



Urban development reduces bee abundance and diversity

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Abstract

Wild bee communities persist in cities despite major disruption of nesting and food resources by urban development. Bee diversity and abundance is key for urban agriculture and maintenance of plant diversity, and assessing what aspects of cities enhance bee populations will promote our capacity to retain and provision bee habitat. Here, we assessed how variation in land cover and neighborhood development history affected bee communities in the midwestern US urban landscape of Madison, Wisconsin. We sampled bee communities across 38 stratified sites with relatively high (>55%) or low (<30%) levels of impervious surface, and assessed effects of land use and neighborhood development history on bee abundance and species richness. We show abundance and richness of soil nesting bees was lower in newer neighborhoods. Soil nesting bees and bee community richness decreased as cover of impervious surface increased, but above ground nesting bees were minimally impacted. Bee community similarity varied spatially and based on dissimilar local land cover, only for soil nesting bees, and the overall bee community. Impervious surface limited bee abundance and diversity, but new neighborhoods were associated with greater negative effects. We suggest that enhancing the structural diversity of new neighborhoods in urban ecosystems may imitate the structural benefits of older neighborhoods for bee populations.

Keywords Urban ecosystems · Bee community · Habitat guilds · Habitat filtering · Impervious surface · Development history

Introduction

Urban development is rapidly transforming the Earth's surface. Impervious surfaces and fragmented patches of vegetation that typify urban ecosystems can threaten species diversity while irrigation and cultivated gardens also supplement habitat resources (Rebele 1994). In cities, ecological communities may experience loss of food and nesting resources, unless habitat is provided within the developed extent. (Rebele 1994; Rosenzweig 2003). Urban habitat fragmentation can lead to the loss of plants and associated pollinators, particularly plants reliant on animal pollination (Biesmeijer et al. 2006), yet organisms

differ in their sensitivity to urbanization, and small, mobile animals like pollinators can thrive despite extremely high rates of habitat disturbance and species turnover (Frankie et al. 2009, Theodorou et al. 2020; Sexton et al. 2021; Ferrari and Polidori 2022; Gathof et al. 2022). More research is thus needed to assess relationships between ecological community structure and land use in urban landscapes to protect biodiversity and ecosystem services in the ecosystems that support most of the human population (Daily 1997).

As urban development expands, urban agriculture grows, emphasizing the need to maintain urban pollinators to produce food where people live (Hoehn et al. 2008; Hodgson et al. 2011). Habitat simplification and competition from honey bee apiaries in urban systems can negatively affect wild bees (González-Varo et al. 2013, Martins et al. 2013; Renner et al. 2021), but high bee diversity has been observed in cities like New York and Chicago, US (e.g., Matteson et al. 2008; Fetridge et al. 2008). This shows urban land can provide ample floral resources for pollinators, especially when gardens provide flowers for a longer duration than other ecosystems (Goddard et al. 2010; Tonietto et al. 2011; Threlfall et al. 2015).

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Urbanization may have different impacts on bees with different phenology and nesting ecology, however (Wojcik et al. 2008; Winfree et al. 2009).

Within urban ecosystems, variation in pollinator nesting strategy may predict sensitivity of species to the high levels of disturbance in urban systems. In many cases, below-ground nesting cavity bees are expected to be more affected by urbanization than bees that nest above ground given the prevalence of impervious surfaces (Cane et al. 2006; McFrederick and LeBuhn 2006; Jha and Kremen 2013; Fortel et al. 2014). For example, many bees excavate or construct their own nesting cavities using mud, wood or pithy stems, or dig cavities in the soil, and these habitats are often less available in urban compared to natural or rural landscapes. However, man-made structures can in some cases supplement nesting habitat, by providing stone walls, wooden structures, and various other cavities, as well as bare ground and loosened soil (Wilson and Jamieson 2019; Ferrari and Polidori 2022). By investigating what aspects of land cover and land use underlie trends in species filtering, we can increase our capacity to restore the resources that are lost along with associated taxa.

