Article

BEES IN A HEAT ISLAND: BEE ASSEMBLAGES ON *CERCIS CANADENSIS* AND *CORNUS FLORIDA* IN URBAN AND EXURBAN SITES

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Journal of Pollination Ecology,
38(1), 2025, pp 110-131
DOI: 10.26786/1920-7603(2025)822

Received 5 October 2024,
accepted 21 April 2025

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Abstract—The predicted effects of climate change on pollination processes are multiple, including earlier blooming times and decoupling from pollinators. Yet, little research has been conducted, especially in urban areas where the heat island effect is known to speed up warming. Our aim is to investigate which bee species visit two native, vernal-blooming tree species with continuous distributions from urban to exurban sites. In 2019 and 2020, we collected bees on the native, mass-flowering *Cercis canadensis* and *Cornus florida* in the St. Louis metropolitan and exurban areas in Missouri, USA. A total of 434 bees carrying pollen were collected identifying 54 species representing five families. An additional 123 specimens which did not carry any pollen at all were captured representing 37 species within five families. We observed a greater species diversity among pollen carrying bees at exurban sites while the numbers of male bees collected were proportionately higher in urban versus exurban sites. Although flowering periods of the two tree species overlapped, the pollen of both tree species was identified on only 34 bees.

Keywords—Bees, *Cercis canadensis*, *Cornus florida*, Heat Island Effect, Pollen Load, Urban-Exurban Gradient

INTRODUCTION

The conversion of natural areas to urbanized environments across the world represents a major threat to biodiversity (Grimm et al. 2008; McDonald et al. 2008, 2013; Simkin et al. 2022). Over 55% of the world's human population already lives in cities and that proportion is expected to exceed by two-thirds by the middle of this century (United Nations, 2005; United Nations Department of Economic and Social Affairs Population Division, 2019). That implies that the world's urban infrastructure will double in the next thirty years (Simkin et al. 2022). Cities represent challenging environments to many of the organisms native to the original habitats. Dramatic alterations in physical, chemical, and biological conditions (Aronson et al. 2016; Lambert et al. 2021) have led to challenges in the life histories of native species (Fenoglio et al. 2020).

The spatial configuration of cities can affect how urban environments alter local energy budgets (Debbage & Shepperd 2015). Urban areas exhibit the so-called heat island effect where overall temperatures in the city tend to be higher than surrounding non-urbanized areas (Manoli et al. 2019). The principal cause of the heat island effect is the absorption of heat by impervious surfaces and infrastructures, which radiate at night (Memon et al. 2008). The heat island effect is also influenced by the progress of global climate change (Sachindra et al. 2016). Steadily increasing warming temperatures across the world are intensifying, making temperatures in cities more extreme (Parker 2010). As urbanization increases and natural land areas decrease, heat islands will escalate (Manoli et al. 2019).

One consequence of the interaction between global warming and the heat island effect is that the annual spring bloom now arrives earlier in cities than in surrounding rural and natural areas (Zipper et al. 2016; Meng et al. 2020), and these differences are growing larger over time (Wohlfahrt et al. 2019). Studies have shown that for many, if not most cities the spring blooming season now starts over a week earlier than a century ago (Li et al. 2019). Finally, phenological sensitivity to temperature mediates many insect-plant interactions (Meineke et al. 2021) and can lead to the decoupling of pollination processes (Settele et al. 2016).

The floral diversity of most cities represents a mixture of native, non-native and invasive species (Pearse et al. 2018). In general, people tend to select trees for their features, such as ornamental value, shade, capacity for soil retention, etc. (Lowenstein & Minor 2016). Consequently, the urban plant community represents a combination of “familiar” and “unfamiliar” floral cues, edible rewards, etc., to the native and naturalized community of pollinators (Lowenstein et al. 2019). This can lead to rearrangements, or even the disruption, of pollination systems (Prendergast & Ollerton 2021). Nonetheless, cities can host a large diversity of insect pollinators (Hall et al. 2017) that at times appear much higher in surrounding rural areas (Baldock et al. 2015; Wenzel et al. 2020). Alternatively, some researchers have found that the heat island effect can decrease the abundance of pollinators in urban settings (Hamblin et al. 2018; Zeballos et al. 2022). Therefore, disentangling the effects of the urban heat island from the seasonal structure of the urban plant community is an important research question that needs to be addressed.

Given the high diversity of life-history strategies, sociality, and nesting habits that bees exhibit (Michener 2000; Danforth et al. 2019), we expect that different species will have a broad range of responses to heat island effects. As certain traits can be favored in warmer urban settings, the functional diversity of the bee community should shift to represent the warming urban environment (Geppert et al. 2023). For example, bumblebees (*Bombus* spp.) in the greater St. Louis metropolitan area showed increased body size in urban locations compared to adjacent rural and natural areas (Austin et al. 2022). This increase was independent of the lack of genetic differentiation across the urban landscape. In Switzerland, two common bumblebees *Bombus pascuorum* (Scopoli 1763) and *B. lapidarius* (Linnaeus 1758), were found to be smaller in urban sites when compared to populations in rural areas (Eggenberger et al. 2019). The same study also found that their urban populations showed a higher phenotypic diversity leading to higher functional trait divergence.

Throughout the central and eastern United States there are two species of native ornamental trees which are common in urban areas, the eastern redbud, *Cercis canadensis* L. (Fabaceae; Fig. 1A), and the flowering dogwood, *Cornus florida* L. (Cornaceae; Fig. 1B). They are well established as sentimental favorites in urban and rural Missouri (Randolph 1964). While both species commence flowering in early spring, *C. canadensis* blooms earlier than *C. florida* (Reed 2004; Ony et al. 2020). We took advantage of the extensive incidence and high abundances of these two species to assess how the heat island effect is altering blooming times, pollinator visitation diversity, and plant-pollinator interactions.

The objectives of this study were: 1) determine the differences between the start of blooming between urban and more natural, i.e., exurban areas for each of our two focal tree species; 2) assess the identity, diversity, sex and abundance of bees foraging on the focal trees in urban and exurban areas; 3) assess foraging bee diversity on both tree species to determine if the later flowering *C. florida* shares bee species with the earlier flowering *C. canadensis*; 4) assess and identify the pollen load of bee foragers in urban and exurban areas. We expect that the urban environment will affect bee visitor assemblages, either directly, via habitat alteration, e.g. impervious surface, or indirectly, via the urban heat island effect. We hypothesize that the focal tree species populations in exurban sites will bloom later than the urban ones. Finally, we hypothesize that we should observe more specialist foragers in the exurban sites than in the urban sites.

MATERIALS AND METHODS

STUDY AREAS

The research was conducted at four sites in the greater St. Louis metropolitan area, Missouri, USA

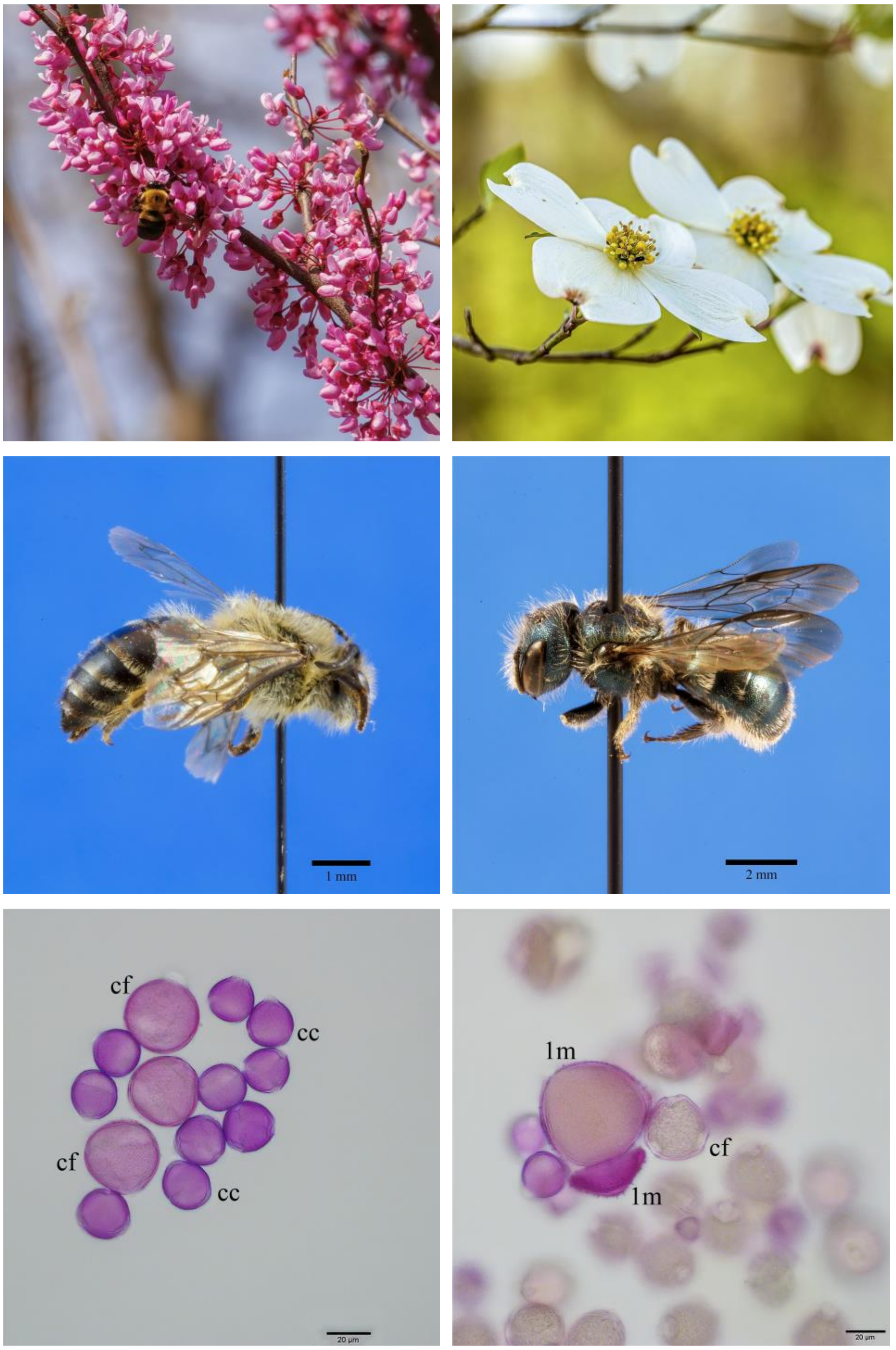

Figure 1. Photo plate of focal tree species floral presentations, representative foragers and comparative pollen grains. (A) Flowering branch of *Cercis canadensis* with *Xylocopa virginica.* (B) Flowering twig of *C. florida.* (C) Pinned specimen of *Colletes inaequalis.* (D) Pinned specimen of *Osmia pumila.* (E) Portion of a pollen wash from a bee captured from SNR site with a combination of grains of *C. canadensis* (cc) and *C. florida* (cf). (F) Portion of a pollen wash from a bee collected from SNR (exurban site) with a grain of *Lonicera maackii* (lm) and a deflated grain of *L. maackii.*
Photo credits: A-D Retha Edens-Meier; E-F Bernhardt/ Meier Laboratory.

