Reap what you sow: local plant composition mediates bumblebee foraging patterns within urban garden landscapes

Megan O'Connell[1] · Zachariah Jordan[2] · Erin McGilvray[1] · Hamutahl Cohen[2] · Heidi Liere[3] · Brenda B. Lin[4] · Stacy M. Philpott[2] · Shalene Jha[1]

Abstract

Although urban gardens are often celebrated for supporting bee abundance and diversity within cities, little is known about how garden management and urbanization levels influence bee foraging behavior and ability to utilize resources within these landscapes. Specifically, the preferences and diet breadth of bees may depend critically on local and landscape conditions in human-managed, urban environments. To understand how foraging patterns and pollen preferences are influenced by urban landscape composition, we first examined if bees visit plants grown within urban gardens and second assessed the relationships between local floral resources, urban land cover, and pollen collection patterns, focusing on 20 community gardens across 125 km of the California central coast. We targeted a well-studied, essential native pollinator in this ecoregion, *Bombus vosnesenskii,* and analyzed pollen on the bodies of individuals collected in our study gardens to compare their contents to local and landscape garden composition factors. We found that greater landscape-level urban cover and greater plant species richness in the garden both drove higher within-garden pollen collection. We also found that *B. vosnesenskii* preferred ornamental plant species over highly available crop species in the gardens. Our study indicates that landscapes that support plant diversity, including both ornamental plants and sustenance-oriented food crops, promote greater within-garden pollen collection patterns, with likely benefits for urban garden food production.

Keywords Urban garden · Pollinator · Ornamental · Floral resource · Foraging · Pollen preference

Introduction

Urban gardens are increasingly recognized as beneficial, multifunctional green infrastructure that contribute to a city's resilience for human inhabitants and biodiversity alike

✉ Megan O'Connell
megan.oconnell@utexas.edu

1 Department of Integrative Biology, University of Texas at Austin, Austin, TX, USA

2 Environmental Studies Department, University of California Santa Cruz, Santa Cruz, CA, USA

3 Department of Environmental Studies, Seattle University, Seattle, WA, USA

4 Division of Marine and Atmospheric Research, Commonwealth Scientific and Industrial Research Organisation (CSIRO), ACT, Canberra, Australia

(Goddard et al. 2010; Barthel and Isendahl 2013; Shwartz et al. 2014). In highly urbanized matrices, gardens that are largely cultivated to provide human sustenance may serve a dual purpose, both as a source of food security for gardeners and as a critical resource-dense patch that helps foster the movement and survival of wildlife across otherwise inhospitable, altered landscapes (Rudd et al. 2002; Sushinsky et al. 2013). These green spaces may be especially important for critical ecosystem service providers such as pollinators, natural enemies of pests, and seed dispersers, but the capacity for urban gardens to support such taxa largely depends on the animals' access to urban gardens and more importantly, their ability to collect and utilize resources once they are in an urban garden (Paker et al. 2014; Philpott and Bichier 2017; Johnson et al. 2018). Despite the high abundance and richness of wildlife recorded in urban gardens (McFrederick and LeBuhn 2006; Baldock et al. 2015; Lin et al. 2015), it is often unclear if garden resources are actually being utilized by these animals, and which local- and landscape-scale management practices might influence resource collection patterns in these spaces (Lowenstein et al. 2019). Elucidating these patterns

could further our understanding of how animals utilize resources in heterogeneous landscapes and would inform urban decision-makers on how to manage green spaces in order to support urban wildlife and associated ecosystem functions.

At the local scale, the composition and species richness of plants grown in urban spaces can have large impacts on the presence and abundance of wildlife (Smith et al. 2006; Kowarik 2011); this is particularly relevant for highly mobile animals found within urban gardens, such as bees (Hulsmann et al. 2015), butterflies (Blair and Launer 1997), and birds (Paker et al. 2014). In particular, there is compelling evidence that plant species composition and vegetative complexity (Lin et al. 2015), as well as access to bare soil and woody plants, correlates with the diversity and richness of beneficial insects that visit urban gardens (Egerer et al. 2017) such as pollinators (Pawelek et al. 2009; Quistberg et al. 2016) and natural enemies of pests (Philpott and Bichier 2017). However, vegetation management within urban gardens is often driven by the needs of the gardeners rather than the needs of wildlife, therefore it is possible that resources provided within urban gardens are not intended or sufficient to support urban-dwelling animals (Loram et al. 2011; Bigirimana et al. 2012; Clarke and Jenerette 2015). For example, urban gardens are often dominated by species that either provide human sustenance (crop species) or aesthetic appeal (exotic ornamental species) (Lowenstein and Minor 2016), even though these same species may not provide optimal resources to urban wildlife with respect to nutrition (Vaudo et al. 2015), habitat requirements (Shapiro 2002), or phenology (Harrison and Winfree 2015). Furthermore, the composition of vegetation within urban gardens is highly variable from garden to garden and may be mediated by extraneous factors, such as the socioeconomic standing of the gardeners (Bigirimana et al. 2012; Clarke and Jenerette 2015), which may further drive plant species compositions in urban gardens to be less similar to naturally occurring plant communities to which native wildlife is accustomed (Thompson et al. 2003; Turo and Gardiner 2019).

