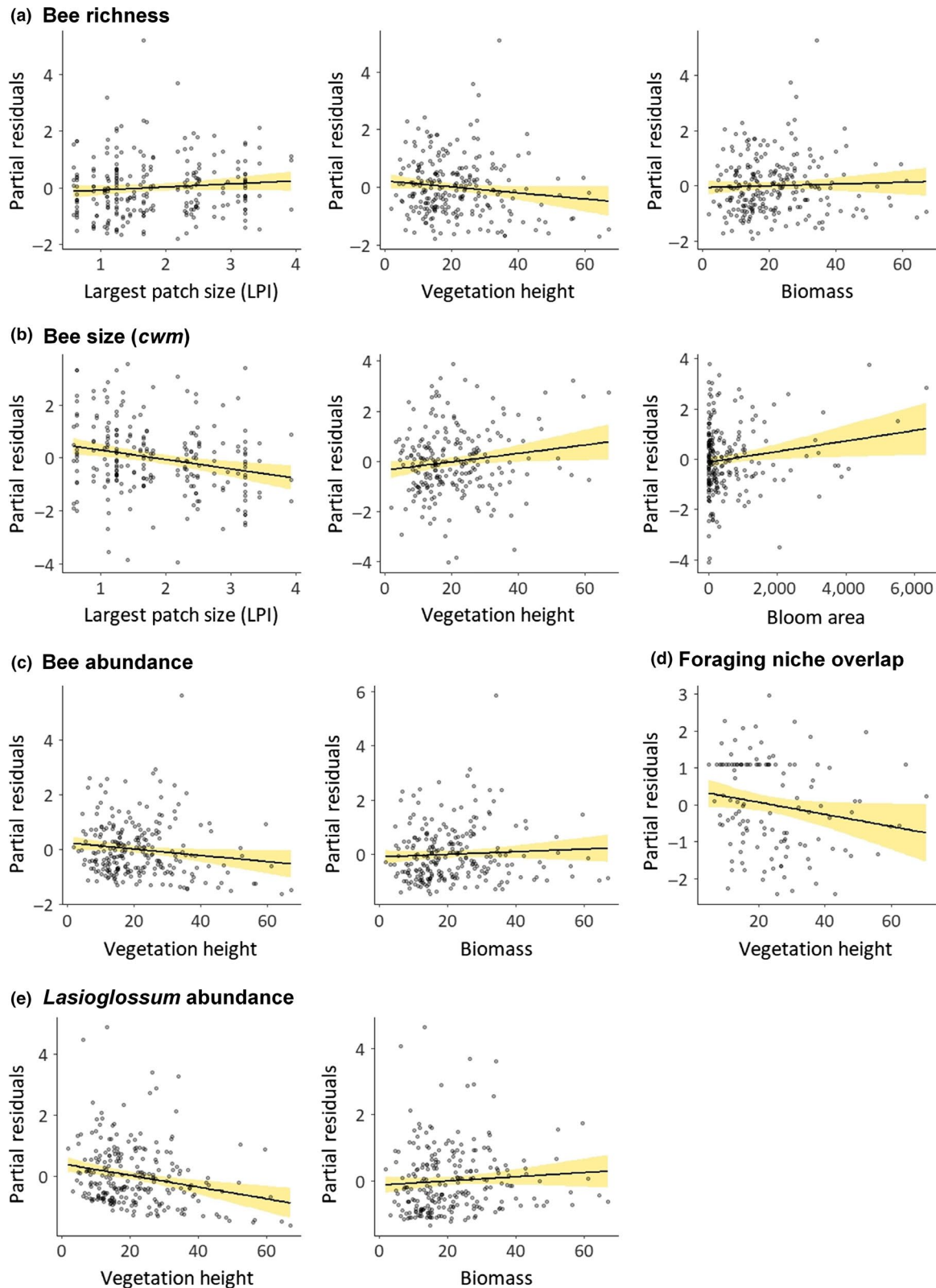
FIGURE 2 Local and landscape characteristics structure urban bee communities. Presence of a large greenspace patch within a landscape (*LPI*) was positively correlated with (a) bee richness and (b) smaller bees (*CWM*). At a local scale, increased biomass significantly predicted increased (a) bee richness, (c) total bee abundance and (e) *Lasioglossum* abundance. However, taller vegetation was negatively correlated with (a) bee richness, (c) total bee abundance, (d) foraging niche overlap and (e) *Lasioglossum* abundance. Lastly, (b) larger sized bees (cwm) were more prevalent in sites with taller vegetation and increased bloom area. Plots show individual variables' partial correlation to response variables after accounting for variation due to all other variables in the full model. Shaded bands indicate 95% confidence intervals for our regressions. Graphs were created from raw data, but analysis used scaled data