(Fig. 2), which has a population of 2.8 million and measures 21,910 km^2. The city was founded along the banks of the Mississippi River and is located near the center of the United States. The annual average precipitation is 86.36 cm.

This study contrasted two levels of organization and two focal tree species (*C. canadensis* and *C. florida*). The two urban sites were located in the core of the city while two were in exurban areas west and southwest of the city. The first urban site was located on the campus of Saint Louis University (SLU; 38.635, -90.232). The campus was landscaped primarily with lawn grasses, non-native ornamentals, and native annuals, perennials, and woody plants. The second urban location was Tower Grove Park (TGP; 38.608, -90.252) with an older and more diverse mixture of native and non-native cultivars. It is approximately 4.5 kilometers south of SLU. Taxonomy for both urban sites follows Yatskievych (1999).

Both exurban sites were secondary and deciduous woodlands retaining the mid-western vernal flora including spring ephemeral perennials, naturalized ruderals, and native and naturalized entomophilous shrubs (Yatskievych 1999). The first exurban site is Shaw Nature Reserve (SNR; 38.478, -90.826) and is owned by the Missouri Botanical Garden. Trees of *C. florida* and *C. canadensis* were located in open *Quercus*-*Carya* woodlands along its 4.82 km loop trail, which borders wetlands, limestone glades, a pinetum, and replanted tall grass prairies. The second exurban site is Babler State Park (BSP; 38.617, -90.688) and is maintained by the Missouri Department of Natural Resources. It consists primarily of *Quercus*-*Carya* closed canopy forests with some open woodlands featuring both of our tree species. BSP is located 30 km west of the SLU campus. All fieldwork was performed during the spring seasons (March through mid-May) of 2019 and 2020.

LANDSCAPE COMPOSITION

Impervious surface has been shown to impact bee richness and abundance at different scales (Bennett & Lovell 2019). For our exurban sites, we used a supervised classification of the National Landcover Dataset of ArcPro (v. 10.6) to classify aerial images of the study sites into seven land use classes. For the urban sites, a 1 m resolution land use land cover dataset for the city of St. Louis (https://moimagery.missouri.edu/arcgis/rest/services/LGov/DOQQ2015_EastWestGateway_6inch/ImageServer) was used. We estimated the surrounding impervious area, forest cover, grassland, open or barren space, and water surface in a 1 km radius. To validate the landscape homogeneity, we compared the forest cover, grassland, and impervious surface in 500 m and 1 km radius, to make sure that the selected individual trees' surrounding landscape was not significantly different from others at the same site.

HEAT ISLAND EFFECT

To establish the presence of the heat island effect, we acquired temperature data for all sites. For the urban sites, SLU and TGP, we used data from the weather station at the St. Louis Science Center (http://agebb.missouri.edu/weather/realtime/stlouissciencecenter.asp) located approximately 3 km away from each site. For the SNR site, we used data from their weather station (https://wcc.sc.egov.usda.gov/nwcc/site?sitenum=2227). Weather data from the Spirit of St. Louis Airport was used for BSP (https://forecast.weather.gov/data/obhistory/KSUS.html), located less than 3 km away from this site. Due to technical problems with the weather stations at SNR and at the St. Louis Science Center, we only had access to the Spring 2020 data for all sites. Raw temperature readings were converted to degree-days (McMaster & Wilhelm 1997), which is a better predictor of plant development (Miller et al. 2001).

FOCAL TREE SPECIES

The common eastern redbud, *Cercis canadensis*, is a deciduous, and emergent tree of temperate-subtropical woodlands distributed through eastern America and northeastern Mexico (Bzdyk 2016). In Missouri, it grows as an emergent or understory species and along limestone ridges (Yatskievych 1999). Indigenous self-seeding populations are found in abundance in natural and conservation areas surrounding the city of St. Louis (Yatskievych 1999). It appears to be insect-pollinated (Lovell 1961), a source of pollen and nectar for honeybees (Pellett 1920), and is self-incompatible (Ony et al. 2020). Horticulturists continue to propagate and register named cultigens (Robertson 1976). People within urban and suburban areas are also encouraged to plant these trees to attract wildlife (Graham 1941; Tallamy 2009). It grows to a height of six to nine meters, flowering in early spring before its new leaves mature. Inflorescences form racemose fascicles with variable numbers of flower buds developing in leaf axils or they are cauliflorous emerging from the bark along trunks or old branches (Fig. 1A). Flowers are complete, bilaterally symmetrical and five-merous with a pink to magenta (rarely white) corolla (Yatskievych 1999). In this study, we did not sample cultivars with the white flower mutation and there were no double-flowered forms.

The dogwood, *Cornus florida*, is also an understory, deciduous and emergent tree of temperate-subtropical, deciduous and/or *Pinus* spp. woodlands ranging from Ontario through eastern America to northeastern Mexico. In Missouri, it appears to grow under the same conditions as *C. canadensis* (see above) producing abundant self-seeding populations located in both urban and exurban areas. As above, it appears to be insect-pollinated (Rhoades et al. 2011), a source of pollen (Fig. 1E) and nectar (Pellett 1920) and is self-incompatible (Reed 2004). *Cornus florida* has been the state tree of Missouri since 1955 and new cultigens continue to be developed and named (Wilde et al. 2015). It grows up to 20 meters in height, flowering early mid-Spring before its seasonal foliage matures (Yatskievych 1999). This species usually flowers one to two weeks after *C. canadensis* peaks in Missouri, but in most years, there is some overlap. Inflorescences of *C. florida* contain 15-30 bisexual flowers within a flat-topped involucre subtended by four large, petaloid, white to cream coloured bracts (Fig. 1B; Yatskievych 1999). When these bracts open, they expose flower buds that may take several days to a week until they open. Individual florets are four-merous, complete, radially symmetrical, and have a short, tubular, yellowish green corolla. In this study, we did not sample bees from pink-bract mutations or otherwise coloured cultivars. All urban and exurban trees of both species used in this study were either self-seeded recruits or showed floral morphologies of the wild types. We recorded the first and last observed open flowers for each tree species at each location for 2019 and 2020.

BEE COLLECTIONS

Bees (Figs. 1C, 1D) were sampled during the complete flowering periods of *C. canadensis* and *C. florida*. The duration of flowering of both species combined lasted three to five weeks each spring. From onset, trees in bloom were not monitored for bee activity every day at all sites. Instead, sampling was conducted on warm, dry days during the morning and/or early afternoon (10:00 - 16:00 CDT) when bee foragers tend to be most active. We sampled a minimum of three individual trees at each location for 15 minutes each via aerial netting. Trees were sampled for a long enough time that bee collections were representative of the bee community. Individual trees were sampled at each location two to three times a week, depending on the weather. As tree height made sampling via standard insect nets difficult, nets were attached to modified paint roller handles that were then screwed onto telescoping painter's poles. Using these extended poles, bees were collected by reaching as far as possible and aiming for bees on flowers within reach. Bees were only collected if they made contact with the inflorescences and/or individual flowers. *Apis mellifera* L. is both a naturalized and commercial species in North America. As *A. mellifera* was numerous at all sites and may be identified visually, bee collections were made selectively. If we saw non-*Apis* bees in the presence of *A. mellifera*, we collected the non-*Apis* bees first. Bees were placed in individual containers to prevent cross contamination of pollen loads. All insects were euthanized in their labeled tubes and stored via freezing at -10°C except for *Bombus* gynes which were identified from their photographs (Arduser 2020) and released. Pollen samples from these *Bombus* gynes were collected but were unfortunately lost. Typically, *Bombus* gynes are not euthanized because of the dramatic decline in *Bombus* populations within the United States. However, collection of *Bombus* gynes was not standardized within this study. A few *Bombus* gynes were sacrificed for voucher specimens and their pollen was identified (Appendix Tables 1-3). Pinned and labelled specimens (see below) were identified using Arduser (2020) and their sex was determined. Specimens were ultimately segregated into the categories; bees with pollen and bees without any pollen (see Appendix Table 4). All subsequent calculations and statistical analyses were based exclusively on those bees that carried pollen as they represent true foragers (see below). Bees lacking pollen showed no evidence of either active or passive contact (sensu Bernhardt, 1996) with dehiscent anthers of host trees.

To determine how complete our sampling of pollen foragers was for each tree species at each location, we used the rarefaction curve method based on coverage to estimate the richness parameter, q^0 (Chao et al. 2020; Roswell et al. 2021). We also calculated the diversity parameters for the forager community for each location using Hill numbers as well as the species turnover among the urbanization level and focal tree species (Chao et al. 2020). Rarefaction curves and Hill numbers were calculated using the iNEXT package (Hsieh et al. 2016) while the turnover was estimated with the package iNEXT.3D (Chao et al. 2021). All statistical and computational analyses were performed in the R computational environment (v.4.0.3, R Core Team 2020).

We compared Hill diversity parameter q^1, which is analogous to the Shannon diversity index, H′ (Roswell et al. 2021), among tree species and locations, by performing a two-way permutation analysis of variance (Anderson & Braak 2003) with urbanization level (urban vs exurban) and focal tree species (*C. canadensis* vs *C. florida*) as the main factors. The analysis was performed with the package “RVAideMemoire” (v. 0.9-83-7, Hervé & Hervé 2020).

In order to ascertain the bee community structural organization among tree species and urbanization levels, we used a cluster analysis. We employed the Bray-Curtis index to calculate dissimilarities among groups using the function 'vegdist' in the package 'vegan' (v. 2.6-4, Oksanen et al. 2013).

POLLEN LOAD ANALYSES

Excluding most *Bombus* gynes, the removal of insect-borne pollen prior to the pinning and labelling process (Figs. 1CD) follows the staining and identification protocols in Goldblatt & Bernhardt (1990) using Calberla’s fluid (Ogden et al. 1974) as basic fuchsin stains the pollen wall pink (Figs. 1DE). Grains that could not be identified to co-blooming species under a compound light microscope were subdivided into morphotypes based on size, shape, exine sculpturing, and the number of visible apertures. To minimize the effects of pollen cross-contamination in the same insect net, a threshold of 20 individual pollen grains from a specific morphotype was used to record a pollen morph as present on an individual bee (Bernhardt et al. 1984). Mounted pollen specimens were photographed under a Zeiss Axio Imager, M2. Washed, pinned, and labelled specimens (Figs. 1BC) were deposited in the insect collection at Saint Louis University, St. Louis, MO, USA, (circa 2024) pending deposition in an entomological museum.

