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ORIGINAL PAPER

Woody flowering plants support early-spring pollinators in urban greenspaces

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Abstract

One threat pollinators face in a rapidly changing climate is the decoupling of their activity period from the blooming period of their host plants. Pollinators active in the earliest part of spring may be especially susceptible, as there are few alternative food resources available if they become active before their host plants begin blooming. Thus, urban landscapes, although often associated with decreased insect biodiversity, may buffer pollinators from such food shortages by offering a diversity of both native and exotic plant species that bloom in the late winter and early spring. However, more data are needed to ascertain the degree to which pollinators utilize flowers of spring-blooming exotic species. Here, we surveyed flower-visiting Hymenoptera and Diptera on 26 flowering plant taxa in three urban botanical gardens in the Oklahoma City metropolitan area in the early spring (March and April). We found that flowers of both native and exotic plants were attractive to Hymenoptera and Diptera, although pollinator visitation rates varied by more than an order of magnitude across plant taxa. Overall, woody plants were more attractive to pollinators compared to herbaceous plants, regardless of whether the plant was native or exotic. Implications for insect conservation: Our results suggest that regardless of native status, urban plants that bloom in the early spring—especially woody species—may be coopted to support pollinators that are especially susceptible to climate change. However, care needs to be taken to select plant species and varieties that pollinators will actually use.

Keywords Botanical gardens · Climate change · Floral visitation · Ornamental plants

Introduction

Climate change has been identified as one of the leading threats to insect species worldwide (Wagner et al. 2021). Changes in climate variables such as temperature lows, winter length, and rainfall quantities may shift the phenology (i.e., the timing of biological events) of individual species, leading to cascading effects in an ecosystem through species interactions (Root et al. 2003; Thackeray et al. 2016). Plant-pollinator mutualisms taking place in the early spring are an example of species interactions that may be jeopardized by climate change (Fitter and Fitter 2002; Duchenne et al. 2019), as both plants and pollinators may risk becoming active too early to encounter their interaction partners (Kudo and Ida 2013; Kudo and Cooper 2019; but see Bartomeus et al. 2011; Iler et al. 2013). Such phenological divergences of spring plants and pollinators may worsen as climate change intensifies (Kehrberger and Holzschuh 2019; Weaver and Mallinger 2022).

In addition to climactic factors, land use change has negatively altered natural habitats and is among the leading causes of pollinator declines (Brown and Paxton 2009). However, some human-modified ecosystems, such as urban landscapes, have the potential to support relatively high pollinator richness and abundance (Theodorou et al. 2020). Urban landscapes often provide abundant floral resources (Lowenstein et al. 2019), as well as diverse nesting and larval habitats that accommodate many different pollinator taxa (Shapiro 2002; Cane et al. 2006). In particular, urban areas may have a greater availability of plant species that bloom in the late winter and early spring compared to adjacent natural or semi-natural habitats, owing to the incorporation of ornamental plants selected from a global species pool (Mach and Potter 2018). However, more data

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are needed to address whether ornamental plants of exotic origin that bloom in the early spring indeed support pollinators active during this time. Although it is known that pollinators in urban areas around the world do utilize exotic floral resources, the relative attractiveness of exotic flowers to pollinators appears to vary across contexts (e.g., Lowenstein et al. 2019; Marquardt et al. 2021; Nabors et al. 2022), and few studies have explicitly compared herbaceous versus woody plants regarding their attractiveness to pollinators (Wang et al. 2024). With these data gaps in mind, we monitored 26 flowering plant taxa that bloom in the early spring for pollinator visitation in three urban botanical gardens in Oklahoma City, Oklahoma, USA to gain a better understanding of (1) whether blooming plants in urban gardens in our study region indeed support diverse early-spring pollinator communities, and (2) whether a plant taxon's attractiveness to pollinators depends on its native status and growth form.

Materials and methods

Our study took place in three botanical gardens in Oklahoma City, Oklahoma, USA: Oklahoma City Zoo and Botanical Garden (approximate centroid: 35.521, -97.473), Myriad Botanical Gardens (35.465, -97.518), and Will Rogers Gardens (35.507, -97.580). Each garden was surveyed for pollinators once in March and once in April 2022, between 10h00 and 16h15 on clear, calm days with air temperatures above 15 °C. During each survey, we walked throughout the botanical garden and recorded each visibly blooming plant taxon, regardless of whether it was a naturally occurring native, a purposefully planted exotic, or a weedy exotic. For each plant taxon, we estimated the number of open flowers at the garden using the same scaling-up approach used by Hung et al. (2019). Here, a plant taxon may correspond to a single species, a distinctive set of cultivars, or groups of species or cultivars within a genus in cases where diverse cultivars obfuscate species boundaries (e.g., genera *Tulipa*, *Narcissus*). We categorized each plant taxon as either a native (i.e., native to Oklahoma, or indistinguishable from an Oklahoma native in the case of purposefully planted ornamentals) or an exotic (not native to Oklahoma), and as either an herbaceous or a woody (i.e., shrubs or trees) species (Table S1 in Online Resource 1.1).