In addition to local-scale resource availability, the presence, abundance, and foraging patterns of urban-dwelling animals are also a function of larger-scale landscape composition and the degree to which this landscape supports animal foraging and habitat needs (McKinney 2002). Within the urban landscape, native vegetation and green spaces are often replaced by impervious substrates such as pavement and buildings, through which mobile wildlife must navigate to find resources and suitable habitat (Blair and Launer 1997; Jha and Kremen 2013a, b). While highly mobile taxa such as birds (McKinney 2002) and flying insects (McFrederick and LeBuhn 2006) can successfully colonize and survive in highly urbanized landscapes, the persistence of these animals is often driven by the distance between resource-rich patches and the landscape composition between these patches. Indeed, the presence of bird and mobile invertebrate species in urban

gardens is sometimes more influenced by the surrounding habitat than by garden features (Chamberlain et al. 2004; Smith et al. 2006). Past studies have suggested that flying insects may indeed be sensitive to landscape composition surrounding urban gardens; for instance, natural habitat cover within 3 km of gardens supports higher insect abundance in gardens, while urban habitat cover in this area supports lower abundance (Winfree et al. 2008; Ahrné et al. 2009). This is likely because these animals often utilize 'partial landscapes', i.e. forage or nesting spaces within a habitat type (sensu Westrich 1996), and thus may travel between several gardens or resource patches to meet their multiple biotic needs (Walther-Hellwig and Frankl 2000; Rudd et al. 2002). Insect use of multiple habitats for nesting and food resources may explain why the impacts of urban land cover on this group seem to be context- and species-specific; for example, past research within urban gardens in coastal California found that overall bee abundance (both ground and cavity-nesting) was negatively impacted by urban land cover, presumably due to lower nest-site availability (Plascencia and Philpott 2017), while research within urban gardens in New York City found that cavity-nesting bees were positively affected by urbanization, assumedly due to their opportunistic use of artificial cavities in built structures (Matteson et al. 2008). While such contrasting responses may be due to differences in animal resource availability and utilization in urbanized landscapes, such as altered floral or nesting resources (as hypothesized in Cane 2005), few studies have explicitly investigated this utilization within urban landscapes.

Beyond the local and landscape dynamics driving the usage of urban gardens by animals, foraging patterns are often dictated by the degree to which each animal displays their dietary preference, where preference is defined as the use of a particular resource in relation to its availability in a landscape (sensu Beyer et al. 2010). For example, many pollinator species prefer foraging at native and 'pollinator-friendly' plant species despite their often relatively low abundance in human-altered landscapes (Frankie et al. 2005; Saifuddin and Jha 2014). Simultaneous reductions in native plant species richness and habitat function are well documented in urbanized areas (Kowarik 2011). As a result, urban wildlife may have very few options when their preferred forage species are no longer available; they can either shift their preferences, find new habitats, or face local extirpation. Thus, in human-dominated landscapes, novel plant communities may drive changes in urban-dwelling wildlife foraging behaviors. For example, pollinator species may shift their foraging behaviors to visit non-preferred, ornamental, and exotic species when native species are locally unavailable; however, these behavioral shifts depend on both plant composition within the landscape and pollinator foraging plasticity (Cane 2005; Williams et al. 2011). More specifically, when found in urban landscapes, some butterflies, bees, hover flies, and hummingbirds

display preferences for highly rewarding ornamentals planted by gardeners, even when these are non-native novel resources (Garbuzov and Ratnieks 2014; Harrison and Winfree 2015). This may explain why pollinator community composition shifts from a broad mix of specialized and generalist consumers to broadly generalist species in urban areas relative to nearby semi-natural areas (Cane 2005; Baldock et al. 2015), indicating that urban plant communities may not support the wide breadth of dietary needs displayed by healthy native wildlife networks (Inouye 1978; Kleijn and Raemakers 2008). Despite the relevance of diet breadth to biodiversity conservation in urban matrices, little is known about the preferences that mobile ecosystem service providers, like pollinators, exhibit in human-altered, resource dense patches such as urban gardens.

Thus, it is of critical importance that we begin to understand more about the foraging patterns and food preferences of pollinators within rapidly urbanizing landscapes. Animal pollinators facilitate the reproduction of ~78–94% of wild plant species and over 75% of global crop species (Klein et al. 2006), worth more than $235–$577 million USD globally (IPBES 2016). In the case of urban gardens, a very high percentage of crop plants depend on animal-mediated pollination services (Matteson and Langellotto 2009); therefore, understanding these dynamics in the urban agricultural context will be crucial in determining the future of urban agroecosystems and urban food security. In this study, we determine if an important native pollinator, *Bombus vosnesenskii*, collects floral resources in urban gardens and how local and landscape-scale factors mediate its foraging patterns. We also quantify and compare this pollinator's forage preference across plant species cultivated at our focal urban gardens. Based on previous findings, we propose three fundamental hypotheses H1) bees collect pollen resources from within urban gardens, H2) Local floral richness and urban land cover positively impact within-garden pollen collection patterns, and H3) Pollinators display a similar preference for the three different plant types (crops, ornamentals, and weeds), relative to their availabilities in the urban gardens.

Methods

Study region and garden metrics

We conducted our study in 20 urban gardens across three counties in the California central coast (Monterey, Santa Clara, and Santa Cruz) from June to August of 2016. Each site consisted of an urban community garden (0.10 to 3.84 ac) separated from other gardens by >2 km. All gardens are organically managed and have produced food for between 2 and 50 years. The region hosts ~1 million people and although the study region is in a single geographic area, the region is heterogeneous and gardens vary in temperature, precipitation, management, landscape conditions, and gardener demographics (Egerer et al. 2019).