RESULTS

LANDSCAPE COMPOSITION, HEAT ISLAND EFFECT, AND FLORAL PHENOLOGY

Urbanization density sharply increased from exurban to urban sites (Fig. 2). Landscape composition within 1 km of the collection sites also varied among all research locations (Fig. 3) but was consistent within urbanization levels. The greatest difference was in the proportion of tree cover and impervious surface at urban and exurban locations. Overall, temperatures in the urban sites ran consistently higher than the exurban sites. The total degree-days for the months of March and April of 2020 were over a full week ahead in the urban sites, whereas the difference was five days by May (Fig. 4). March and April of 2020 were much warmer (15.3°C and 20.6°C) respectively, than in 2019 (11.1°C and 18.4°C). Alternatively, May of 2019 was warmer (24.9°C) than May of 2020 (23.1°C). On March 27, 2020, the maximum urban temperature was 26.7°C. The maximum exurban temperature that day was 25.3°C. Similarly, on April 8, 2020, the maximum urban temperature was 32.2°C, while the maximum exurban temperature was 23.1°C.

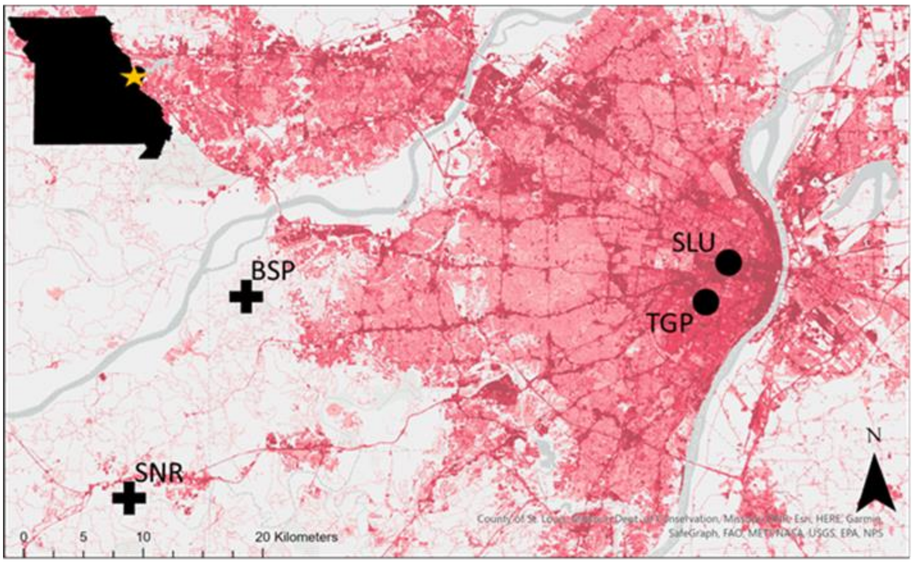

Figure 2. Location of urban (SLU, TGP) and exurban (SNR, BSP) study sites in St. Louis metropolitan area. Upper-left black inset represents the state of Missouri, and the yellow star the location of the city of St. Louis. Red shading areas are urban areas, with darker areas corresponding to higher density of urbanization.

Figure 3. Landscape composition for study sites in the greater St. Louis metropolitan area, MO, USA, at a scale of 1 km. BSP and SNR are exurban sites while TGP and SLU are urban.

Both tree species bloomed up to a week earlier in urban locations compared to exurban trees. In 2019, the first open flower of *C. canadensis* at the urban site was on March 26 and the last flower for this species was on April 26. For the same year, the first flower of *C. canadensis* at the exurban sites was observed on April 3 and the last flower was on April 21. In 2020, the first flower for *C. canadensis* was observed on March 23 and the last flower was on April 21. For the same year, the first flower at the exurban site of this species was observed on April 4 and the last flower was on April 26. In 2019, the first open flower observed for *C. florida* at the urban site was on April 16 and the last flower was documented on May 7. For the same year, the first flower for *C. florida* at the exurban sites was recorded on April 23 and the last flower was on May 6. In 2020, the first flower for *C. florida* was observed on April 19 and the last flower on May 12. For the same year, the first flower of this species at the exurban site was observed on April 19 and the last flower was recorded on May 7.

BEE PHENOLOGY

The first and last collections of pollen-carrying bee species on both tree species are summarized in Table 1. Bee activity on *C. canadensis* occurred earlier in 2020 compared to 2019. The earliest collection of bees (04/16/2019) on *C. canadensis* was identical in urban and exurban sites. In 2020,

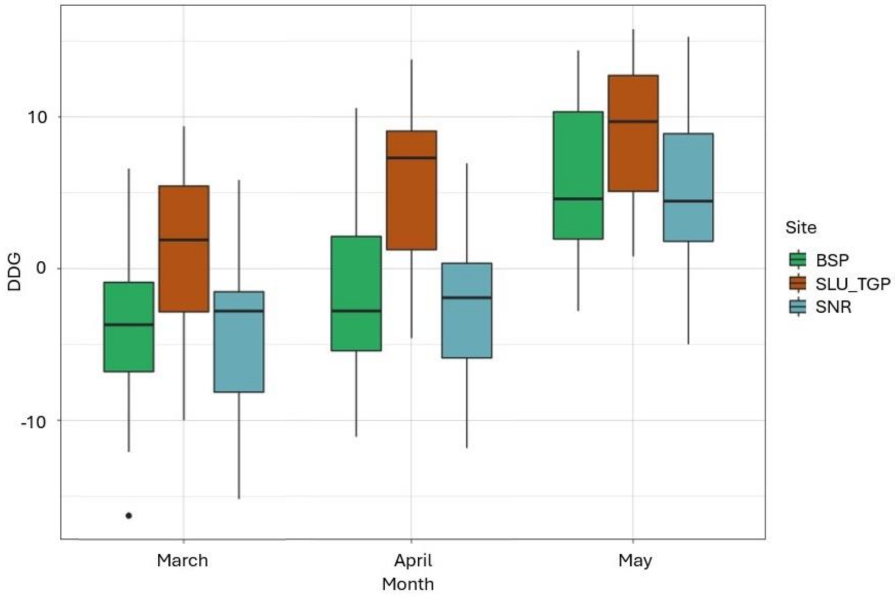

Figure 4. Degree days accumulation per month for study sites in St. Louis, MO, for the year 2020. BSP in green and SNR in blue are the exurban sites while SLU_TGP are the urban sites.

Table 1. Phenology of Pollen-Carrying Bees on Two Tree Species (2019, 2020; F = Female, M = Male)

Site, Bee, Tree	Date of First & Last Bee Captured (2019)	Date of First & Last Bee Captured (2020)
Urban First Bee(s) Caught	04/16/2019	04/07/2020
C. canadensis	*Andrena cressonii* F *Apis mellifera* F	*Andrena imitatrix* F *Andrena forbesii* F *Apis mellifera* F *Colletes inaequalis* M (3x)
Exurban First Bee(s) Caught	04/16/2019	04/04/2020
C. canadensis	*Andrena cressonii* F (3x) *Andrena nuda* F *Apis mellifera* F (4x) *Bombus impatiens* F (2x) *Colletes inaequalis* F (5x) *Osmia lignaria* F (2x) *Osmia georgica* F *Osmia pumila* F *Xylocopa virginica* M (2x)	*Andrena cressonii* M *Colletes inaequalis* F
Urban First Bee(s) Caught	04/19/2019	04/19/2020
C. florida	*Andrena cressonii* F	*Andrena nasonii* M *Xylocopa virginica* F
Exurban First Bee(s) Caught	04/20/2019	04/19/2020
C. florida	*Andrena carlini* F *Andrena cressonii* F *Andrena imitatrix* M *Apis mellifera* F *Colletes inaequalis* F (5x)	*Andrena cressonii* M *Andrena miserabilis* F
Urban Last Bee(s) Caught	04/26/2019	04/21/2020
C. canadensis	*Osmia taurus* F	*Andrena imitatrix* M (2x) *Apis mellifera* F (4x)
Exurban Last Bee(s) Caught	04/21/2019	04/26/2020
C. canadensis	*Andrena mandibularis* F (2x) *Andrena nigrae* F *Andrena perplexa* F *Augochlorella aurata* F *Colletes inaequalis* F (2x) *Osmia georgica* F (2x) *Xylocopa virginica* M	*Colletes inaequalis* F (2x)
Urban Last Bee(s) Caught	05/07/2019	05/12/2020
C. florida	*Hylaeus prosopis* sp. M	*Andrena imitatrix* F
Exurban Last Bee(s) Caught	05/06/2019	05/07/2020
C. florida	*Andrena cressonii* F *Andrena ilicis* M *Andrena imitatrix* F *Andrena nasonii* F (2x) *Andrena nuda* F (2x) *Augochloropsis viridula* F *Apis mellifera* F	*Andrena cressonii* F *Andrena forbesii* F *Andrena miserabilis* F *Apis mellifera* F *Colletes inaequalis* F

exurban bees were caught three days earlier than urban bees. We continued to catch urban bees five days later than the last exurban bees in 2019. However, in 2020, we continued to catch exurban bees five days after the last bee was collected at urban sites. The first pollen-carrying bees collected on *C. canadensis* in 2019 represented two species in urban sites and nine species in exurban sites. In 2020, the first bees collected represented four species in urban sites and two species in exurban sites.

Floral foraging by bees on *C. florida* began on April 19 in 2019 and 2020 (Table 1). In 2019, an urban bee was caught one day earlier than the first exurban bee. We still collected an urban bee one day after we collected bees from the exurban sites in 2019. In 2020, there was a five-day gap between the last bee collected at an urban site (05/12/2020) compared to the exurban sites (05/07/2020). Only one bee species represented our first urban collection in 2019 but five species were collected at our exurban sites. In contrast, in 2020, two bee species were first collected at our urban sites while two bee species were collected at our exurban sites.

Diversity of Foraging Bees

Pooling all four sites and both tree species over a two-year period, we collected a total of 557 bees of which 434 bees representing 54 bee species from five families carried pollen (Tables 2, 3, 4). One hundred and twenty three specimens, representing 36 species and five families from urban and exurban sites, carried no pollen (see Appendix Table 4). The pollen-carrying bee assemblage species richness, q^0, was comparable between *C. canadensis* and *C. florida* (Table 4, Fig. 5A) independent of urbanization level. Alternatively, bee species richness was higher in the exurban locations than in the urban ones (Table 4; Fig. 5B).

A total of 254 pollen-carrying bees was collected on *C. canadensis* representing 37 species (Tables 2, 4, Fig. 5A). Pollen-carrying urban specimens consisted of 47 bees representing 10 species, while pollen-carrying exurban specimens consisted of 207 bees representing 35 species. Comparisons between species from urban and exurban sites on bees collected from *C. canadensis* showed that two bee species in the family Apidae were unique to the urban site while 27 bee species representing four families (Andrenidae, Apidae, Halictidae, Megachilidae) were found foraging only on exurban *C. canadensis* (Table 2). A total of eight species representing four families (Andrenidae, Apidae, Colletidae, Megachilidae) were collected in both urban and exurban sites (Table 2).

A total of 180 pollen-carrying bees were collected on *C. florida* representing 43 species (Tables 3, 4; Fig. 5B). Pollen-carrying urban specimens consisted of 54 bees representing 16 species. Pollen-carrying exurban specimens consisted of 126 bees representing 38 species. Five species representing three families (Andrenidae, Apidae, and Halictidae) collected on *C. florida* were unique to our urban sites. Twenty-seven species representing all five families were found foraging on *C. florida* only at exurban sites (Table 3). Eleven species representing four families (Andrenidae, Apidae, Colletidae, and Halictidae) were collected on *C. florida* at both the urban and exurban sites (Table 3).