Here we assessed effects of land cover and neighborhood development on the urban bee communities associated with the growing urban cityscape of Madison, Wisconsin, United States. Our study tested two main hypotheses related to bee community alpha and beta diversity. First, we predicted that increasing density of impervious surface and recent parcel development would disturb bee habitat and reduce the abundance and species richness of bee communities. In particular, we expected stronger effects of property development (both impervious cover and recency) on below-ground cavity nesting bees that require already excavated cavity spaces, often underground. We also expected surrounding natural vegetation and forest would increase bee species community richness. Second, we predicted that bee community composition would be more dissimilar with greater geographic distance across the city and greater *distance* in other environmental characteristics including land cover and property development, especially for small soil-nesting bees with limited dispersal capacity. By assessing effects of land cover, property development, and spatial scale on species richness and species composition of bee communities, our study contributes to the empirical foundations of pollination ecology as it relates to conservation and restoration efforts in urban ecosystems.

Materials and methods

Study area and sampling design

Madison, Wisconsin is an urban state capital surrounded by agricultural land in one of the fastest growing counties in

the US. In the 1960s, Madison's population climbed from 126 to 173 k, kicking off more than half a century of rapid growth and suburban expansion (<https://data.census.gov>). The primary transition type occurring in the Madison area for the past century is the conversion of agricultural to urban land around the city edge, intermingling many various aspects of land cover and land use change like increased impervious cover and lawn management regimes (Wegener 2001; Carpenter et al. 2007; Riera et al. 2001). Urban land cover analysis has revealed that lower density patterns of single-family development are associated with a larger area of impervious cover than higher density development and monoculture lawn follows an inverted U relationship with population density (Schnore & Klaff 1972; Stone 2004; Locke et al. 2019).

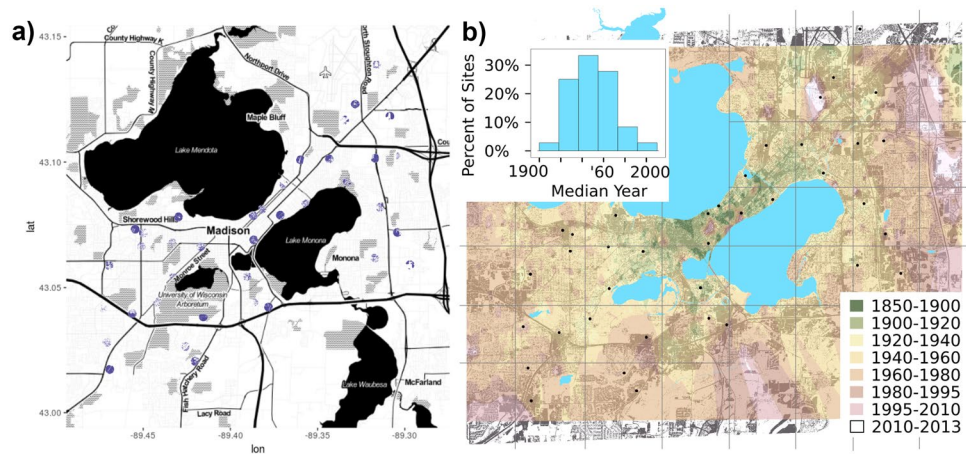
The dominant urban area is typified by mixed residential and commercial zones with small forest patches and city parks. The 123 km² central urban zone of Madison includes 46 km² (37%) of impervious surface, 30 km² (24%) of vegetated space, with the remaining landscape covered by lakes based on unsupervised classification of 1-foot USGS urban aerial imagery from 2010 (via Wisconsin View) into 30 classes, then manual assignment of classes to desired categories of canopy, impervious/built, natural vegetation, and other. The city receives semi-frequent rain and severe thunderstorms throughout the summer months that supports abundant flowering prairie plants in city parks or where native grasslands have been conserved or restored around the city.

Flower-visiting insects were sampled across Madison using a spatially stratified survey to account for changing regional species pools. To select sites, a grid of 2.5 × 2.5 km squares was laid across Madison and cells dominated by lake or agriculture were excluded, leaving 19 cells dominated by high-density residential and urban land (Fig. 1). In each of these cells we used a paired design and selected two sites characterized by either (1) high (>55%) or (2) low (<30%) impervious surface area within the surrounding 200 m land cover (USGS NAIP 2010). Within each cell, paired sites with high or low impervious surface area were separated by at least 400 m. These 38 sites were selected in a stratified-random manner, and permission from property owners (identified from a city parcel database) was requested until appropriate locations were identified. Sample sites included primarily residential properties, as well as commercial properties, urban storm water management areas, and city parks.