Concurrently, for each plant taxon, we performed 3-min timed observations on five patches of blooming flowers measuring approximately 1 m^2 and recorded the numbers and identities of hymenopteran and dipteran pollinators that landed upon the monitored flowers over the course of the 15 min of monitoring. For large trees (*Pyrus*, *Cercis*), we selectively monitored flowers on the lowest branches where we could track pollinators and used binoculars (SkyGenius 10×50) to aid in pollinator identification. We categorized pollinators into one of eight groups: honey bees (*Apis mellifera* L.), bumble bees (Apidae: *Bombus*), carpenter bees (*Xylocopa virginica* L.), mason bees (Megachilidae: *Osmia* spp.), short-tongued bees (Andrenidae, Halictidae, and Colletidae spp.), wasps (winged Hymenoptera other than bees), hover flies (Syrphidae), and other flies (non-syrphid Diptera). Pollinators were recorded as individuals regardless of how many flowers they visited, although individuals that left the monitored patch and returned within the observation period may have been counted multiple times. For plant taxa for which there were fewer than five patches, we repeatedly monitored a haphazardly selected subset of patches, with successive rounds of monitoring at the same patch separated by a minimum of 3 min.

To investigate the factors that influence pollinator visitation, we constructed negative binomial generalized linear mixed-effects models (GLMMs). The first GLMM tested how the number of pollinators visiting each 1-m^2 observation patch of flowers (dependent variable) varied with plant native status (native versus exotic), growth form (herbaceous versus woody), $\log_{10}$-transformed patch-level flower abundance (i.e., the average number of blooming flowers across monitored 1-m^2 observation patches), and scaled garden-level flower abundance (i.e., the estimated number of blooming flowers within the garden, scaled to a mean of 0 and standard deviation of 1 to facilitate model fitting); the four independent variables were included without interactions. In this GLMM, we also included survey round (March versus April) as an additional covariate, the amount of time spent observing each plant taxon as an offset variable (to account for one instance in which a plant taxon was observed for only 9 min instead of 15 min due to logistical constraints), and garden identity and plant taxon identity as random-intercept effects. A second GLMM examined pollinator visitation on a per-flower basis rather than at the level of 1-m^2 observation patches and was structured like the first, except the average patch-level flower abundance was included within the offset variable (multiplied by time spent observing the plant taxon) instead of as an independent variable. All models were constructed in R version 4.3.2 (R Core Team 2023), using package *lme4* (Bates et al. 2015) for fitting GLMMs and package *lmerTest* (Kuznetsova et al. 2017) for assessing *P*-values. Results were visualized using package *ggplot2* (Wickham 2016).

Results

We observed 879 pollinating insect individuals representing all eight pollinator groups (Table S2 in Online Resource 1.2), although no plant taxon was visited by all eight pollinator groups (Fig. 1). Pollinator visitation rates to the 5 native and 21 exotic plant taxa we monitored varied by over an order of magnitude (Fig. 1). Visitation at the 1-m^2 patch level was higher in woody than in herbaceous plants ($Z=3.23$, $P=0.001$), positively correlated with each plant taxon's $\log_{10}$-transformed patch-level flower abundance ($Z=3.18$, $P=0.001$), and negatively correlated with each plant taxon's scaled garden-level flower abundance ($Z=2.59$, $P=0.010$; although this negative correlation was driven entirely by one plant species that attracted no hymenopteran or dipteran pollinators despite having the highest recorded garden-level flower abundance, see Online Resource 1.3); there was no effect of native status ($Z=0.14$, $P=0.89$) or survey round ($Z=0.21$, $P=0.83$). Visitation at the single-flower level was also higher in woody than in herbaceous plants ($Z=2.21$, $P=0.027$) and negatively correlated with each plant taxon's scaled garden-level flower abundance ($Z=3.67$, $P=0.002$); and there was no effect of native status ($Z=0.31$, $P=0.75$) or survey round ($Z=0.32$, $P=0.75$). Visualization of model outputs is provided in Online Resource 1.4.