FIGURE 3 Spontaneous non-native vegetation provides valuable forage for urban pollinators. Networks illustrate common foraging patterns between the most abundant bee genera and plant species during early (a, b) and late season (c, d) samples within vacant lot control sites (a, c) and *High Diversity* pocket prairies (b, d)
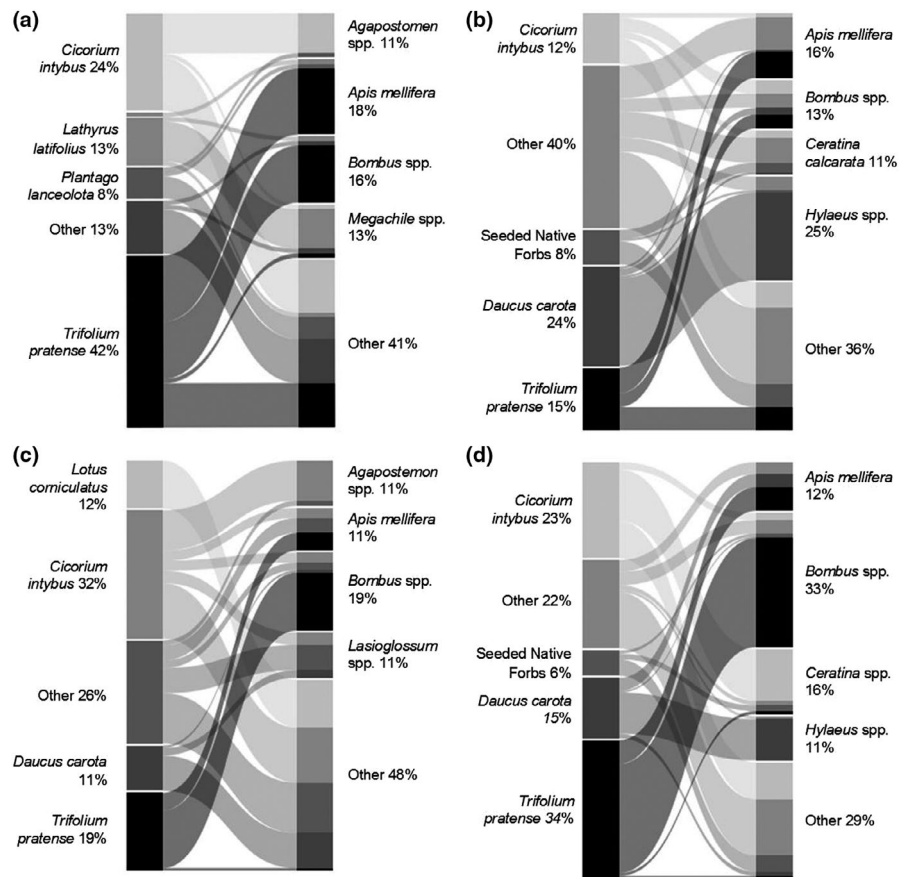
differences between our *Control* and *High* and *Low Diversity* prairies in 2016 may be due, in part, to observed differences in multivariate spread.