Bee community sampling

Bees were sampled six times between early June and late August 2013. Pan traps were distributed every two weeks during clear, sunny days when bees were foraging. All traps were distributed across the same evening to early morning

Fig. 1 Map of urban bee community sampling sites selected in a spatially stratified design across the City of Madison, **a** surrounded by 200 m buffers, filled with impervious land cover and **b** overlaid on a kriged property development year surface



period (after 17:00-dark and before dawn-8:00), and collected 4 d later. Six bee traps were placed at least 5 m apart within a 40 m area in each site, with two dark blue, two canary yellow, and two white; bees were also trapped in 0.5 L pan traps suspended 20 cm or 2.5 m from the ground to match the height of flowering vegetation. Bees were identified to species using the discover life online key and a comprehensive dichotomous key available for *Lasioglossum* (Ascher & Pickering 2013; Gibbs 2011).

We classified bee taxa as soil-nesting, below-ground cavity-nesting, and above-ground nesting bees, based on available observations. The below ground cavity-nesting bees included 7 species of bumble bees (*Apidae: Bombus*). Above-ground nesting bees included small carpenter bees (*Ceratina spp.*), yellow faced bees (*Hylaeus spp.*), carder, mason, and leafcutter bees (*Megachilidae*), and two sweat bees that nest in decaying wood, *Lasioglossum cressonii* (Mitchell 1960) and *L. oblongum* (Sakagami & Michener 1962). Above-ground nesting bees included 22 species. The rest of the bees were classified as soil nesting bees, which included 69 species across several groups: (i) long-horned bees (Tribe Eucerini), (ii) mining bees (*Andrena spp.*), (iii) green bees, (iv) all of the other sweat bees, and (v) any others were classified as soil nesting bees, although natural history observation of many species could not be located.

Measuring land cover and neighborhood development around study sites

Fine-scale land cover was described in terms of impervious surface (e.g. roads, parking lots, and built structures), tree canopy, and open canopy natural vegetation (excluding lawn) at two scales (200 m and 1000 m), as well as a composite land cover distance matrix based on these three classes at each of the two scales. One-foot resolution digital aerial imagery of the study extent from (USGS via Wisconsin-View) was used to generate these classes of land cover based

on the following procedure. Unsupervised classification was initiated with 30 classes that were visually assessed and classified into the land cover types of interest. The impervious surface layer from this classification procedure was added to the City of Madison building footprint and road layer to recover impervious surface obscured by tree canopy. Natural vegetation was identified visually within 1000 m of each site and included open-canopy, perennial grasses and forbs in greenways, parks, or transportation corridors, digitized elements were added to classified “natural vegetation”. Closed canopy forest was captured well by this classification procedure. Each land cover variable was measured as a percent of the 200 m or 1000 m radius landscape sectors surrounding each site, then variables were standardized with a mean of zero and standard deviation of 1 for comparison in analyses. The three land cover types were also consolidated in a distance matrix at each scale for the final analysis applying multiple regression on distance matrices.

To characterize neighborhood development history, publicly accessible tax assessment data was obtained and property development year was extracted for parcels located within a 200 m radius of each site. For the first and second hypothesis, the median year of parcel development was extracted from the parcels within 200 m of the study site. For the third analysis, a Bray–Curtis distance matrix was constructed to contrast sites based on the area-weighted average development year, median development year, and most recent property development year within the 200 m buffer. The area-weighted average development year for each site was calculated by weighting the parcel development year of each parcel within the 200 m surrounding landscape sector by the area of the parcel.

Data analysis

Individual-based rarefaction curves were constructed for each site using the ‘vegan’ R package, and rarefaction-

based species richness estimates were compared to observed richness (Oksanen et al. 2018). Rarefied richness did not reach an asymptote, so raw abundance and richness values were used as sampling effort was standardized (Fig. 2). To investigate the first hypothesis, we used segmented regression and breakpoint analysis of bee abundance based on median neighborhood development year to split older and newer neighborhoods if a transition point was detected. Segmented regression models were fitted using the R package ‘segmented’ (Muggeo 2008). Bee abundance and species richness were plotted for each nesting guild group.