The two tree species shared 34 bees representing all five families. Eleven species representing three families (Apidae, Halictidae, Megachilidae) were captured exclusively on *C. canadensis* (Tables 2, 3). Seventeen species representing four families (Andrenidae, Apidae, Colletidae, Halictidae) foraged only on *C. florida* (Tables 2, 3).

The most commonly observed but not always captured visitor, independent of location, was the honeybee, *A. melifera*. The most commonly collected native species (N = 80) at exurban areas was *Colletes inaequalis* Say remaining rare in urban sites and represented by only three male specimens (Tables 2, 3; Fig 1C). Likewise, *Augochlora pura* Say was the most commonly collected member of the Halictidae (N = 15) on both exurban tree species. It was absent from our urban sites, although it was collected previously and often from May through September in the St. Louis area by Camilo et al. (2017).

Skewed distributions of bees preferring *C. canadensis* to *C. florida* were noted for *Bombus* gynes (8:1), the combined five *Osmia* species (30:3) and *Colletes inaequalis* (72:11). The most commonly collected *Andrena* species on both tree species at urban and exurban sites was *Andrena cressonii*

Table 2. Pollen-Carrying Bee Species Identity and Abundance Collected on *Cercis canadensis*, Urban vs. Exurban (Exurb = Exurban). Parentheses differentiate female and male bees from total number of bees per site.

Bee Species	Urban	Female Urban	Male Urban	Exurban	Female Exurb	Male Exurb	TOTAL
Andrenidae							
Andrena carlini	0			0			0
A. crataegi	0			0			0
A. cressonii	4	(4)		6	(5)	(1)	10
A. forbesii	1	(1)		2	(2)		3
A. hippotes	0			0			0
A. ilicis	0			1		(1)	1
A. illini	0			0			0
A. illini/sayi	0			2		(2)	2
A. imitatrix	3	(1)	(2)	4	(4)		7
A. mandibularis	1	(1)		4	(4)		5
A. miserabilis	0			1	(1)		1
A. nasonii	0			1	(1)		1
A. nigrae	0			1	(1)		1
A. nuda	0			1	(1)		1
A. perplexa	0			1	(1)		1
A. pruni	0			4	(2)	(2)	4
Apidae							
Anthophora ursina	1		(1)	0			1
Apis mellifera	14	(14)		39	(39)		53
Bombus bimaculatus	1	(1)		0			1
B. griseocollis	0			1	(1)		1
B. impatiens	0			5	(5)		5
Bombus spp.	0			1	(1)		1
Ceratina calcarata	0			2	(1)	(1)	2
C. strenua	0			0			0
Eucera dubitata	0			1		(1)	1
Nomada cressoni/sayi	0			1		(1)	1
N. luteoloides	0			1	(1)		1
N. pygmaea	0			0			0
Xylocopa virginica	17	(4)	(13)	7		(7)	24
Colletidae							
Colletes inaequalis	3		(3)	69	(62)	(7)	72
Hylaeus (*Prosopis*) sp.	0			0			0
Halictidae							
Halictus rubicundus	0			0			0
Augochlora pura	0			5	(5)		5
Augochlorella aurata	0			2	(2)		2
Augochloropsis viridula	0			2	(2)		2
Lasioglossum birkmani	0			0			0
L. callidum	0			0			0
L. cattellae	0			1	(1)		1
L. coeruleum	0			2	(2)		2
L. cressonii	0			0			0
L. fuscipenne	0			0			0
L. gotham	0			2	(2)		2
L. hitchensi	0			2	(2)		2
L. illinoense	0			0			0
L. imitatum	0			8	(8)		8
Lasioglossum sp. 1	0			0			0
L. tegulare	0			0			0
L. versatum	0			0			0
L. weemsi	0			0			0

Table 2 continued

Bee Species	Urban	Female Urban	Male Urban	Exurban	Female Exurb	Male Exurb	TOTAL
Megachilidae							
Osmia atriventris	0			1	(1)		1
O. taurus	2	(2)		3	(3)		5
O. georgica	0			10	(10)		10
O. lignaria	0			8	(8)		8
O. pumila	0			6	(5)	(1)	6
Total	47	(29)	(18)	207	(183)	(24)	254

Robertson ($N = 39$) but it appears to prefer *C. florida* ($N = 29$) to *C. canadensis* ($N = 10$; Tables 2, 3).

There was no significant difference between bee visitor communities' diversity parameter q^1 ($F = 2.3$, $DF = 1, 11$, $P = 0.1573$; Table 4) between the two tree species. Alternatively, there was a significant difference in overall diversity between urban and exurban treatments ($F = 26.3$, $DF = 1, 11$, $P = 0.0003$; Table 4), with the exurban sites having over a 50% greater estimate than the urban sites. Finally, there was a significant interaction effect between tree species and urbanization level with the urban *C. canadensis* having lower diversity than all other combinations ($F = 7.3$, $DF = 3, 11$, $P = 0.0058$; Table 4).

The cluster analysis revealed a clear dichotomy in bee visitor assemblages between urban and exurban sites (Fig. 6). In the urban areas, bee assemblages were segregated by the focal tree species overriding the local habitat effect. Alternatively, in exurban sites, the visitor assemblages within each location were more similar to each other than to the same species at the other location (Fig. 6) showing a stronger local effect.

FREQUENCIES AND DISTRIBUTIONS OF FEMALE AND MALE POLLEN-CARRYING BEES

More females than males were collected on both tree species during both years regardless of sites (Tables 2, 3). A total of 72 females were collected from both *C. canadensis* and *C. florida* at the urban sites, with 29 females from *C. canadensis* and 43 females from *C. florida*. We collected 29 males from both research trees at urban sites, 18 males from *C. canadensis* and 11 males from *C. florida* (Tables 2, 3). Females of five species were collected and identified from both *C. canadensis* and *C. florida* (Tables 2, 3). Only females of *Andrena mandibularis* Robertson, *Bombus bimaculatus* Cresson, and *Osmia taurus* Smith representing three families (Andrenidae, Apidae, Megachilidae) were collected only on *C. canadensis*. Only females of *Andrena miserabilis* Cresson, *Lasioglossum hitchensi* Gibbs, *L. illinoense* Robertson, *L. imitatum* Smith, *Lasioglossum* sp. 1, *L. tegulare* Robertson representing the Andrenidae and the Halictidae were captured only on *C. florida* (Tables 2, 3).

When males were compared between the two research tree species at urban sites, we found one species (*Andrena imitatrix* Cresson; Andrenidae) was collected from both *C. florida* and *C. canadensis* (Tables 2, 3). Two species (*Anthophora ursina* Cresson, *Xylocopa virginica* L; Apidae) were unique to *C. canadensis* (Tables 2, 3). Seven species representing three families (Andrenidae, Apidae, Colletidae) were unique to *C. florida* (Tables 2, 3). More males of *X. virginica* ($N = 13$) were collected on *C. canadensis* at urban sites than females ($N = 4$; Table 2). More females of *A. cressonii* bees ($N = 12$) were collected on *C. florida* at urban sites than males of the same species ($N = 1$; Table 3).

A total of 293 females were collected from both *C. canadensis* and *C. florida* at the exurban sites, consisting of 183 females from *C. canadensis* and 110 females from *C. florida*. We collected 40 males from both research trees at exurban sites, 24 males from *C. canadensis* and 16 males from *C. florida* (Tables 2, 3).

When females at exurban sites were compared for both trees, we found that 18 species in all five families were collected on both *C. canadensis* and *C. florida* (Tables 2, 3). Twelve female bee species in all families excluding Colletidae were collected only on *C. canadensis* (Table 2; Fig. 1D). Eleven female species representing the Andrenidae and Halictidae were found only on *C. florida* (Table 3).

Table 3. Pollen-Carrying Bee Diversity on *Cornus florida*, Urban vs. Exurban (Exurb = Exurban)

Bee Species	Urban	Female Urban	Male Urban	Exurban	Female Exurb	Male Exurb	TOTAL
Andrenidae							
Andrena carlini	0			1	(1)		1
A. crataegi	0			2		(2)	2
A. cressonii	13	(12)	(1)	16	(15)	(1)	29
A. forbesii	1	(1)		1	(1)		2
A. hippotes	3		(3)	0			3
A. ilicis	0			2	(1)	(1)	2
A. illini	0			1	(1)		1
A. illini/sayi	0			1		(1)	1
A. imitatrix	5	(4)	(1)	6	(4)	(2)	11
A. mandibularis	0			2	(2)		2
A. miserabilis	13	(12)	(1)	5	(5)		18
A. nasonii	2		(2)	10	(10)		12
A. nigrae	0			1		(1)	1
A. nuda	0			3	(3)		3
A. perplexa	1		(1)	1		(1)	2
A. pruni	0			1		(1)	1
Apidae							
Anthophora ursina	0			0			0
Apis mellifera	8	(8)		24	(24)		32
Bombus bimaculatus	0			0			0
B. griseocollis	0			0			0
B. impatiens	0			1	(1)		1
Bombus spp.	0			0			0
Ceratina calcarata	0			3		(3)	3
C. strenua	1		(1)	0			1
Eucera dubitata	0			0			0
Nomada cressoni/sayi	0			0			0
N. luteoloides	0			0			0
N. pygmaea	0			1		(1)	1
Xylocopa virginica	1	(1)		0			1
Colletidae							
Colletes inaequalis	0			11	(11)		11
Hylaeus (*Prosopis*) sp.	1		(1)	1		(1)	2
Halictidae							
Halictus rubicundus	0			1	(1)		1
Augochlora pura	0			10	(10)		10
Augochlorella aurata	0			1	(1)		1
Augochloropsis viridula	0			2	(2)		2
Lasioglossum birkmani	0			1	(1)		1
L. callidum	0			1	(1)		1
L. cattellae	0			0			0
L. coeruleum	0			1	(1)		1
L. cressonii	0			1	(1)		1
L. fuscipenne	0			2	(2)		2
L. gotham	0			0			0
L. hitchensi	1	(1)		1	(1)		2
L. illinoense	1	(1)		0			1
L. imitatum	1	(1)		2	(2)		3
Lasioglossum sp. 1	1	(1)		1	(1)		2
L. tegulare	1	(1)		0			1
L. versatum	0			4	(4)		4
L. weemsi	0			1	(1)		1

Table 3 continued

Bee Species	Urban	Female Urban	Male Urban	Exurban	Female Exurb	Male Exurb	TOTAL
Megachilidae							
Osmia atriventris	0			1	(1)		1
O. taurus	0			1		(1)	1
O. georgica	0			1	(1)		1
O. lignaria	0			0			0
O. pumila	0			0			0
Total	54	(43)	(11)	126	(110)	(16)	180

When males were compared between the two research tree species at exurban sites, we found five species representing two families (Andrenidae, Apidae) were collected from both *C. florida* and *C. canadensis* (Tables 2, 3). Five species representing three families (Apidae, Colletidae, Megachilidae) were unique to *C. canadensis* (Tables 2, 3). Seven species representing all families except Halictidae were netted only on *C. florida* (Tables 2, 3).