Discussion

We found that urban botanical gardens harbored diverse early-spring pollinator assemblages, highlighting the value of these greenspaces for supporting insect populations. Additionally, we found that exotic plants did not inherently differ from native plants with respect to their attractiveness to pollinators, corroborating prior research elsewhere in the world (Marquardt et al. 2021; Wang et al. 2024; but see Salisbury et al. 2015; Nabors et al. 2022) and greatly expanding the pool of candidate species that may be considered for urban pollinator conservation. Although the exotic honey bee

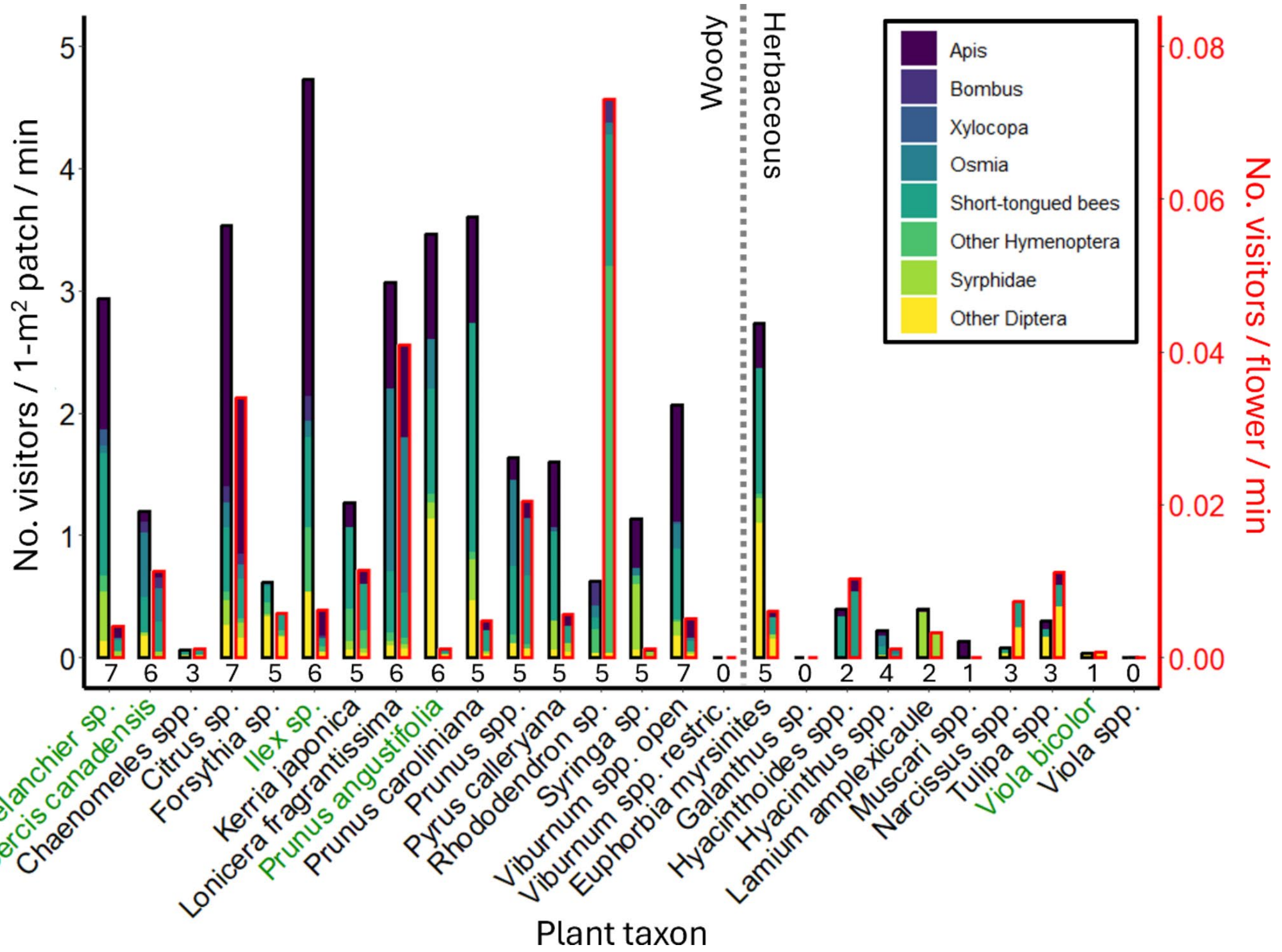

Fig. 1 Stacked bar plot depicting pollinator visitation to 26 plant taxa included in our study. For each plant taxon, the left-side bars with black borders scale to the left axis and depict pollinator visitation rates per 1-m^2 patch, whereas right-side bars with red borders scale to the right axis and depict pollinator visitation rates per flower. Woody plant taxa are arranged to the left of the dotted grey line, and herbaceous taxa to the right; taxa native to Oklahoma are depicted in green text, and exotic taxa in black. Numbers below bars report the numbers of pollinator categories observed visiting each taxon. *Prunus* and *Viola* taxa are each separated into native and exotic taxa; *Viburnum* taxa are separated based on flower morphology ("open" = open flowers permitting pollinator access, "restric." = narrowed flowers restricting pollinator access)