At the local scale, we measured habitat characteristics (e.g. vegetation and ground cover) within a 20×20 m plot placed at the center of each garden. We measured canopy cover with a convex spherical densiometer at the center of the plot, and 10 m to the North, South, East, and West. We counted and identified all trees and shrubs in the plot and noted the number of individuals in flower. In each plot, we randomly selected eight 1×1 m quadrats within which we identified all herbaceous plants (except grasses) to morphospecies, measured height of the tallest non-woody vegetation, noted which species were in flower and counted their flowers, and assessed percent ground cover of bare soil, grass, herbaceous plants, leaf litter, rocks, mulch, and straw. Due to high levels of collinearity between many of these metrics, we only included the following in our regression model development: the number of trees and shrubs in the 20×20 m plot at each garden, the percent mulch cover in the 1×1 m quadrats in each garden, the average number of flowers in the 1×1 m quadrats in each garden, the size of the garden, and the estimated herbaceous plant species richness in the 1×1 m quadrats in each garden (model composition similar to past studies in this region, Plascencia and Philpott 2017). Herbaceous and woody plant species were identified using the USDA PLANTS database and were binned into the following categories according to human usage: crop species, ornamental species, and weed species (as designated by the USDA PLANTS database). Because these vegetation surveys were conducted on one day in each garden across three time periods (June 6th–9th, July 1st-5th, Aug 1st-3rd) surrounding the pollinator survey (June 27th - July 11th), we included all three vegetation surveys in our analyses to comprehensively describe the plant community. Further, of the 93 plant species in our vegetation surveys, 11 were not observed flowering during the survey dates but are known to flower in the summer; for these species we confirmed with resources at the Missouri Botanical Gardens that flowering typically occurs between May and July (Kemper Center for Home Gardening 2020).

At the landscape scale, we calculated the proportional cover of four main land-use categories within 2 km buffers surrounding each garden with data from the 2011 National Land Cover Database (NLCD, 30 m resolution)(Homer et al. 2015). Specifically, we selected 2 km buffer zones as this is the largest landscape scale that has been shown to be predictive of resource usage for bees (Steffan-Dewenter et al. 2002) and is utilized by many other urban bee studies (Cusser et al. 2019, Egerer et al. 2017, Quitsberg et al. 2016). We created four land-use categories and calculated the proportion of area represented for each in the 2 km buffer: 1) semi-natural (deciduous, evergreen and mixed forests, dwarf scrub, shrub/scrub, and grassland/herbaceous), 2) open (lawn grass, parks, and

golf courses), 3) urban (low, medium, and high intensity developed land), and 4) agricultural habitat (pasture/hay and cultivated crop). Other land cover types covered <5% of the total area and were not included. Due to collinearity between these four main land-use categories, for our initial model development we only included semi-natural habitat and urban habitat cover. Additionally, we estimated total garden size by ground-truthing GPS points around each garden. We assessed both garden size and land cover with spatial statistics tools in ArcGIS v.10.1.

Pollinator survey

We focused our foraging study on *Bombus vosnesenskii,* an annual, primitively eusocial, ground-nesting, central place foraging bee native to the Pacific Coast states of the United States (Thorp et al. 1983). As with many genera in the Apidae family, *Bombus* species are buzz-pollinators, meaning they sonicate the poricidal anthers of many plant species, which allows them to be effective generalist pollinators for a wide variety of plant species in urban, rural, and agricultural landscapes (De Luca and Vallejo-Marin 2013; McFrederick and LeBuhn 2006). We selected *B. vosnesenskii* as a representative *Bombus* species given its abundance across the region, its proficiency as a crop and greenhouse pollinator (Dogterom et al. 1998; McFrederick and LeBuhn 2006), and its sensitivity to land-use change and urbanization (Jha and Kremen 2013a, b). Further *B. vosnesenskii* is a dominant forager in the region (McFrederick and LeBuhn 2006) and dominant bumble bees are of particular ecological interest as they often drive specialization in their native pollinator communities, with subsequent positive impacts on plant reproductive success (Brosi and Briggs 2013). While European honeybees (*Apis mellifera*) were also observed in our study system, their abundances were relatively low and previous work in urban gardens has shown that competition between bumble bees and honey bees is often low in resource rich patches like gardens (Gunnarsson and Federsel 2014) and is thus unlikely to drive individual bumblebee foraging patterns.

We collected 10 *B. vosnesenskii* individuals from each garden between 8 am and 5 pm between the dates of 27th of June and 11th of July 2016. Given this mid-summer collection period, we were likely sampling the second cohort of *B. vosnesenskii* workers, since colonies of *B. vosnesenskii* tend to see their highest numbers of workers from late May to mid-July (Koch 2012). We focus on this season for *B. vosnesenskii* as it directly precedes the production of the next generation of queens and the establishment of new colonies (Crone and Williams 2016), and thus is an important season to study foraging patterns for the species (Pope and Jha 2018). Other species of *Bombus* have been found to engage in up to six 60-min foraging bouts per day (Minahan and Brunet 2018), and because extensive pollen removal and

deposition occurs at the colony after each bout (e.g., Malfi et al. 2019), we posit that pollen found on the body likely describes one of the more recent foraging bouts within the day. After capturing *B. vosnesenskii* individuals with a net, we transferred them to a 'kill jar' with ethyl acetate for analysis in the lab. In order to examine pollen that is representative of floral visitation (as in Alarcón 2010), we first removed corbicula pollen from the specimen (less than 15% of individuals were carrying corbicula pollen loads) and then placed individuals into 5 mL test tubes and submerged them in a 95% ethanol solution. We rinsed the forceps with 95% ethanol between the processing of each individual to avoid pollen contamination. A few of the samples experienced ethanol leakage and degradation, leaving a total of 189 bees for subsequent analysis (mean = 9.45, SE = 0.08, per garden).