We used linear regression models to test whether single land cover type variables and median year of neighborhood development (median property development year) affected bee species richness (α -diversity); separate analyses were conducted for the overall community and three bee guilds. All variables were scaled to a mean of 0 and standard deviation of 1 and top models were selected using stepwise AIC model selection using the ‘MASS’ R package (Ripley et al. 2018). The Moran’s I test was used to check for spatial autocorrelation in model fit for each full and final models, applied using the ‘car’ R package (Fox et al. 2018).

We used multiple regression on distance matrices (MRM) to assess effects of the various explanatory variables on bee community composition at the landscape scale (β -diversity), which was implemented through the R package ‘ecodist’ (Legendre and Legendre 1998; Goslee and Urban 2017). This allowed us to capture the various multifaceted explanatory variables reflecting heterogeneity of composite land cover and land use history variables. MRMs measure the effect magnitude of each explanatory distance matrix using

a non-parametric framework and pseudo *t*-tests are used to assess significance of explanatory variables (Goslee and Urban 2017).

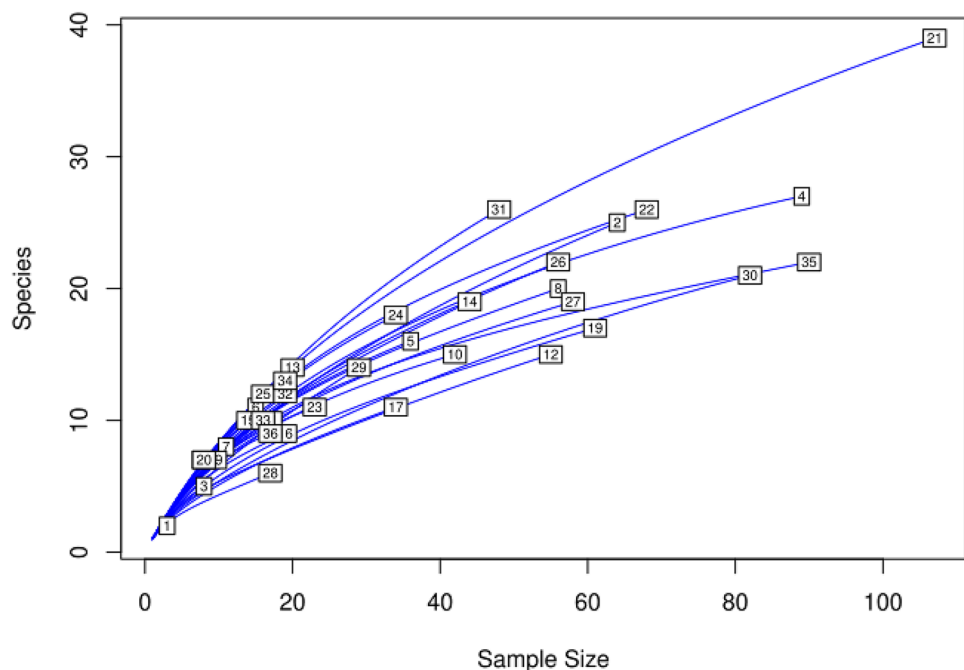
Results

We captured 1331 bees at the 38 sites. Across families, 31% were Apidae, 3% Andrenidae, 55% Halictidae, 8% Megachilidae, and 3% Collitidae. Sites were surrounded by 0 to 43% natural vegetation (Mean = 10.3; SD = 9.1) and 0 to 28% forest (Mean = 5.0; SD = 6.3) with median property development varying between 1920 and 2003 (Mean = 1947; SD = 22). All full bee community and soil nesting bee community analyses were performed across all sites ($n = 38$). Above ground nesting bee and below ground cavity nesting bee analyses were performed across sites where bees from the nesting guild were present, 32 and 17 sites, respectively.

Effects of recent property development on bee abundance and diversity

Segmented regression models fitted for each group of bees based on bee abundance, resulting in the following breakpoints: 1953 for all bees, 1958 for soil nesting bees, 1951 for above-ground nesting bees, and 1933 for below-ground nesting bees (Fig. 3). Bee abundance and species richness split into older and newer neighborhood categories based on these breakpoints for all bees as well as each nesting guild of bees showed no differences in bee abundance

Fig. 2 Species accumulation curves for overall site species richness with site numbers



or species richness between older and newer neighborhoods based on Welsh's t-tests (Fig. 3, panel C). Differences in bee abundance and species richness were also assessed based on older and newer neighborhoods split at year 1960, the beginning of a period of rapid population growth in Madison, WI. Based on this split, we observed a decline in soil bee species richness, but no other significant differences in bee abundance or species richness between older and newer neighborhoods based on Welsh's t-tests (Fig. 3, panel D). In multiple variate linear regression models including development and land cover variables, a negative influence of recent property development was the strongest predictor of overall bee and soil nesting bee species richness, and the term was included with the negative influence of impervious surface in top models (Tables 1 and 2).