POLLEN LOAD ANALYSES

Of the bees foraging on *C. canadensis*, we found 195 exurban bees representing all five families and 45 urban bees representing four families (Andrenidae, Apidae, Colletidae, Megachilidae) carrying pollen of *C. canadensis* (Fig. 1E; Appendix Tables 1-2; 5-6). In addition, 24 exurban bees and 6 urban bees collected on *C. canadensis*, also carried pollen of *C. florida* (Fig. 1E; Appendix Tables 1-2, 5-6).

A total of 111 exurban bees representing all five families and 42 urban bees representing four families collected on *C. florida* carried this tree's pollen (Fig. 1E; Appendix Tables 3, 7-9). Thirty exurban bees representing four families (Andrenidae, Apidae, Colletidae, Halictidae) and 13 urban bees representing three families (Andrenidae, Apidae, Halictidae) collected on *C. florida* also carried pollen of *C. canadensis* (Fig. 1E; Appendix Tables 3, 7-9).

Female bees collected on *C. florida* at the SLU site carried the greatest mean number of pollen morphotypes (mean = 2.30, *SD* = 1.70) compared to males (mean = 0.93, *SD* = 1.07) when compared with male and female bees at our three remaining sites. When male bees were eliminated and female and worker bees were combined, similar results were obtained (mean = 2.18, *SD* = 1.66). The bee carrying the greatest number of different pollen morphotypes was a female *Andrena miserabilis* collected at the urban SLU site on *C. florida* (04/22/2019) with five recognizable morphotypes. An additional three bees collected on *C. florida* carried four different pollen morphotypes apiece. Bees collected foraging on *C. canadensis* never carried more than three pollen morphotypes. When only female and worker *Apis* are considered for *C. canadensis* at the urban TGP site, bees carried more pollen morphotypes (mean = 1.30, *SD* = 0.95) than those caught at the remaining sites [SLU (mean = 1.24, *SD* = 0.54; BSP (mean = 1.25, *SD* = 0.73); SNR (mean =1.19, *SD* = 0.86).

	q^0	q^1(±se)	q^2(±se)
Cercis canadensis	37	19.1(1.6)	10.3(1.1)
urban	10	8.1(0.7)	4.5(0.6)
exurban	35	17.7(1.2)	7.6(0.8)
Cornus florida	43	22.2(2.0)	13.9(1.4)
urban	16	11.1(1.0)	5.1(0.6)
exurban	38	17.9(1.2)	7.8(0.8)
Urban total	30	14.9(1.9)	10.0(1.1)
Exurban total	51	22.8(1.5)	12.2(1.1)

Table 4. Hills diversity parameter estimates for bee community assemblages from *Cercis canadensis* and *Cornus florida*, as well as urbanization level, from the St. Louis, MO, USA, metropolitan region. The parameter q^0 is species richness, while q^1 is analogous to Shannon's H', and q^2 is analogous to Simpson's D.

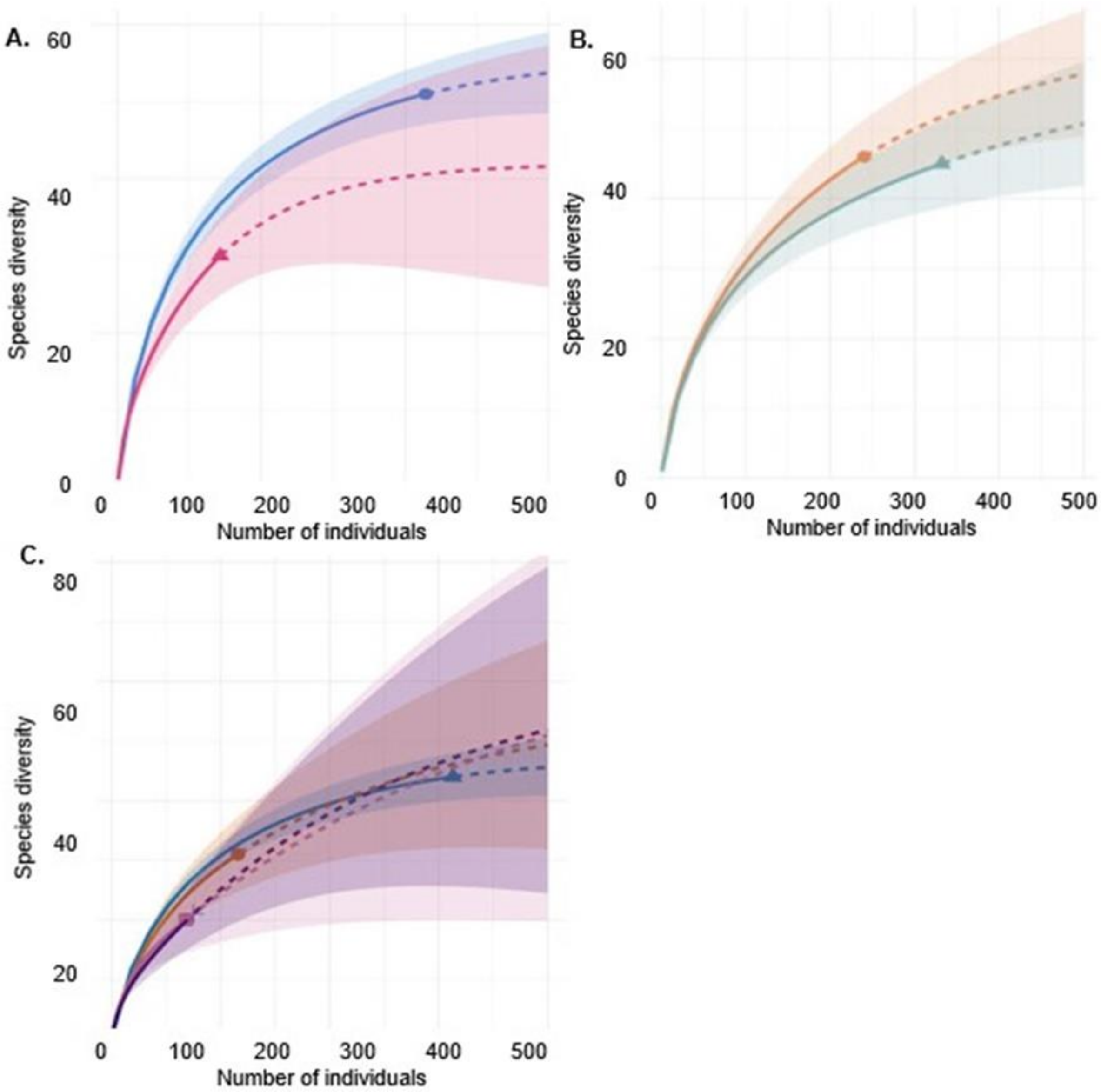

Figure 5. Species rarefaction curves for bee communities sampled in the greater St. Louis metropolitan area. The solid lines represent the observed while the dashed lines are the extrapolated values. Shaded areas represent the confidence intervals. (A) Rarefaction curves for *Cercis canadensis* (blue) and *Cornus florida* (red); (B) Rarefaction curves for urban (green) and exurban (yellow) sites; (C) Rarefaction curves for the individual locations, SLU (pink square), TGP (violet cross), BSP (orange circle), and SNR (blue triangle).

DISCUSSION

THE IMPACT OF THE HEAT ISLAND EFFECT ON TREE PHENOLOGY AND BEE DIVERSITY

We expected that the urban environment will affect bee visitor assemblages, either directly, via habitat alteration, e.g. impervious surface, or indirectly, via the urban heat island effect. We also hypothesized that the focal tree species populations in exurban sites will bloom later than the urban ones. Results supported our hypotheses. The significantly warmer urban environment resulted in earlier blooming for both tree species as compared to the exurban sites. The earlier blooming could have resulted in decreased insect richness and abundance of potential foragers for both tree species in the urban areas. This gap between the time when the first urban flower buds open and the time in which the first urban bees are collected on *C. canadensis* may represent a challenge to bees provisioning their nests. We suggest that the extra early flowering of urban *C. canadensis* limits the species pool of potential bee visitors because much of the flowering period has already elapsed. The overall differences in species

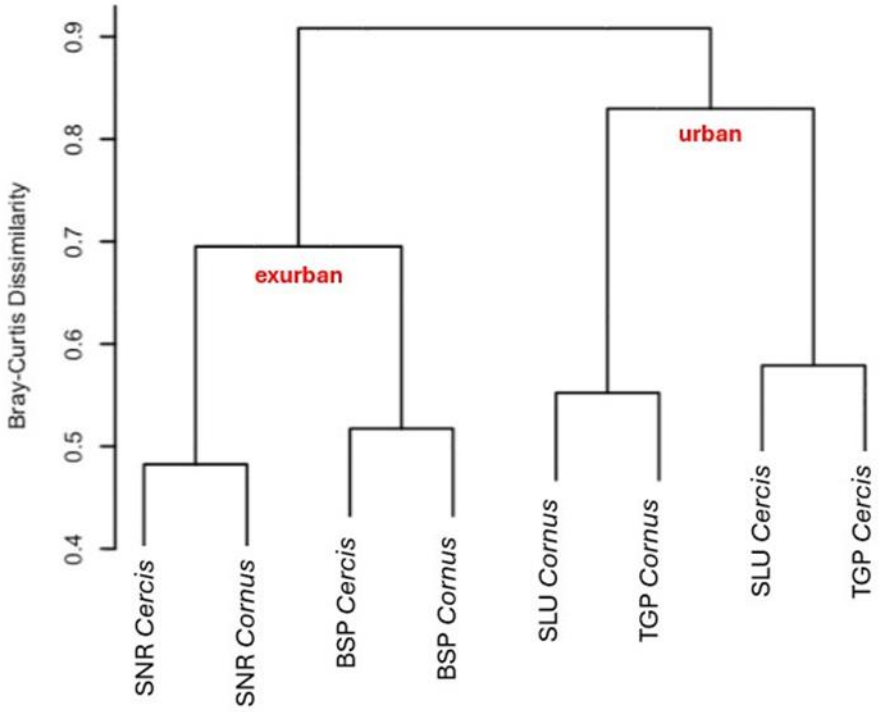

Figure 6. Dendrogram of bee assemblages visiting *Cercis canadensis* and *Cornus florida* in urban and exurban sites in the St. Louis metropolitan region, MO, USA. The greatest dissimilarity was between urbanization level.

richness (Fig. 5), diversity (Appendix Table 1), and species turnover (Fig. 6) suggest that the effects of urbanization, including the heat island effect, are significant. This, in turn, leads to similarity in assemblage composition between urban sites (Fig. 6). The urban *C. florida* follows a similar pattern although not as drastic. Alternatively, in the exurban sites, the later and longer blooming periods allow for the enlargement of the visitor species pool, and consequently, greater similarity in bee visitor assemblages (Fig. 6).