3.2 | Community analysis

We found several consistent trends between the pan-trapped bee community and local and landscape variables (Table 1). Vegetation *biomass* was positively correlated with *bee richness* ($z = 1.99$, $p = 0.047$; Figure 2a), *bee abundance* ($z = 1.99$, $p = 0.047$; Figure 2c) and *Lasioglossum abundance* ($z = 2.18$, $p = 0.029$; Figure 2e). Likewise, *vegetation height* was negatively correlated with *bee richness* ($z = -2.19$, $p = 0.029$; Figure 2a), *bee abundance* ($z = -2.18$, $p = 0.029$; Figure 2c) and *Lasioglossum abundance* ($z = -2.85$, $p = 0.004$; Figure 2e), and positively correlated with bee size (*cwm*; $t = 2.08$, $p = 0.038$; Figure 2b). Lastly, bee size (*cwm*) was also positively correlated with average *bloom area*, wherein sites with larger bloom areas had increased abundances of larger bees ($t = 2.07$, $p = 0.040$; Figure 2b).

Vacant lots embedded within landscapes with a larger patch of greenspace (*LPI.gs*) supported higher *bee richness* ($z = 1.98$, $p = 0.048$; Figure 2a) and smaller sized bees (*CWM bee size*; $t = -3.17$, $p = 0.002$; Figure 2b), and neared significance for *bee diversity* ($t = 1.91$, $p = 0.058$). However, landscape variables were not significant predictors of *bee abundance*, *Lasioglossum abundance*,

or *cavity* and *ground nesting* guilds. Across our best models, time of collection (i.e. *year* and *season*) also frequently influenced bee samples (Table 1).

3.3 | Urban bee foraging

We recorded 1,752 bee visits from 76 species to 52 plant taxa (see Table S5). Average network size was 8.62 for 2016 and 10.29 for 2015. Across all visitations, foraging primarily occurred on three non-native species, *T. pratense* (21.2%), *C. intybus* (19.2%) and *Daucus carota* L. (13.4%; Figure 3). Fewer than 5% of all bee vacuum samples were collected from native seeded prairie plants. We found that foraging frequency was correlated with bloom area for *T. pratense* ($z = 3.79$, $p < 0.001$) and *D. carota* ($z = 2.81$, $p = 0.027$), whereas *C. intybus* foraging was not influenced by bloom area at a given site ($z = -1.59$, $p = 0.112$). Increased bee foraging also occurred on *D. carota* in late season samplings ($z = 2.81$, $p = 0.005$).

In our analysis of foraging patterns, mixed-effect models revealed a significant interaction between *treatment* and *season*. When comparing our *High Diversity Prairies* to our *Control* vacant lots, the mean number of plant species visited by a bee species (*generality*) decreased in late season within the pocket prairies but not in the control lots ($t = -2.13$, $p = 0.036$; Figure 4). *Niche overlap* between foraging bee species also tended to decrease in
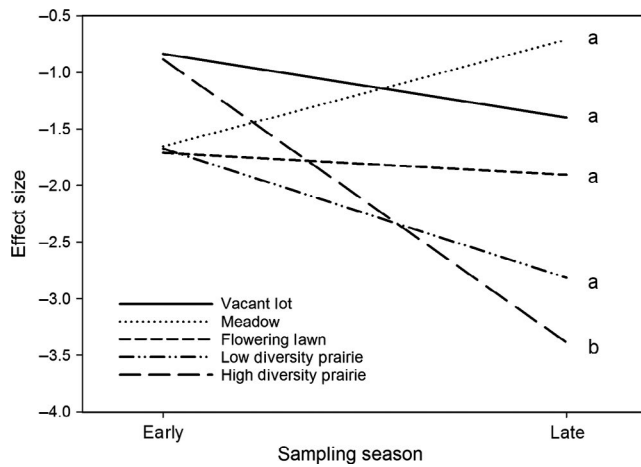
FIGURE 4 Bee foraging changed with habitat type and sampling season. *Network generality*, (i.e. mean number of plant species visited) was significantly decreased in late summer within our *High Diversity* prairies, as compared to our *Control* vacant lots ($p = 0.03$)

late season within our *High Diversity* pocket prairie habitats as compared to our control lots ($t = -1.70$, $p = 0.092$). Landscape and local vegetation variables were not predictive of foraging generality, but niche overlap was significantly decreased in sites with taller vegetation ($t = -2.00$, $p = 0.048$; Table 1; Figure 2d).