Effects of surrounding land cover on bee species diversity

In addition to effects of neighborhood development, the proportion of impervious surface also reduced the species richness (α -diversity) of the overall bee community, soil-nesting bees, and above-ground nesting bees (Tables 1 and 2). The negative influence of impervious surface on the overall richness of bee species and soil-nesting bees were each about half the magnitude of the property development effect in the scaled regression model. For the overall bee community, the regression model indicates a 2.9 factor decrease in bee species richness per 23% increase in the proportion of impervious surface. The below-ground cavity-nesting bee species richness was negatively associated with surrounding forest

Table 1 Results of top AICc-selected multiple linear regression models for species richness of a. the full bee community, b. soil-nesting bees, c. above-ground bees and d. below-ground cavity-nesting bees

Variable	Estimate	Std Error	P	Model R ²	P
Intercept	14.97	1.19	<0.001	0.16, 0.14	0.02
Imp200	-3.06	1.19	0.02		
Soil bee community					
Variable	Estimate	Std Error	P	Model R ²	P
Intercept	10.48	0.74	<0.001	0.14, 0.12	0.02
Imp200	-1.77	0.74	0.02		
Above-ground cavity nesting bee community					
Variable	Estimate	Std Error	P	Model R ²	P
Intercept	3.63	0.49	<0.001	0.12, 0.10	0.04
Imp200	-1.03	0.50	0.04		
Below-ground cavity nesting bee community					
Variable	Estimate	Std Error	P	Model R ²	P
Intercept	1.46	0.11	<0.001	0.38, 0.29	0.03
Forest200	0.43	0.11	0.02		
Forest1000	-0.29	0.16	0.02		

cover with a 1.0 factor decrease in bumble bee species with each 12% increase in surrounding forest cover.

Variation in bee community composition across the study extent

Finally, the multiple regression on distance matrix model (MRM) for the full bee community composition included only the effect of the composite land cover variable ($P=0.03$) (Table 3). For the soil nesting bee community, there was a clear influence of geographic distance on

Table 2 Model average coefficients for the 95% confidence model set of AICc-selected multiple linear regression models for species richness of a. the full bee community, b. soil-nesting bees, c. cavity-nesting bees, and d. above-ground bees

Full bee community								
Variable	Intercept	Forest (1 km)	Nat Veg (1 km)	Imp (1 km)	Forest (200 m)	Nat Veg (200 m)	Imp (200 m)	MedYr
Model Avg Coef	27.2	0.5	-0.1	0.0	-1.5	-0.8	-3.3	-0.0
Sum of Weights		0.20	0.19	0.20	0.33	0.22	0.90	0.21
Soil nesting bee community								
Variable	Intercept	Forest (1 km)	Nat Veg (1 km)	Imp (1 km)	Forest (200 m)	Nat Veg (200 m)	Imp (200 m)	MedYr
Model Avg Coef	19.14	0.47	0.44	-0.14	-0.66	-0.44	-1.84	-0.02
Sum of Weights		0.22	0.22	0.20	0.26	0.22	0.84	0.22
Above-ground nesting bee community								
Variable	Intercept	Forest (1 km)	Nat Veg (1 km)	Imp (1 km)	Forest (200 m)	Nat Veg (200 m)	Imp (200 m)	MedYr
Model Avg Coef	-3.88	-0.23	-0.62	-0.21	-0.09	-0.34	-1.05	0.02
Sum of Weights		0.20	0.35	0.20	0.18	0.22	0.71	0.22
Below-ground nesting bee community								
Variable	Intercept	Forest (1 km)	Nat Veg (1 km)	Imp (1 km)	Forest (200 m)	Nat Veg (200 m)	Imp (200 m)	MedYr
Model Avg Coef	2.99	-0.25	0.09	-0.14	0.37	0.08	-0.01	-0.0
Sum of Weights		0.51	0.17	0.20	0.50	0.14	0.13	0.14