Bumble bee pollen load

Bees were vortexed in their original 5 mL test tube for 30 s, then after removing the bees, the pollen was centrifuged for 2 min at 1800 rpm. We then pipetted 15 μL of ethanol plus the suspended pollen pellet into a new tube, added 40 μL of Fuchsine dye, and vortexed the mixture for 10 s (Kearns and Inouye 1993). We added 50 μL of the vortexed solution to the slide and allowed this to sit for 10 s before the cover slip was placed on top and allowed to set for at least 24 h. We examined each microscope slide at 20x magnification by beginning at the top left corner and moving down to the bottom edge, then moving over to ensure that the first column of surveyed area was not in view. Then, we moved back up the slide and repeated this pattern to cover the entire slide without covering the same area twice. For up to the first 300 grains encountered, we examined and identified the species of each pollen grain using the reference collection as a comparison. We chose to maintain this 300-grain cutoff to ensure our sampling efforts were consistent across individuals (as per Williams and Kremen 2007, Ritchie et al. 2016). If the original slide had fewer than 300 grains, we counted and identified grains on an additional slide made with the same dye protocol as the original slide until we reached 300 grains. If fewer than 250 grains were found on the first two slides, no more slides were analyzed as we observed diminishing returns in the number of grains on each new slide made from the original sample solution. We were able to collect pollen and makes pollen slides for all 189 of our study bees. When we found a pollen grain that could not be identified as any of the species in the reference collection, we counted that grain as a morphological species, assigned it a number, and followed the same protocol described below to add it to the reference collection. We were able to successfully identify the majority of the pollen grains collected in the pollen loads to species: less than 0.1% of the collected grains remained unidentified. For all grains identified to species, grains were binned into three categories based

on the USDA PLANTS database: crop species (species that were planted intentionally for the production of fruits and vegetables for human sustenance), ornamental species (species that were planted intentionally, but do not produce fruits that are consumed by humans), and weedy species (species that occurred in the gardens but were not planted intentionally) (Green 2009).

Reference collection

We created a pollen reference collection by collecting pollen samples from the 160 most abundant floral resources (based on inflorescence counts within the 20 × 20 m plots) in the urban gardens. Specifically, anthers from these plants were collected from the gardens and placed in ethanol, and later centrifuged for 1 min at 1800 rpm to separate pollen. We combined 15 μL of this pollen solution with 40 μL of Fuchsine dye, vortexed this for 10 s, and pipetted 50 μL onto a slide. After 10 s, we placed a slide cover on top and allowed 24 h to set. We then viewed these slides using a Leica light microscope to find and photograph pollen grains for the reference collection using the LAS v4 software. We took one picture of each pollen species at 20x magnification, and two pictures at 63x magnification at different focal planes. We made some exceptions for very large grains, instead taking pictures at 40x magnification for clarity in viewing significant features. The 20x photographs included a scale bar in micrometers and were kept to scale for a comparative size reference. We set the saturation of the photographs to 101 and the Gamma setting to 0.55. We adjusted the brightness as needed to see the details of the pollen grains but tried to keep the brightness near 80%. This reference collection then served as a guide to identify pollen grains found on bumble bees.

Impacts of local and landscape features on pollinator diversity

We used binomial generalized linear mixed effects models (Bates et al. 2011) to examine relationships between local and landscape predictor variables on the following four pollen load response variables: the proportions of pollen from within and outside of the gardens and the proportions of crop, ornamental, and weed pollen. We used linear mixed effects models to examine relationships between local and landscape predictor variables on the Shannon-Weiner Diversity of each pollen load. Given that bumble bees make multiple foraging bouts in a single day and heavily groom themselves between bouts (Holmquist et al. 2012) and that individual bumble bees in urban gardens tend to forage within the same gardens where they were originally collected (Matteson and Langellotto 2009), we assume that a plant species present in a garden and found on a pollinator was likely collected from that garden (as per Matteson and Langellotto 2009). To ensure an