In contrast, by the time the urban bees begin to forage on *C. canadensis*, a significant period of flowering time of *C. canadensis* has already elapsed. Once these bees begin to forage on *C. canadensis*, they have missed a significant proportion of the tree's pollen and nectar supply. Perhaps this heat island effect is evidence of the early stages of decoupling between foraging bees and selected species of mass flowering trees in a city (see Freimuth et al. 2022). This would help explain the comparatively low diversity of urban bees on both tree species compared to our exurban sites.

Of course, bees can achieve high diversities in urban centers (Baldock et al. 2015; Hall et al. 2017; Buchholz et al. 2020) despite the challenges that urban infrastructure represents (Lambert et al. 2021). Some studies have suggested that this increased diversity is associated with the warmer urban centers (Banaszak-Cibicka 2014; Geppert et al. 2023). However, Banaszak-Cibicka (2014) and Geppert et al. (2023) studied urban bee diversity later in the flowering season compared with this study. We found decreased diversity and abundance from late March through early May in the urban centre compared to exurban locations. Furthermore, the results of the cluster analysis suggest that the local microhabitat effect observed in the exurban sites is overturned completely by the urban infrastructure and associated heat island effect (Fig. 6).

BEE ABUNDANCE AND DIVERSITY OF POLLEN-CARRYING BEES

Both tree species had a significantly higher diversity of bee foragers (Fig. 5B), and a greater number of males, at the exurban sites (Table 4, Fig. 5). *Cornus florida* in exurban areas received a greater bee species richness compared to *C. canadensis* (Fig. 5A).

In this study, urban bee collections on *C. canadensis* started in April, two to three weeks earlier than the previous studies conducted in St. Louis by Camilo et al. (2018), yet this present study adds only three new species to the Camilo et al. (2018) bee checklist. This included two female, pollen-carrying specimens of *Osmia taurus*, a Eurasian species first identified on the east coast of the United States in 2002 (Gutierrez et al. 2022). We also added *Andrena rugosa* but it was not carrying pollen of either tree species (see Appendix Table 4). As the urban bee checklist did not identify *Nomada* specimens to species, we are unable to match them to our four exurban species (see Appendix Table 4). In addition, the St. Louis bee species checklist (Camilo et al. 2017) lacks several species (Andrenidae: *Andrena miserabilis*, *Andrena nigrae* Robertson, *Andrena pruni* Robertson; Apidae: *Ceratina mikmaqi* Rehan & Sheffield, *Eucera dubitata* Cresson; Halictidae: *Lasioglossum birkmanii* Crawford, *L. fuscipenne* Smith, *L. gotham* Gibbs, *L. weemsi* Mitchell) found only in our two exurban sites.

However, our exurban collections also show that as in other mass-flowering canopy tree species, our two, smaller tree species also attract a diverse cast of polylectic females and pollinivorous males (Urban-Mead et al. 2021, 2022). This may be comparable to bee collections from mass-flowering trees of the Neotropics (Frankie et al. 1998) and temperate Australia (Bernhardt 1989). As daily temperatures increase in temperate zones, the abundance and diversity of vernal bees increases with the abundance and diversity of the vernal flora (Bernhardt 1989). Consequently, bee diversity is higher in exurban *C. florida* compared to exurban *C. canadensis*.

FREQUENCIES AND DISTRIBUTIONS OF POLLEN-CARRYING FEMALE AND MALE BEES

The percentage of male to female bees was disproportionately higher in our urban sites compared to our exurban sites for both tree species (*C. canadensis* 38% urban, 12% exurban; *C. florida* 20% urban, 13% exurban). As in most winged, hibernating-pupating insects, we expect that male bees will emerge from hibernation before females. While this suggests that the males of a few bee species (e.g., *Colletes inaequalis*, *X. virginica*) may be particularly sensitive to the long-term stimulus of the urban heat island effect as winter grades into spring, it must be treated with caution. The abundance of male *X. virginica* at the urban sites may be based in part on its overwintering preferences in wood and twigs exposing the developing males to the earlier cycle of urban heat. If this is true, though, it fails to explain the rarity of males of *Osmia* species on urban *C. canadensis*, as bees in this genus are also wood and twig nesters. When the sex ratios of female:male bees are combined for both tree species at our exurban sites, females dominate overwhelmingly, as usual, but 14 species were represented only by males. However, with the exception of *X. virginica*, males of each of the remaining 13 species were represented by only one to three specimens.

In eastern North America, female and male bees collect and/or eat pollen from canopy, wind-pollinated trees (Urban-Mead et al. 2023). Consequently, we presumed that we would capture more female than male bees on our two species of subcanopy, nectariferous and mass-flowering trees. Smith et al. (2019) emphasized that male and female bees behave differently. Based on sex, this includes foraging preferences, periods of foraging activity and flight distances. Food consumed by males is converted into fuel for flight, mating, and competition with other males. In addition, some males merely scout flowers for incoming females, so their contact with anthers and stigmas may be minimal. The same cannot be stated for females. We note that males of *X. virginica* were more common on *C. canadensis* than females of the same species (Fig. 1A). In contrast, males of *X. virginica* were not attracted to *C. florida*. Males of *Bombus* species were not collected from either tree species because they do not emerge until later in the year.

In fact, the two tree species in this research attract many of the same bee species that forage on the vernal, herbaceous flora of the Midwestern United States. Our results contribute to recent reconsiderations of the roles of male bees as consumers of floral rewards (Smith et al. 2019; Urban-Mead, 2023). Previous studies also show varying ratios of male to female bees as prospective pollinators of the Midwestern herbaceous flora (see Bernhardt et al. 2016; Edens-Meier et al. 2018; Edens-Meier et al. 2020; Edens-Meier et al. 2021).

TREES SHARING BEE SPECIES VS. URBAN/EXURBAN BEE FORAGING PREFERENCES

With more bees (*N* = 254) collected on *C. canadensis* than on *C. florida* (*N* = 180), we suspect this is another consequence of seasonal warming. As more bee-pollinated plants are in bloom later in the season with *C. florida*, there must be some competition for the limited pollinator guild (see below). In addition, there was only a 48% overlap of bee species shared by the two tree species.

An interaction effect in bee species diversity between tree species and location showed a significant decrease in bee diversity on urban *C. canadensis*. We attribute that decrease to the limited species pool available given this tree species' earlier bloom cycles. Of the shared bee species, the skewed density of *Colletes inaequalis* in exurban versus urban sites is surprising. While the most commonly collected exurban species, it was absent on urban *C. florida* and almost completely absent from urban *C. canadensis* although large nesting aggregations have been found in several residential areas in St. Louis city (Camilo unpublished). We conclude that even generalist foragers have preferences based on the availability of plants in bloom. Batra (1980) found that *C. inequalis* prefers to forage on native trees in the genus *Acer* in the eastern United States, especially *Acer rubrum* L., as soon as the soil defrosts. *Acer* species are not native to the oak-hickory woodlands in either of our exurban sites (Yatskievych 1999). In contrast, at least four *Acer* species native to North America are grown as ornamentals in the city of St. Louis, MO (Yatskievych (1999). Most likely, the urban *Colletes inaequalis* in the present study ignored *C. canadensis* in favor of co-blooming *Acer* species. Likewise, the comparative absence of *Osmia* species and *Bombus* gynes on *C. florida* in exurban sites would also appear to reflect pollen and nectar preferences. Previous studies by Rhoades et al. (2011) also found that suburban stands of *C. florida* were visited primarily by members of the Andrenidae and Halictidae. In this study all of the 16 *Andrena* species identified as pollen foragers visited *C florida* while nine of the 14 pollen carrying *Lasioglossum* species (Halictidae) were collected only on *C. florida*.

We hypothesized that we should observe more specialist foragers in the exurban sites than in the urban sites. Consequently, our data did not support the hypothesis of specialized exurban foragers as none of the bee species collected are regarded as oligolectic on either tree species or specialists on the Fabaceae or Cornaceae (Fowler 2016). Our pollen load analyses indicated that most of our bee species are more likely to visit more than one plant species during the same foraging bout, especially when *C. florida* blooms.

It is also understood that some of the polylectic bee species divide their foraging bouts between woodlands and adjacent habitats (Urban-Mead et al. 2023; Edens-Meier et al. 2011). Furthermore, our exurban bee collections indicate that bees foraging on trees that are between six and twenty meters in height are also foraging on and pollinating the native, vernal, herbaceous flora of the Midwestern United States. Based on past identification of pollinators, no vertical barriers are obvious between the low growing herbs and our taller trees (Edens-Meier et al. 2011; Bernhardt et al. 2016; Edens-Meier et al. 2018; Edens-Meier et al. 2020). We note that out of 88 native bees collected on *Hypoxis hirsuta* L. Coville, 25 specimens carried the pollen of *H. hirsuta* mixed with *C. florida* (Ren et al., 2019).

URBAN VS. EXURBAN POLLEN LOAD ANALYSES

Bees in exurban sites were more likely to carry mixed loads of pollen when they visited *C. florida*, compared to when they visited *C. canadensis*. As our foraging females all belonged to polylectic species, the mixed pollen loads they carried are predictable, reflecting previous pollination studies (see above; Bernhardt et al. 2016; Edens-Meier et al. 2011, 2018, 2020, 2021). However, why does the diversity of pollen morphotypes found on urban bees foraging on *C. florida*, exceed those of the more diverse bee species collected on exurban trees? Once again, by the time *C. florida* blooms in St. Louis the urban landscape offers polylectic foragers additional mass-flowering woody plants based on many cultivars in the Rosaceae (*Malus, Prunus, Spiraea*) and *Syringa* (Oleaceae) unavailable at the exurban sites. In contrast, bees collected on urban *C. canadensis* foraged too early to exploit these ornamental species with the possible exception of nectar secreting *Chaenomeles*, *Pyrus calleryana* Decaisne (Dolan et al. 2023) and *Forsythia*.

Nineteen bees (12 species) carried the large and distinctive pollen grains of the invasive Asian shrub *Lonicera maackii* (Rupr.) Maxim (Fig. 1F) in both urban and exurban sites. This included *A. mellifera* and 17 bees dominated by eight *Andrena* species. Only two bees collected on *C. canadensis* carried pollen of *L. maackii* as their flowering periods do not have a broad overlap during the

Missouri spring (Yastkievich 1999). The role of some native bees in the pollination of *L. maackii* deserves further investigation since many factors appear to influence the foraging preferences of native bees on exotic flora (Frankie et al. 2019; Staab et al. 2020).

IMPLICATIONS

The small sample size of sites investigated is a limitation of this study. We encourage potential future research to address this issue and add to the existing knowledge base of bees visiting vernal blooming native trees in urban and exurban areas. There are more opportunities globally because the domestication of native species of mass- and spring-flowering plants for ornamental display is virtually pandemic (Bauer & Carlquist 1965; Goody 1990; Robbin 2002). As the overall scientific consensus insists that urbanization is altering ecosystems and biodiversity at unprecedented rates (Peng et al. 2017; Simkin et al. 2022), this should also be true of plant-pollinator interactions (Marcacci et al. 2023).