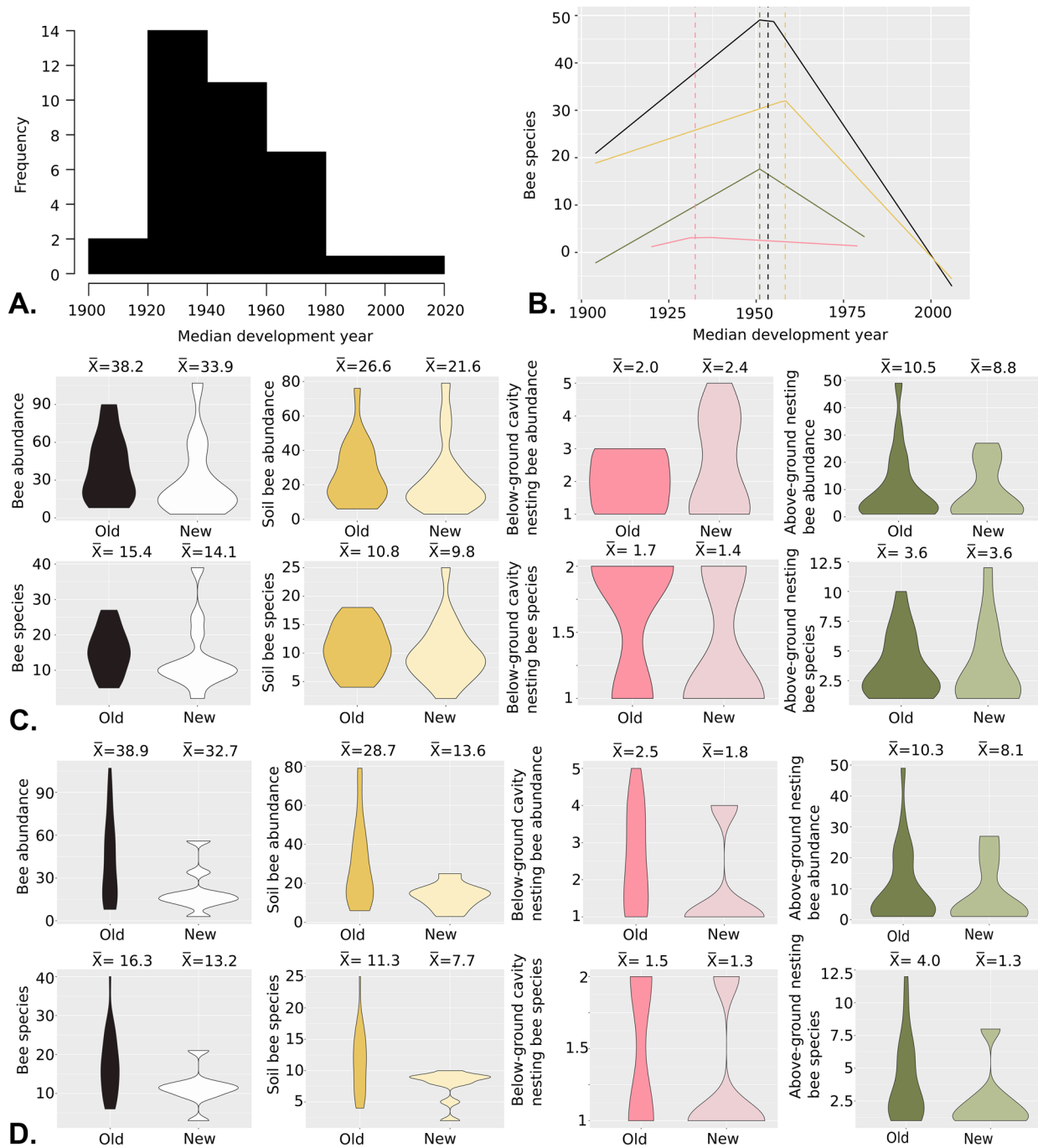


Fig. 3 Sample sites and neighborhood property development described with **A** a histogram of median neighborhood property development year in the surrounding 200 m landscape sector for all study sites, **B** segmented regression and breakpoint analysis for bee abundance by median neighborhood development year for each nesting guild (All bees: 1953, Soil nesting bees: 1958, Below ground nesting bees: 1933, Above ground nesting bees: 1951) and **C** Bee abundance and species richness for all bees and nesting guilds

in older and newer neighborhoods based on guild-specific breakpoints, none were significantly different based on Welch's t-tests. **D** Bee abundance and species richness for all bees and nesting guilds in older and newer neighborhoods based on a breakpoint of 1960, soil bee abundance declined from 28.7 to 13.6 ($t=-3.38$, $df=40.0$, $p=0.002$) and species richness declined from 11.3 to 7.7 ($t=-2.87$, $df=27.5$, $p=0.008$), no other groups differed significantly based on Welch's t-tests