appropriate characterization of proportions and preference, we only retained pollen loads for which we were able to identify a total of 300 grains to species for our statistical analyses (as per Harmon-Threatt et al. 2017, Saifuddin and Jha 2014). We calculated Shannon-Weiner Diversity using the 'vegan' package in R (Oksanen et al. 2018) to calculate diversity within each pollen load. The predictor variables we originally included in our model development were the following: at the landscape scale, the percent of urban land cover and semi-natural habitat within 2 km of the garden, and at the local scale, the number of trees and shrubs in the 20 × 20 m plot at each garden, the percent mulch cover in the 1 × 1 m quadrats mulch in each gardens, the average number of flowers in the 1 × 1 m quadrats in each garden, the size of the garden, and the estimated herbaceous plant species richness in the 1 × 1 m quadrats in each garden. After developing this set of initial predictor variables, we ran tests to identify collinearity of predictors in all of our models by calculating a variance inflation factor (VIF) for each model set using the *car* package in R (Fox and Weisberg 2018). We used a VIF cutoff score of 2 and removed the variables with the highest value in a stepwise fashion until all variables received a score below the cutoff. Using this process, our three full models contained all of the aforementioned predictor variables except the number of flowers in the garden (which positively correlates with herbaceous plant species richness, retained in the model) and the amount of semi-natural habitat within 2 km of the garden (which negatively correlates with percent urban land cover within 2 km, retained in the model). We considered each of the 189 pollen loads collected from an individual bee as a replicate response variable in each garden and we included the garden as a random effect in our models. We ran GLMs in R using the 'glmer' function for the four response variables that represent pollen proportions (binomial distribution) and the 'lmer' function for the Shannon-Weiner Diversity index (normal distribution) in the 'lme4' package (Bates et al. 2011). We then ran model selection using the MuMin package (Barton 2018) and selected the top model based on the AICc values and model averaging for models that were within 2 AICc of the top model.

Within-garden preference analysis

We calculated plant species preferences for 189 individuals of *B. vosnesenskii* to determine which plant species the bee is more likely to visit, relative to its availability in the gardens. Specifically, we assessed the species-level composition of pollen loads according to a framework developed for habitat or resource use analysis (Johnson 1980) that is also frequently used for pollinators (e.g., Davis et al. 2012; Jha et al. 2013). These analyses rank resource collection (i.e. proportion of each pollen species) relative to its availability (i.e. percent cover of each plant species) in the garden; pollen species that

are collected significantly more than expected respective to the plant species' floral availability are ranked the highest. We ran these preference analyses using the adehabitatHS package in R (Aebischer et al. 1993; Calenge 2006) by comparing a matrix of floral species availability per garden with a matrix of pollen species use per bee using Wilks' lambda. From this we constructed a preference matrix, which was evaluated using a randomization test (500 repetitions) to determine significant preference for one plant species over each other species (Aebischer et al. 1993). For herbaceous plants, we estimated the floral availability in each garden by averaging the percent cover of each plant species that occurred within our eight 1 × 1 m quadrats and averaged these across the three sampling periods. For woody plants, we estimated floral availability in each garden by using shrub count data from our 20 × 20 m survey plot. For these species, we calculated each species' average circular area available (as per average plant spread measures provided by the Kemper Center for Home Gardening, Missouri Botanical Garden 2020), summed these values per plot, then divided these totals by the area of the 20 × 20 m plot and averaged this across the three sampling dates. Total percent cover of each plant type (crop, ornamental, weed) was calculated by summing the plant species percent cover within each category. Preference was only analyzed for plant species documented both in the garden and in the pollen load of each *B. vosnesenskii*, therefore, of the 93 plant species identified in the pollen loads, 25 plant species were excluded from the preference analysis portion of the study because they were not present in the gardens where the bees were collected. Of the remaining 68 species included in the preference analyses, three were removed due to their infrequency (<2 individual occurrences) within the garden or pollen load data (as per Ritchie et al. 2016); this minimum occurrence threshold was set due to the constraints in calculating variance for compositional analysis (Calenge 2006). We also conducted this preference analysis excluding the most common pollen species, strawberry, to evaluate whether

remaining preference rankings remained the same and found similar overall results (Table S1).

Results

Across our 20 study gardens, we observed a variety of landscape contexts, garden compositions, and *B. vosnesenskii* pollen collection patterns. Our study gardens were located across a gradient of urbanization ranging from 7.7% to 97.3% urban cover within a 2 km radius and ranged in size from 0.04 to 1.55 ha. Our garden plots had anywhere from 7 to 24 herbaceous plant species and on average hosted 60.7% crop cover (SE = 0.125), 21.7% ornamental cover (SE = 0.116), and 17.6% weed cover (SE = 0.009). *B. vosnesenskii* individuals across these gardens collected pollen from 3 to 35 plant species. On average, 39.2% (SE = 0.020) of the pollen loads were composed of pollen from plant species identified as being in the study gardens and 60.8% (SE = 0.020) of pollen from plants that were designated as being outside of the gardens, with the average pollen load being composed of 49.9% crop species (SE = 0.131), 45.7% ornamental species (SE = 0.139), and 4.4% weed species (SE = 0.046) (Figs. 1 and 2).

We found a positive relationship between the percent of urban land cover within a 2 km radius and the proportion of pollen collected from within the gardens (X = 0.392, P = 0.020)(Fig. 3a, Table 1). Additionally, we found a positive relationship between the number of herbaceous plant species in the garden and the proportion of pollen collected from within the garden (X = 0.472, P < 0.001)(Fig. 3b, Table 1). An increase in herbaceous plant species richness negatively correlated with the collection of pollen from crop plants (X = −0.480, P < 0.001), but positively influenced the collection of pollen from ornamental plants (X = 0.570, P < 0.001)(Fig. 4a, Table 1). An increase in the percent urban land cover within a 2 km radius positively correlated with crop plant pollen collection (X = 0.300, P = 0.028), but had no effect on the