4 | DISCUSSION

An estimated 25% of Ohio's bee fauna have been collected from residential vacant lots across the city of Cleveland, OH, USA (Sivakoff et al., 2018). Bee abundance, richness and *Lasioglossum* abundance were enhanced with increased biomass and shorter vegetation within these habitat patches, but we did not find that seeding vacant lots with native vegetation increased their conservation value for bees. Instead, we identified that non-native species, including *T. pratense*, *C. intybus* and *Daucus carota* (native to Eurasia, North Africa and Western/Central Asia) consistently provided forage for bees across all treatments. Urban landscape configuration also influenced bee communities, and presence of larger greenspaces within 1,500 m of a site supported bee richness and appeared influential for colonization by smaller bees. Importantly, these patterns inform urban planning in post-industrial cities and can guide re-investment in green infrastructure to support urban bee biodiversity.

We identified a consistent, positive relationship between *plant biomass* and *bee richness*, *total bee abundance* and *Lasioglossum abundance*. We anticipated this pattern as decreased site management, that is, mowing, can lessen disturbance and increase forage opportunities, resulting in increased bee abundances (Lerman et al., 2018; Wastian et al., 2016). However, we also documented another seemingly contradictory pattern wherein shorter vegetation was also correlated with increased bee richness and abundances. We attribute observed increases to greater visibility of pan traps in these shorter habitats, and thus higher catch-rates.

Alternatively, shorter vegetation may reflect increased access to low-lying forage resources (Dylewski et al., 2019; Lerman et al., 2018), such as *T. pratense*, which was prominent in our foraging networks. This is further supported by our observation of increased *niche overlap* in shorter habitats where bees tended to forage on a few consistent resources.

Our plant–pollinator interaction networks illustrated that non-native spontaneous vegetation provided much of the foraging resources for bees within our study area. We found that three species, *C. intybus*, *D. carota* and *T. pratense*, accounted for over 50% of all foraging observations. This is unsurprising as previous research has identified non-native forage as crucial for urban bees (Garbuzov & Ratnieks, 2014; Larson et al., 2014; Salisbury et al., 2015; Sivakoff et al., 2018). It is less evident, however, whether foraging frequency is due to bee preferences or based solely on plant species density. We addressed this question for the three most frequently visisted foraging resources and found that bee collections from *T. pratense* and *D. carota* were correlated with their total bloom area within a site. However, foraging on *C. intybus* exceeded expectations based on its bloom area (see Table S5). While two bee species, *Ceratina calcarata* Robertson and *Agapostemon virescens* (Fabricius), accounted for half of all *C. intybus* interactions, 26 other native taxa were recorded from this flower, including several *Lasioglossum* spp. which were otherwise rarely collected. This suggests that *C. intybus* is an important forage species for these two common species and some rarer urban bees. Thus, plant identity, possibly tied to nutritional quality, may be more important than relative abundance or origin in some instances. Furthermore, even though foraging on *D. carota* was influenced by its bloom area, 77% of all recorded interactions occurred from *Hylaeus* spp. bees, the majority of which were native, indicating that this spontaneous non-native plant likely has a role in supporting a unique subset of the urban bee community.

While foraging primarily occurred on spontaneous non-native vegetation, we did document a treatment effect wherein bees exhibited more specialized foraging within *High Diversity* pocket prairies during late season collections. However, upon further examination of *High Diversity* foraging networks (Figure 3d), we suspect that specialization trends are likely driven by bumble bees feeding on non-native *T. pratense* in late season 2015, as 90% of all bumble bee/*T. pratense* interactions in the *High Diversity* prairies were recorded during this time period. It is possible that praire site preparation in 2014, including tillage, addition of micronutrients and herbiciding, created a favorable environment for *T. pratense* growth. Thus, while seeded plants did not influence bee community patterns or foraging to-date, we infer that management of a site could influence the quality or longevity of available spontaneous forage. Moreover, as frequent mowing can reduce blooms, may disturb ground nesting species and has been documented as a negative driver of bee abundance and richness (Lerman et al., 2018), we conclude that limited site management may improve bee outcomes.