Table 3 Multiple regression on distance matrices to assess the influence of geographic distance, neighborhood development, and land cover on the full bee community, soil-nesting bees, above-ground nesting bees, and d. below-ground cavity nesting bees

Full bee community						
Variable	Regression Coefficients	<i>P</i>	<i>F</i> -value	Model <i>R</i> ²	<i>P</i>	
Intercept	5.55×10^{-1}	0.81	2.78	0.02	0.007	
Geographic distance	1.03×10^{-6}	0.28				
Neighborhood Development	8.61×10^{-4}	0.18				
Land cover (200m)	-1.83×10^{-4}	0.04*				
Land cover (1000m)	1.53×10^{-4}	0.43				
Full bee community – Final model						
Variable	Regression Coefficients	<i>P</i>	<i>F</i> -value	Model <i>R</i> ²	<i>P</i>	
Intercept	0.570	0.030	9.690	0.02	0.09	
Land cover (200m)	-1.86×10^{-4}	0.03*				
Soil nesting bee community						
Variable	Regression Coefficients	<i>P</i>	<i>F</i> -value	Model <i>R</i> ²	<i>P</i>	
Intercept	4.92×10^{-1}	1.000	4.160	0.030	0.020	
Geographic distance	2.16×10^{-6}	0.04*				
Neighborhood Development	7.51×10^{-4}	0.260				
Land cover (200m)	-1.70×10^{-4}	0.04*				
Land cover (1000m)	-1.26×10^{-4}	0.500				
Soil nesting bee community – Final model						
Variable	Regression Coefficients	<i>P</i>	<i>F</i> -value	Model <i>R</i> ²	<i>P</i>	
Intercept	4.91×10^{-1}	0.97	7.390	0.020	0.010	
Geographic distance	-1.70×10^{-4}	0.04*				
Land cover (200m)	2.18×10^{-6}	0.04*				
Above ground nesting bee community						
Variable	Regression Coefficients	<i>P</i>	<i>F</i> -value	Model <i>R</i> ²	<i>P</i>	
Intercept	8.13×10^{-1}	0.110	1.590	0.01	0.36	
Geographic distance	-1.84×10^{-6}	0.210				
Neighborhood Development	1.65×10^{-4}	0.480				
Land cover (200m)	3.33×10^{-4}	0.680				
Land cover (1000m)	-3.71×10^{-4}	0.170				
Above ground nesting bee community – Final model						
Variable	Regression Coefficients	<i>P</i>	<i>F</i> -value	Model <i>R</i> ²	<i>P</i>	
Intercept	7.69×10^{-1}	0.270	2.130	0	0.14	
Land cover (1000m)	-4.00×10^{-4}	0.140				
Below ground cavity nesting bee community						
Variable	Regression Coefficients	<i>P</i>	<i>F</i> -value	Model <i>R</i> ²	<i>P</i>	
Intercept	3.76×10^{-1}	0.95	5.810	0.070	0.040	
Geographic distance	5.07	0.08				
Neighborhood Development	-2.55	0.63				
Land cover (200m)	-4.30×10^{-4}	0.92				
Land cover (1000m)	-3.60×10^{-3}	0.6				
Below ground cavity nesting bee community – Final model						
Variable	Regression Coefficients	<i>P</i>	<i>F</i> -value	Model <i>R</i> ²	<i>P</i>	
Intercept	3.72×10^{-1}	0.96	3.810	0.030	0.070	
Land cover (1000m)	5.23×10^{-6}	0.07				

* indicates the probability of observing the obtained results by random chance is less than 5%

community dissimilarity ($P=0.040$) and a land cover effect ($P=0.04$) (Table 3). The below-ground cavity nesting community composition included a weakly significant influence of geographic distance ($P=0.07$) (Table 3). And there were

no observed effects of geographic distance or land cover on the above-ground bees (Table 3). None of the bee community final models included significant effects of property development on community composition (Table 3).