Fig. 1 The proportion of pollen grains in the pollen loads collected from *B. vosnesenskii* that were composed of pollen identified as being from plants within the garden versus plants that were outside of the garden plots. Pink represents pollen collected from species located within the study gardens and blue represents pollen collected from species that were not identified as growing in the study gardens
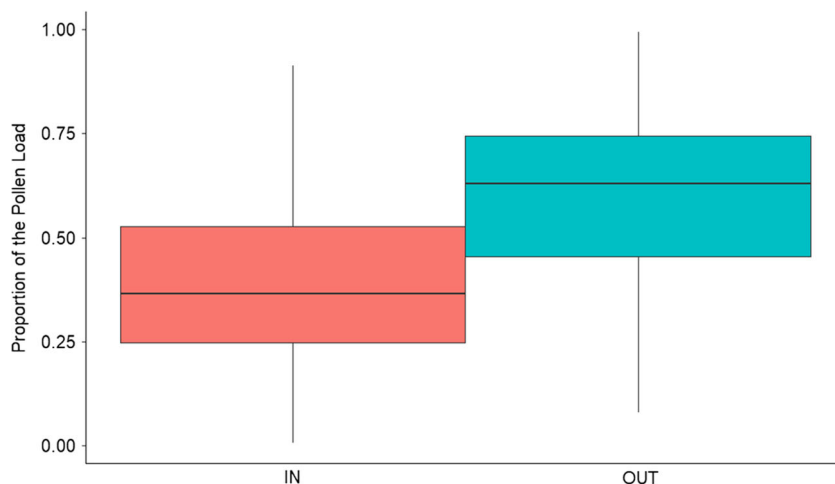
Fig. 2 The availability versus usage of crop, ornamental, and weed plants in our study gardens by *B. vosnesenskii.* These groupings were determined using the USDA PLANTS database and floral resource availability was determined by summing the total percent cover of each classification as a proportion of the garden. Usage was calculated as the proportion of the pollen load that composed of each type. Pink represents plant availability and blue represents plant usage
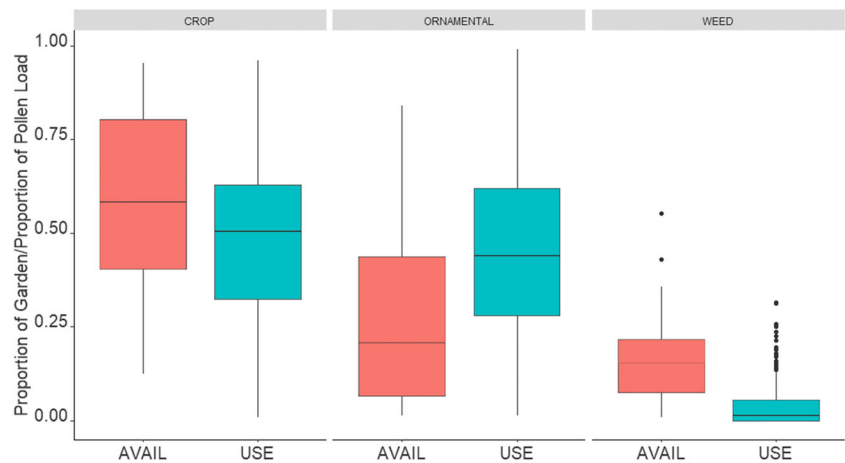
collection of pollen from ornamental plants (Fig. 4b, Table 1). To this end, we verified that no significant correlations (Pearson correlation coefficients) existed between our measure of urbanization and the percent cover of crop (r = −0.187) versus ornamental (r = 0.107) versus weed (r = −0.338) species in our study gardens. Lastly, an increase in garden size negatively impacted the diversity of pollen collected as measured via the Shannon-Wiener species diversity index (X = −1.047, P = 0.020)(Table 1).

From our preference analysis, we found that *B. vosnesenskii* highly preferred strawberry (*Fragaria x ananassa)* and California poppy (*Eschscholzia californica*) above the other plant species in our study gardens (λ = 0.017, P = 0.002)(Table 2). Beyond this common crop species, over half of the species preferred were ornamental and weed species that were present in low availabilities relative to many of the crop species in the gardens. Regarding ornamentals, *B. vosnesenskii* preferred California poppy (*Eschscholzia californica*), snapdragon (*Antirrhinum majus*), rose bush (*Rosa L.*), and California buckwheat (*Eriogonum fasciculatum*)(Table 2, Table S2). *B. vosnesenskii* also

displayed a preference for two weed species: wild mustard (*Brassica L.*) and wild radish (*Raphanus raphanistrum*) which are widely distributed introduced species in the region. Lastly, *B. vosnesenskii* also displayed a weak preference for crop plants such as American red raspberries (*Rubus idaeus*), arugula (*Eruca vesicaria*), and eggplant (*Solanum melongena*) despite their lower percent coverage compared to crops such as tomatoes and peppers. Overall, the dominance of ornamentals and weeds in the top ten preferred plants relative to their lower overall availability in the gardens, shows that *B. vosnesenskii* exhibits strong foraging preference for non-crop plant species (Fig. 2).