Furthermore, we expect that as seeded native plants establish within our sites, they may play a greater role in future foraging networks. At the time of this investigation, seeded species composed ~ 1% of total quantified bloom area in our study, but native plants may

become more influential at higher bloom densities (see Table S5). Certainly, some urban studies have found that native plants support native bee commmunities in the city (Salisbury et al., 2015; Threlfall et al., 2015). It remains to be seen, however, whether planting native plants will encourage recruitment of bee species not currently found within vacant lots and what timescale such restorations might occur. Nonetheless, it is likely that spontaneous non-native vegetation will continue to provide important forage for urban bees. For example, in a recent examination of urban foraging in Chicago, IL, USA simplification of plant–pollinator interaction networks resulted in a reduced list of two native plants and two non-native weeds (*D. carota* and *Convolvulus* spp.) that supported all sampled bees (Lowenstein et al., 2019). Furthermore, even if non-natives are not primary resources, they may still extend seasonal plantings (Salisbury et al., 2015).

At a landscape scale, we identified that larger patches of greenspace predicted higher abundances of smaller bees and were associated with increased bee richness and diversity within vacant lots. This result suggests that smaller bees, which drove richness trends, might be more sensitive to urbanization pressures, and thus require a larger greenspace refuge. In large patches, it is likely that smaller bees, which typically forage at short distances (100–300 m; Zurbuchen et al., 2010), could encounter both nesting and foraging resources and build up source populations that spill over into adjacent habitats. Larger patches of greenspace have been implicated as important factors in previous urban bee studies across several countries and contexts (Beninde et al., 2015; Marini et al., 2014; Quistberg et al., 2016). For instance, in the shrinking city of Poznań, Poland, greater bee richness occurred with increased proximity to a large patch of greenspace with direct connection to suburban land cover (Banaszak-Cibicka et al., 2016). Likewise, larger patch sizes were associated with increased bee richness and abundances in the growing city of Bangkok, Thailand (Stewart et al., 2018). In part, patch sizes are likely influential because they affect nesting site availability (Stewart et al., 2018). Indeed, simultaneous work in Cleveland documented that native bees and wasps exhibit increased reproduction when a larger patch of greenspace was available within the urban landscape (KJ Turo, unpublished data), suggesting that habitat area may be a limiting factor for some urban bees.

4.1 | Synthesis and applications

Our study offers several takeaways for the creation of urban conservation habitat. First, we recommend practitioners consider landscape context and prioritize those sites closer to larger patches of greenspace, as these refuge habitats have been correlated with greater bee richness, especially for smaller bees. While site decisions may be constrained by availability or zoning, a priori consideration of landscape context is likely to improve habitat outcomes (Gilby et al., 2018). Thus, we emphasize that post-industrial cities have an important role in creating optimal conservation habitat. As much of the land in shrinking cities is flexibly held by city land banks,

opportunities exist for developing conservation habitat in locations which are better primed to achieve success. We also echo past calls for increased investigation into how bloom characteristics, such as pollen and nectar quantity and quality, affect bee fitness (Knight et al., 2018; Lowenstein et al., 2019; Vaudo et al., 2015). Current guidelines for pollinator plantings can include unattractive species (Garbuzov & Ratnieks, 2014) and bee richness and abundance metrics fail to account for long-term population viability. Given that this study took place during native forb establishment, we highlight that further investigation into the role of native flora in supporting urban bees is required. Finally, our study also implies that spontaneous non-native vegetation has value as urban bee forage. Thus, reducing management (e.g. frequent mowing) of spontaneous vegetation in private or publicly owned urban greenspaces is an important consideration for urban bee conservation.

AUTHORS' CONTRIBUTIONS

K.J.T., M.M.G. and M.R.S. conceived the ideas and designed methodology; Y.A.D., M.R.S. and K.J.T. collected the data; Y.A.D., F.S.S. and K.J.T. analysed the data; K.J.T. led manuscript writing, with editing from M.M.G. and contributions from other authors. All authors gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository https://doi.org/10.5061/dryad.8cz8w9gn5 (Turo et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.