was the most abundant pollinator species observed (Table S2), our conclusions remain unchanged when we excluded this species from our analyses (Online Resource 1.5). The lack of effect of plant native status on pollinator attraction may be in part due to our studied botanical gardens lacking spring-blooming host plants of pollen-specialist bees in our region (Fowler 2020). In the absence of plants that support pollen-specialists, the pollinator assemblages that persisted in our studied gardens were likely dominated by diet generalists (see also Tonietto et al. 2011), which would opportunistically forage from accessible flowers regardless of native status (but see Erickson et al. 2020).

Woody plant species in our study tended to present densely packed inflorescences containing many flowers, such that patch-level flower density was higher on average in woody than in herbaceous plants (Online Resource 1.6). However, it is noteworthy that our woody plant taxa were comparatively more attractive to pollinators at the patch level than were herbaceous taxa even after accounting for the expected positive relationship between pollinator visitation and patch-level flower abundance (e.g., Salisbury et al. 2015; Marquardt et al. 2021). In fact, when modeled separately, growth form better predicted pollinator visitation than did patch-level flower density (Online Resource 1.6). Although various complex, idiosyncratic traits associated with the flowers of our woody species (e.g., flower color, morphology, and orientation) may have contributed to this difference in pollinator visitation between growth forms (Wang et al. 2024), it seems plausible that woody plants' three-dimensional spatial arrangement of inflorescences, coupled with their often large, contiguous expanse of conspecific blooms (in the case of trees and large, spreading shrubs), facilitated pollinator foraging. Across our studied botanical gardens, plant taxa that attracted the highest diversity and abundance of pollinators were native *Prunus angustifolia*, *Amelanchier* sp., and *Ilex* sp.; as well as exotic *Prunus* spp., *Lonicera fragrantissima*, and *Citrus* sp., all of which were large shrubs or small trees with clusters of small to medium-sized, white flowers. Multiple studies to date have investigated the attractiveness of different ornamental plant blooms (e.g., Salisbury et al. 2015; Mach and Potter 2018; Erickson et al. 2020; Marquardt et al. 2021), but few have explicitly compared across distinct growth forms (Lowenstein et al. 2019; Wang et al. 2024). Our results suggest that such comparisons may be valuable when attempting to optimize limited space to support pollinators, especially since a given plant species' relative attractiveness to pollinators may differ depending on whether the measurement occurs at the level of unit of area occupied or single flowers (Fig. 1).

Our finding that a plant taxon's garden-level flower abundance was negatively correlated with pollinator visitation rate (at least when considering visitation at the single-flower level, see Online Resource 1.3) contrasts with results from several other studies (e.g., Erickson et al. 2020; Marquardt et al. 2021). This counterintuitive finding perhaps suggests that pollinators occurring within our studied gardens were not visiting flowers at random but were rather directing their foraging activity toward preferred plant taxa. In such a scenario, pollinators that preferentially visited plants with the highest garden-level flower abundance would be consistently dispersed amidst the largest numbers of flowers, thereby "diluting" their visitation to our monitored patches. A negative relationship between flower abundance and pollinator visitation rates has also been previously reported in other systems (Campbell and Husband 2007; Delmas et al. 2014).

In conclusion, our results suggest that exotic plants that bloom in the early spring—especially woody species—may be coopted to support early-spring pollinators in urban landscapes. However, care needs to be taken in the selection of plants, as some popular, widely grown exotic taxa proved to be unattractive to pollinators (Fig. 1; see also Lowenstein et al. 2019), especially when considering the number of flowers that can be borne per unit of area available for planting. Similarly, care needs to be taken when incorporating exotic species, as some may become invasive when not contained in a horticultural context (e.g., *Lonicera fragrantissima* in our study). Future research across larger geographical areas will shed light on the generality of our findings with respect to the attractiveness of specific plant taxa to pollinators.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-024-00635-7.

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Data availability Raw data included in this study are available via the Open Science Framework: https://osf.io/a7gnv/?view_only=08ec874750e7490e96ddbe61a75b7d24.

Declarations

Competing interests The authors declare no competing interests.

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