Discussion

We conducted one of the first analyses of urban bee pollen collection and preference to reveal strong predictors of urban garden floral usage at both the landscape and local scale, as well as distinct foraging preferences for ornamental and weedy plants available within these gardens. Specifically,
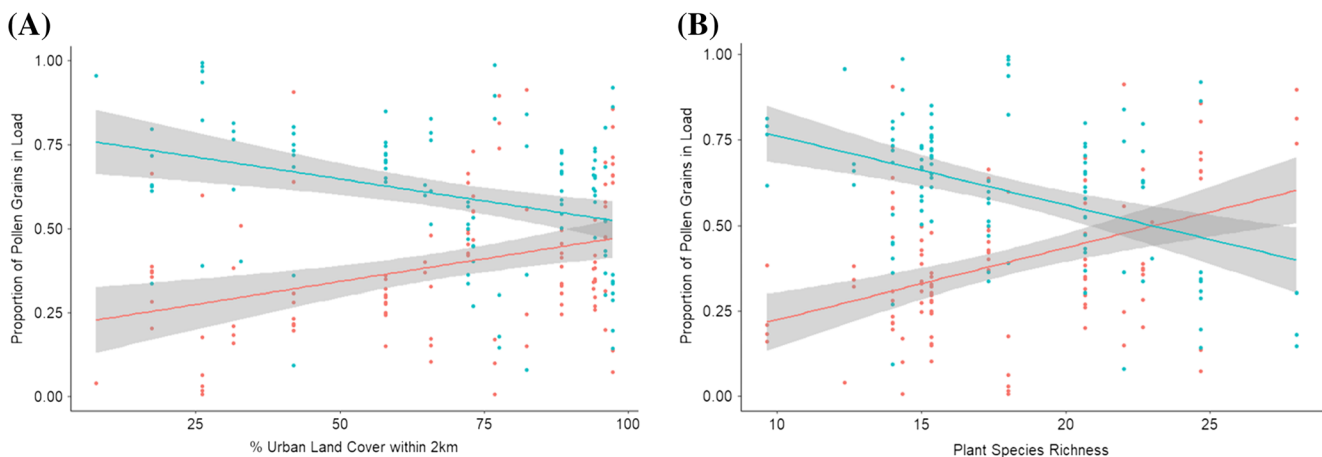
(A)

(B)

Fig. 3 **a**: The influence of % urban land cover within 2 km of the study garden plots and **b**: plant species richness in the garden plots on the proportion of pollen collected from within (pink) and outside (blue) of the garden plots by *B. vosnesenskii*

Table 1 Top models after MuMin model selection for each of our five response variables related to pollen load composition. Models 1–4 were run as general linear mixed effects models with a binomial distribution and model 5 was run as a linear mixed effects model with a normal distribution. Garden identity was included in all models as a random effect. Significant *p* values are bolded

Response variables	Predictor variables	Est.	Std.Err	Z value	Pr(>|z|)
Model 1: Proportion Pollen from Within Garden	Model 1: Garden Size + Urban 2 km + Herbaceous Plant Richness				
	GardenSize	−0.257	0.144	−1.787	0.074
	Urban2km	0.326	0.140	2.336	**0.0195**
	HerbPlantRich	0.472	0.133	3.565	**<0.001**
Model 2: Proportion Crop Pollen	Model 2: Number Trees/Shrubs + Urban 2 km + Herbaceous Plant Richness				
	NumTreesShrubs	0.235	0.121	1.949	0.051
	Urban2km	0.300	0.137	2.195	**0.028**
	HerbPlantRich	−0.480	0.128	−3.738	**<0.001**
Model 3: Proportion Ornamental Pollen	Model 3: Garden Size + Herbaceous Plant Richness				
	GardenSize	0.319	0.177	1.802	0.072
	HerbPlantRich	0.570	0.159	3.584	**<0.001**
Model 4: Proportion Weed Pollen	Model 4: Herbaceous Plant Richness				
	HerbPlantRich	−0.450	0.297	−1.518	0.129
Model 5: Shannon's Pollen Species Diversity	Model 5: GardenSize + Herbaceous Plant Richness				
	GardenSize	−1.047	0.401	−2.610	**0.020**
	HerbPlantRich	−0.673	0.383	−1.757	0.096

our results show that the composition of the pollen loads of *B. vosnesenskii* in urban gardens were largely influenced by two factors: the percent urban cover within 2 km of the gardens (landscape) and the number of herbaceous plant species planted within the gardens (local). Additionally, we found that this key native pollinator exhibits a strong preference for ornamental and weedy plants, indicating that urban gardeners should consider cultivating a suite of ornamental plants and allowing some flowering weeds to persist, in addition to their food crops, in order to attract pollinator visitation and services in urban gardens.