ACKNOWLEDGEMENTS

We wish to thank Mike Arduser for his assistance in the identification of bee specimens. A special thanks goes to Dr. Zong-Xin Ren of the Kunming Institute of Botany, Yunnan, for his help in organizing and labelling our photographic plate. We thank employees of Shaw Nature Reserve for making it possible for us to do research at that site. We thank the librarians at the Peter Raven Library of the Missouri Botanical Garden for their professional services and kindness. We thank Dr. Charlotte Taylor of the Bayer Herbarium of the Missouri Botanical Garden for helping us organize the bee collection data sets.

AUTHOR CONTRIBUTION

All authors contributed to the data collection and analyses, as well as writing. Peter Bernhardt had the original idea while Gerardo Camilo designed the study. Peter Bernhardt, Gerardo Camilo and Retha Edens-Meier did the editing and reviewing.

DISCLOSURE STATEMENT

All authors declared no conflict of interest.

DATA AVAILABILITY STATEMENT

The data used to write this paper are available by contacting Gerardo Camilo at Lamponius@gmail.com. Please contact this author for data requests.

APPENDICES

Additional supporting information may be found in the online version of this article:

Appendix 1: Tables 1-3, 5-9: Pollen Loads collected on male and female bees

Appendix 2: Table 4. Captured bees without pollen

REFERENCES

Anderson M, Braak CT (2003) Permutation tests for multi-factorial analysis of variance. Journal of statistical computation and simulation. 72:85-113. https://doi.org/10.1080/00949650215733

Arduser M (2020) Keys to bee genera in the tallgrass prairie region and greater midwest. Version 3.0. https://conservationresearchinstitute.org/files/keys/3_bee_genera.pdf

Aronson MF, Nilon CH, Lepczyk CA, Parker TS, Warren PS, Cilliers SS, Goddard MA, Hahs AK, Herzog C, Katti M, others (2016) Hierarchical filters determine community assembly of urban species pools. Ecology, 97:2952-2963. https://doi.org/10.1002/ecy.1535

Austin MW, Tripodi AD, Strange JP, Dunlap AS (2022) Bumble bees exhibit body size clines across an urban gradient despite low genetic differentiation. Scientific Reports, 12:1-12. https://doi.org/10.1038/s41598-022-08093-4

Baldock KC, Goddard MA, Hicks DM, Kunin WE, Mitschunas N, Osgathorpe LM, Potts SG, Robertson KM, Scott AV, Stone GN, Vaughan IP, (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. Proceedings of the Royal Society B: Biological Sciences, 282:20142849. https://doi.org/10.1098/rspb.2014.2849

Banaszak-Cibicka W (2014) Are urban areas suitable for thermophilic and xerothermic bee species (Hymenoptera: Apoidea: Apiformes)? Apidologie, 45:145-155. https://doi.org/10.1007/s13592-013-0232-7

Batra SWT (1980) Ecology, behavior, pheromones, parasites and management of the sympatric vernal bees *Colletes inaequalis, C. thoracicus,* and *C. validus*. Journal of the Kansas Entomological Society, 53:509-538.

Bauer H, Carlquist S (1965) Japanese Festivals. Doubleday. Garden City, New York.

Bennett AB, Lovell ST (2019) Landscape and local site variables differentially influence pollinators and pollination services in urban agricultural sites. PLoSONE, 14(2):e0212034. https://doi.org/10.1371/journal.pone.0212034

Bernhardt P, Kenrick J, Knox R (1984) Pollination biology and the breeding system of *Acacia retinodes* (Leguminosae: Mimosoideae). Annals of the Missouri

Botanical Garden 17-29. https://doi.org/10.2307/2399054

Bernhardt P (1989) The floral ecology of Australian Acacia. In: Advances In Legume Biology. Stirton CH, Zarucchi JL Monographs in Systematic Botany from the Missouri Botanical Garden, St. Louis, Missouri, pp 127-155.

Bernhardt P (1996) Anther adaptations in animal pollination. In: The Anther. D'Arcy WG, Keating RC Cambridge University Press, Great Britain, pp 192-220.

Bernhardt P, Edens-Meier R, Jocson D, Zweck J, Ren Z-X, Camilo GR, Arduser M (2016) Comparative floral ecology of bicolour and concolour morphs of *Viola pedata* L (Violaceae) following controlled burns. Journal of Pollination Ecology 19:57-70. https://doi.org/10.26786/1920-7603(2016)3

Buchholz S, Gathof AK, Grossmann AJ, Kowarik I, Fischer LK (2020) Wild bees in urban grasslands: Urbanisation, functional diversity and species traits. Landscape and Urban Planning 196:103731. https://doi.org/10.1016/j.landurbplan.2019.103731

Bzdyk K (2016) Eastern Redbud. LoudonWildlife Conservancy 21. https://loudounwildlife.org/2016/04/eastern-redbud

Camilo G R, Muniz PA, Arduser, MS, Spevak, EM (2017) A checklist of the bees (Hymenoptera; Apoidea) of St. Louis, Missouri, USA. Journal of the Kansas Entomological Society 90:175-188. https://doi.org/10.2317/0022-8567-90.3.175

Chao A, Kubota Y, Zelený D, Chiu C-H, Li C-F, Kusumoto B, Yasuhara M, Thorn S, Wei C-L, Costello MJ, others (2020) Quantifying sample completeness and comparing diversities among assemblages. Ecological Research 35:292-314. https://doi.org/10.1111/1440-1703.12102

Chao A, Henderson PA, Chiu C-H, Moyes F, Hu K-H, Dornelas M, Magurran AE (2021) Measuring temporal change in alpha diversity: A framework integrating taxonomic, phylogenetic and functional diversity and the iNEXT. 3D standardization. Methods in Ecology and Evolution 12:1926-1940. https://doi.org/10.1111/2041-210X.13682

Danforth BN, Minckley RL, Neff JL, Fawcett F (2019) The solitary bees: biology, evolution, conservation. Princeton University Press, Princeton, New Jersey. https://doi.org/10.1515/9780691189321

Debbage, N, Shepherd, JM (2015) The urban heat island effect and city contiguity. Computers, Environment and Urban Systems 54:181-194. http://dx.doi.org/1-.1016/j.compenvurbsys.2015.08.002.

Dolan BJ, Kalkstein, AL, Haase M, Chernisky P, Niese A, Hicks AN, Miller D (2023) Pollinator communities of planted and feral *Pyrus calleryana*. Ecologies 2:1-10. https://doi.org/01.3390/ecologies4010001.

Edens-Meier R, Joseph M, Arduser M, Westhus E, Bernhardt P (2011) The pollination biology of an annual endemic herb, *Physaria filiformis* (Brassicaceae), in the Missouri Ozarks following controlled burns. The Journal of the Torrey Botanical Society 138:287-297. https://doi.org/10.3159/TORREY-D-11-00024.1

Edens-Meier R, Arduser M, Camilo GR, Bernhardt P (2018) Comparative pollination ecology between two populations and two varieties of *Cypripedium parviflorum* (Orchidaceae) in Missouri, United States of America-does size matter? Botanical Journal of the Linnean Society 186:544-559. https://doi.org/10.1093/botlinnean/boy001

Edens-Meier R, Arduser M, Camilo GR, Bernhardt P, Ren Z-X (2020) Breeding systems and pollination ecology of *Uvularia grandiflora* (Colchicaceae). The Journal of the Torrey Botanical Society 147:38-48. https://doi.org/10.3159/TORREY-D-19-00015.1

Edens-Meier R, Arduser M, Camilo GR, Tackett MJ (2021) Pollination ecology and breeding systems of *Cypripedium kentuckiense* (Orchidaceae) in Tennessee. The Journal of the Torrey Botanical Society 148:53-74. https://doi.org/10.3159/TORREY-D-20-00033.1

Eggenberger H, Frey D, Pellissier L, Ghazoul J, Fontana S, Moretti M (2019) Urban bumblebees are smaller and more phenotypically diverse than their rural counterparts. Journal of Animal Ecology 88:1522-1533. https://doi.org/10.1111/1365-2656.13051

Fenoglio MS, Rossetti MR, Videla M (2020) Negative effects of urbanization on terrestrial arthropod communities: A meta-analysis. Global Ecology and Biogeography 29:1412-1429. https://doi.org/10.1111/geb.13107

Fowler J (2016) Specialist bees of the Northeast: Host plants and habitat conservation. Northeastern Naturalist 23:305-320. https://doi.org/10.1656/045.023.0210

Frankie G, Vinson SB, Rizzardi MA, Griswold JL, O'Keefe S, Snelling RR (1998) Diversity and abundance of bees visiting a mass flowering tree in disturbed seasonal dry forest Costa Rica. Journal of the Kansas Entomological Society 70:281-296.

Frankie G, Feng I, Thorp R, Pawelek J, Chase MH, Jadallah CC, Rizzardi M (2019) Native and non-native plants attract diverse bees to urban gardens in California. Journal of Pollination Ecology 25. https://doi.org/10.26786/1920-7603.

Freimuth J, Bossdorf O, Scheepers JF, Willems FM (2022) Climate warming changes synchrony of plants and pollinators. Proceedings of the Royal Society 289:20212142. https://doi.org/10.1098/rspb.2021.2142

Geppert C, Cappellari A, Corcos D, Caruso V, Cerretti P, Mei M, Marini L (2023) Temperature and not landscape composition shapes wild bee communities in an urban environment. Insect Conservation and Diversity 16:65-76. https://doi.org/10.1111/icad.12602

Goldblatt P, Bernhardt P (1990) Pollination biology of *Nivenia* (Iridaceae) and the presence of heterostylous self-compatibility. Israel Journal of Plant Sciences 39:93-111.

Goody J (1990) The Culture of Flowers. Cambridge University Press, Cambridge, United Kingdom.

Graham EK (1941) Legumes for erosion control and wildlife. United States Department of Agriculture, Miscellaneous Publications 412:1-153.

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319:756-760. https://doi.org/10.1126/science.1150195

Gutierrez GM, LeCroy KA, Roulston TH, Biddinger DJ, López-Uribe MM (2023) *Osmia taurus* (Hymenoptera: Megachilidae): A Non-native bee species with invasiveness potential in North America. Environmental Entomology 52:149-156. https://doi.10.1093/33/nvad005

Hall D M, Camilo GR, Tonietto RK, Ollerton J, Ahrné K, Arduser M, Ascher JS, Baldock KC, Fowler R, Frankie G, others (2017) The city as a refuge for insect pollinators. Conservation Biology 31:24-29. https://doi.org/10.1111/cobi.12840

Hamblin, AL, Youngsteadt, E, Frank, SD (2018) Wild bee abundance declines with urban warming, regardless of floral density. Urban Ecosystems, 21, 419-428. https://doi.org/10.1007/s11252-018-0731-4

Hervé M, Hervé MM (2020) Package 'RVAideMemoire'. https://CRANR-projectorg/package= RVAideMemoire.