Discussion

Bees from each nesting guild were observed throughout the City of Madison at both low and high impervious surface sites. This result suggests that in general, bees are able to use small patches of habitat within the most urbanized landscapes of the city (Theodorou et al. 2016; Hall et al. 2016, Daniels et al. 2020). Our observation of an association between impervious surface and reduced bee community richness, especially for soil nesting bees, reflected patterns reminiscent of a 60-year study in Brazil, which documented an increase of impervious surface and decrease in soil bee nests, abundance, and declines of species richness and phylogenetic diversity (Pereira et al. 2021). The negative influence of impervious surface on soil-nesting bees, above-ground cavity-nesting bees, and the entire bee community, may stem from a loss of exposed soil used for nesting habitat, and associated decreases in flowering forbs that bees use as a food resource.

Our finding that more recently developed neighborhoods exhibited lower bee abundance and diversity was not based on our initial expectations of mechanistic associations between land cover transformation and bee habitat provisioning. A negative influence of recent development was observed for the full bee community and soil-nesting bees. While this negative effect may be due to disturbance and soil compaction, we also observed a reduction of structural complexity in recently developed neighborhoods surrounded by more grass lawn and less gardens that may provision diverse types of bee habitat (Ossola et al. 2019). More established neighborhoods more frequently offered more complex built habitat including rock walls and gardens rather than simple lawn land cover.

While we expected that below-ground cavity nesting bees would be the most impacted by urbanization and impervious surface, we did not observe that result. Bumble bees that comprised this nesting habitat guild can forage long distances, and other studies have observed bumble bee foraging presence to be strongly influenced by floral resources (Turo et al. 2019; Reeher et al. 2020; Cohen et al. 2020). In fact, greater urban cover can sometimes increase the abundance of urban bumble bees in urban gardens, and promote higher in-garden foraging, alongside plant richness as another contributing factor (O'Connell et al. 2021). Another study of urban bumble bees in the American Midwest found that bumble bee abundance and richness were unaffected by the amount of impervious surface across several cities (Reeher et al. 2020).

While geographic distance did not explain the dissimilarity of the full bee community, it contributed to the dissimilarity in soil-nesting and below-ground cavity-nesting bee community composition. This confirmed our

hypothesis that generally smaller, soil-nesting bee communities would vary more across the urban study extent. Past studies have confirmed that bee foraging distances are correlated with body size, contributing to patchy distributions of small bee species (Steffan-Dewenter et al. 2002; McKinney 2008). A recent study of pollinators around cotton farms in Texas found no geographic pattern of isolation by distance for bees, but these patterns were observed for beetles and other more movement limited insect taxa (Cusser et al. 2018).

Urbanization can also filter bee community composition, with some evidence that urban bee communities are more homogenous subsets of nearby rural bee communities (Banaszak-Cibicka and Zmihorski 2020). In the models for the species composition of the full bee community as well as each nesting habitat guild, property development did not appear to filter the species composition. Surrounding land cover did affect the full bee and soil-nesting bee community dissimilarity. While the influence of land cover significantly influenced the dissimilarity of species assemblages, these factors did not explain much of the variation overall. High species richness of bees was observed across the city, as well as patchy distributions of rare species.

Research documenting responses of bee communities to urbanization is on the rise, but a recent meta-analysis only discovered three published studies assessing the relationships between bee traits and urbanization (Buchholz and Egerer 2020). As urbanization processes continue to transform landscapes around the world, improving our understanding of habitat provisioning and ecosystem services in urban ecosystems is of great importance. Globally, urban bee research is heavily biased towards cities in developed countries with temperate climates (Silva et al. 2021). Improving the targeted nature of urban pollinator research and accomplishing this research in diverse urban landscapes will bolster our capacity to integrate habitat that supplies pollination services and biodiversity to cityscapes around the world.

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Author contributions VWP designed study, performed analysis and drafted manuscript, JSB and DWC participated in manuscript review. All authors gave final approval for publication.

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Availability of data and material Bees are submitted to the University of Wisconsin-Madison insect museum.

Code availability <https://github.com/verawp>.

Declarations

Conflict of interest The authors declare they have no conflict of interest.

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