Hsieh T, Ma K, Chao A (2016) iNEXT: An R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods in Ecology and Evolution 7:1451-1456. https://doi.org/10.1111/2041-210X.12613

Lambert MR, Brans KI, Des Roches S, Donihue CM, Diamond SE (2021) Adaptive evolution in cities: progress and misconceptions. Trends in Ecology & Evolution 36:239-257. https://doi.org/10.1016/j.tree.2020.11.002

Li D, Stucky BJ, Deck J, Baiser B, Guralnick RP (2019) The effect of urbanization on plant phenology depends on regional temperature. Nature Ecology & Evolution 3:1661-1667. https://doi.org/10.1038/s41559-019-1004-1

Lovell HB (1961) Let's talk about honey plants. Gleanings Bee Culture 89:99-100.

Lowenstein DM Minor ES (2016) Diversity in flowering plants and their characteristics: integrating humans as a driver of urban floral resources. Urban Ecosystems 19:1735-1748. https://doi.org/10.1007/s11252-016-0563-z

Lowenstein DM, Matteson KC, Minor ES (2019) Evaluating the dependence of urban pollinators on ornamental, non-native, and 'weedy' floral resources. Urban Ecosystems 22:293-302. https://doi.org/10.1007/s11252-018-0817-z

Manoli G, Fatichi S, Schläpfer M, Yu K, Crowther TW, Meili N, Burlando P, Katul GG, Bou-Zeid E (2019) Magnitude of urban heat islands largely explained by climate and population. Nature 573:55-60. https://doi.org/10.1038/s41586-019-1512-9

Marcacci G, Westphal C, Rao VS, Kumar SS, Tharini KB, Belavadi VV, Nölke N, Tscharntke T, Grass I (2023) Urbanization alters the spatiotemporal dynamics of plant–pollinator networks in a tropical megacity. Ecology Letters 26:1951-1962. https://doi.org/10.1111/ele.14324

McDonald RI, Kareiva P, Forman RT (2008) The implications of current and future urbanization for global protected areas and biodiversity conservation. Biological Conservation 141:1695-1703. https://doi.org/10.1016/j.biocon.2008.04.025

McDonald RI, Marcotullio PJ, Güneralp B (2013) Urbanization and global trends in biodiversity and ecosystem services, In: Urbanization, Biodiversity and Ecosystem Services: Challenges and Opportunities. Springer, Dordrecht, pp 31-52. https://doi.org/10.1007/978-94-007-7088-1_3

McMaster GS, Wilhelm W (1997) Growing degree-days: one equation, two interpretations. Agriculture and Forest Meteorology 87:291-300. https://doi.org/10.1016/S0168-1923(97)00027-0

Meineke EK, Davis CC, Davies TJ (2021) Phenological sensitivity to temperature mediates herbivory. Global Change Biology 27:2315-2327. https://doi.org/10.1111/gcb.15600

Meng L, Mao J, Zhou Y, Richardson AD, Lee X, Thornton PE, Ricciuto DM, Li X, Dai Y, Shi X, others (2020) Urban warming advances spring phenology but reduces the response of phenology to temperature in the conterminous United States. Proceedings of the National Academy of Sciences of the United States of America 117:4228-4233. https://doi.org/10.1073/pnas.1911117117

Memon RA, Leung DYC, Chunho L (2008) A review on the generation, determination and mitigation of urban heat island. Journal of Environmental Sciences 20:120-128. https://doi.org/10.1916/S1001-0742(08)60019-4.

Michener CD (2000) The bees of the world. John Hopkins University Press, Baltimore, Maryland, USA.

Miller P, Lanier W, Brandt S (2001) Using growing degree days to predict plant stages. AgExtension Communicatoin Coordinator, Communication Services, Montana State University-Bozeman, Bozeman MO 59717, 406:994-2721.

Ogden EC, Museum NYS, Service S, Commission, U.S.A.E. (1974). Manual for sampling airborne pollen. Hafner Press.

Oksanen J, Simpson G, Blanchet F, Kindt R, Legendre P, Minchin P, O'Hara R, Solymos P, Stevens M, Szoecs E, Wagner H, Barbour M, Bedward M, Bolker B, Borcard D, Carvalho G, Chirico M, De Caceres M, Durand S, Evangelista H, FitzJohn R, Friendly M, Furneaux B, Hannigan G, Hill M, Lahti L, McGlinn D, Ouellette M, Ribeiro Cunha E, Smith T, Stier A, Ter Braak C, Weedon J (2022) Vegan: Community Ecology Package. R package version 2.6-4, https://CRAN.R-project.org/package=vegan.

Ony MA, Nowicki M, Boggess SL, Klingeman WE, Zobel JM, Trigiano RN, Hadziabdic, D (2020) Habitat fragmentation influences genetic diversity and differentiation: Fine-scale population structure of *Cercis canadensis* (eastern redbud). Ecology and Evolution 10:3655-3670. https://doi.org/10.1002/ece3.6141

Parker DE (2010) Urban heat island effects on estimates of observed climate change. Wiley Interdisciplinary Reviews: Climate Change 1:123-133. https://doi.org/10.1002/wcc.21

Pearse WD, Cavender-Bares J, Hobbie SE, Avolio ML, Bettez N, Chowdhury R, Darling LE, Groffman PM, Grove JM, Hall SJ others (2018) Homogenization of plant diversity, composition, and structure in North American urban yards. Ecosphere 9:e02105. https://doi.org/10.1002/ecs2.2105

Pellett FC (1920) American Honey Plants. American Bee Journal. Hamilton, Illinois, USA.

Peng J, Tian L, Liu Y, Zhao M. Wu J (2017) Ecosystem services response to urbanization in metropolitan areas: Thresholds identification. Science of the Total Environment 607:706-714. https://doi.org/10.1016/j.scitotenv.2017.06.218

Prendergast K S, Ollerton J (2021) Plant-pollinator networks in Australian urban bushland remnants are not structurally equivalent to those in residential gardens. Urban Ecosystems 24:973-987. https://doi.org/10.1007/s11252-020-01089-w

R Core Team (2020) R: A language and environment for statistical computing. R foundation for statistical computing. Vienna, Austria.

Randolph V (1964) Ozark Magic and Folklore. Dover Press. New York, USA.

Reed SM (2004) Self-incompatibility in Cornus florida. HortScience 39:335-338. https://doi.org/10.21273/HORTSCI.39.2.335

Ren Z-X, Bernhardt P, Edens-Meier R, Zweck J, Arduser M, Li H-D, Wang H (2019) Comparative pollen-pistil interactions and insect pollination in two *Hypoxis* species (Hypoxidaceae) in China and North America. Plant Systematics and Evolution 305:115-126. https://doi.org/10.1007/s00606-018-1556-6

Rhoades PR, Klingeman WE, Trigiano EB, Skinner JA (2011) Evaluating pollination biology of *Cornus florida* L. and *C. Kousa* (Buerger ex. Miq.) Hance (Cornaceae: Cornales). Journal of the Kansas Entomological Society 84:285-297. https://doi.org/10.2317/JKES110418.1

Robbin L (2002) Nationalising nature: Wattle days in Australia. Journal of Australian Studies 26:13-26. https://doi.org/10.1080/14443050209387762

Robertson KS (1976) Cwecis: The redbuds. Arnolida 36:37049.

Roswell M, Dushoff J, Winfree R (2021) A conceptual guide to measuring species diversity. Oikos 130:321-338. https://doi.org/10.1111/oik.07202

Sachindra D, Ng A, Muthukumaran S, Perera B (2016) Impact of climate change on urban heat island effect and extreme temperatures: a case-study. Quarterly Journal of the Royal Meteorological Society 142:172-186. https://doi.org/10.1002/qj.2642

Settele J, Bishop J, Potts SG (2016) Climate change impacts on pollination. Nature Plants 2:1-3. https://doi.org/10.1038/nplants.2016.92

Simkin RD, Seto KC, McDonald RI, Jetz W (2022) Biodiversity impacts and conservation implications of urban land expansion projected to 2050. Proceedings of the National Academy of Sciences of the United States of America 119: e2117297119. https://doi.org/10.1073/pnas.2117297119

Smith PS, Bronstein JL, Papaj DR (2019) Sex differences in pollinator behavior: Patterns across species and consequences for the mutualism. Journal of Animal Ecology 88:971-985. https://doi.org/10.1111/1365-2656.12988

Staab M, Pereira-Peixoto MH, Klein A-M (2020) Exotic garden plants partly substitute for native plants as resources for pollinators when native plants become seasonally scarce. Oecologia 194:465-480. https://doi.org/10.1007/s00442-020-04785-8

Tallamy DW (2009) Bringing nature home: How you can sustain wildlife with native plants, updated and expanded. Timber Press, Portland, Oregon.

United Nations (2005) Millennium ecosystem assessment. Washington, DC: New Island 13: 520.

United Nations Department of Economic and Social Affairs Population Division (2019) World Urbanization Prospects: The 2018 Revision (ST/ESA/SER.A/420). UnitedNations, New York, NY.

Urban-Mead KR, Muñiz P, Gillung J, Espinoza A, Fordyce R, van Dyke M, McArt SH, Danforth BN (2021) Bees in the trees: Diverse spring fauna in temperate forest edge canopies. Forest Ecology and Management 482:1-10. https://doi.org/10.1016/j.foreco.2020.118903

Urban-Mead KR, Walter E, McArt SH, Danforth BN (2022) Nearly half of spring-flying male Andrena bees consume pollen, but less than female conspecifics. Apidologie 53: 49. https://doi.org/10.1007/s13592-022-00951-4

Urban-Mead KR, van Dyke M, Muñiz P, Young AD, Danforth BN, McArt SH (2023) Early spring orchard pollinators spill over from resource-rich adjacent forest patches. Journal of Applied Ecology 60:553-564. https://doi.org/10.1111/1365-2664.14350

Wenzel A, Grass I, Belavadi VV, Tscharntke T (2020) How urbanization is driving pollinator diversity and pollination-A systematic review. Biological Conservation 241:108321. https://doi.org/10.1016/j.biocon.2019.108321

White J, Son Y, Park Y-L (2009). Temperature-dependent emergence of *Osmia cornifrons* (Hymenoptera: Megachilidae) Adults. Journal of Economic Entomology 102: 2026-2032. https://doi.org/10.1603/029.102.0602.

Wilde H, Gandhi K, Colson G (2015) State of the science and challenges of breeding landscape plants with ecological function. Horticultural Research 2: 14069. https://doi.org/10.1038/hortres.2014.69.

Wohlfahrt G, Tomelleri E, Hammerle A (2019) The urban imprint on plant phenology. Nature Ecology and Evolution 3:1668-1674. https://doi.org/10.1038/s41559-019-1017-9

Yatskievych G (1999) Steyermark's Flora of Missouri. Missouri Botanical Garden Press. St. Louis, MO, USA.

Zeballos, M, Calviño, AA, Zamudio, F (2022) Is the flight and foraging activity of small-size stingless bee affected by the urban heat island? The case of *Plebeia catamarcensis* (Meliponini) in Cordoba City (Argentina). Journal of Apicultural Research 61:632-641. https://doi.org/10.1080/00218839.2022.211043.

Zipper SC, Schatz J, Singh A, Kucharik CJ, Townsend PA, Loheide II SP (2016) Urban heat island impacts on plant phenology: intra-urban variability and response to land cover. Environmental Research Letters 11: 054023. https://doi.org/10.1088/1748-9326/11/5/054023