The proportion of pollen that *B. vosnesenskii* collected from within the study gardens was strongly positively correlated with the percent of urban land cover within 2 km of the garden. In other words, we found that in landscapes with more urban land cover, a greater proportion of the bee's pollen load came from plant species cultivated within the focal urban garden. This trend seems intuitive, considering that these gardens may be acting as highly rewarding resource islands in otherwise forage-poor landscapes (McFrederick and LeBuhn 2006). Because the degree of urbanization often correlates with the homogenization of floral communities (McKinney 2002; Shwartz et al. 2014), urban gardens in highly urbanized
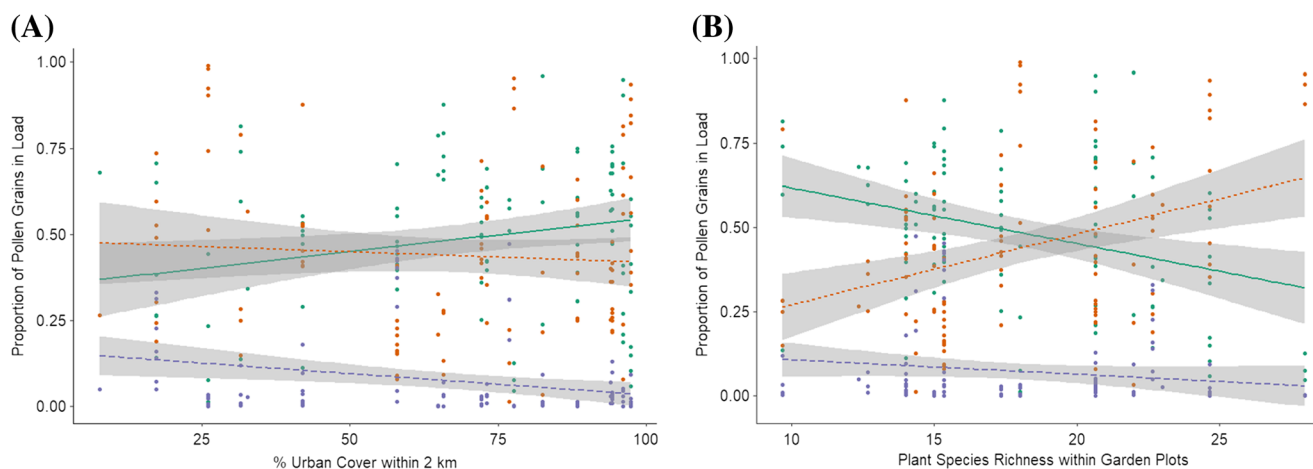

Fig. 4 The effects of landscape (**a**: % urban land cover within 2 km of garden plots) and local (**b**: plant species richness within garden plots) features on the proportion of crop (pink), ornamental (green), and weed (blue) pollen in *B. vosnesenskii* pollen loads

Table 2 Assessed pollen preference for *Bombus vosnesenskii*. The overall preference selection test (*p* value and Lambda, left column) and the top ten preferred floral species are listed, with rank denoting the level of preference for that species with "A" being the most preferred species and each letter indicating a significantly different level of preference

	Preferred plant species	Plant common name	Crop/Ornamental/Weed	Rank
Analysis 1	*Fragaria x ananassa*	Strawberry	Crop	A
P = 0.002	*Eschscholzia californica*	California poppy	Ornamental	A
λ = 0.017	*Brassica sp.*	Mustard	Weed	B
	Raphanus raphanistrum	Wild radish	Weed	C
	Antirrhinum majus	Snapdragon	Ornamental	C
	Rosa L.	Rose bush	Ornamental	C
	Rubus idaeus	American red raspberry	Crop	C
	Eruca vesicaria	Arugula	Crop	C
	Solanum melongena	Eggplant	Crop	C
	Eriogonum fasciculatum	California buckwheat	Ornamental	D

landscapes may contain a higher plant richness relative to their surrounding landscapes (Hulsmann et al. 2015). Increased pollinator visitation to high-reward floral resource patches within resource-poor landscapes has been documented in classic patch dynamics (Goulson 2000; Blaauw and Isaacs 2014) and spatial memory literature (Cartar 2004; Burns 2005; Ohashi et al. 2007); however, its relevance for pollinators within urban landscapes had not been previously been determined. Bees are central place foragers (Michener 2000) and although the literature claims that larger bee species can forage at greater distances from their nests (Greenleaf et al. 2007), even large-bodied species, including several *Bombus* species, predominantly exhibit shorter-distance foraging, with 78% of foraging bouts made within 500 m of nests (Walther-Hellwig and Frankl 2000). In a study of *B. impatiens* in urban gardens in New York City, Matteson and Langellotto (2009) found that 45% of marked individuals were later collected in the gardens where they had initially been documented, indicating that bumble bees in highly urbanized areas may largely forage within a single garden. This is perhaps partially due to the capacity for bumble bees to display 'area-restricted foraging', repeatedly traveling along the same foraging routes in a landscape until they optimize and integrate resource location in their spatial memories (Ohashi et al. 2007). Our findings similarly suggest that bumble bees foraging within urban landscapes, like *B. vosnesenskii,* may respond to landscape-scale resource distribution when selecting high-resource patches, as seen in rural systems for this species (Jha and Kremen 2013a, b; Pope and Jha 2018) and/or additionally experience strong nest site fidelity, as suggested in past landscape genetic studies (e.g., Schenau and Jha 2017).

Interestingly, greater urban cover around our study gardens also correlated with greater proportions of pollen collected from crop plants in the garden; this is particularly interesting given that crop cover was not higher in gardens within more urbanized landscapes. This trend could be a result of lower or more homogenized resources in more urbanized landscapes combined with the greater relative floral availability of crops in our urban gardens. This pattern also may be due to greater levels of generalism or novel-plant visitation by bees in more urbanized landscapes. For certain species of bumble bees, pollen load composition can shift with land-use change over time (Cane 2005). Sustained exposure to novel, but more readily available food sources (such as crops and invasive plants) can lead to these shifts (Kleijn and Raemakers 2008; Williams et al. 2011). In suburban and rural Northern California, *B. vosnesenskii*, the same species studied here, did not show a preference for native over non-native pollen, suggesting that the species might be more resilient to shifts in vegetation composition (Jha et al. 2013; Saifuddin and Jha 2014). In this study, we could not compare native and non-native pollen collection since more than 80% of the species in our study were non-native, but we were able to document substantial variability in pollen collection in response to urban landscape cover. Additionally, it has been found that urban areas with a higher human population density can host a high diversity of plant species (Lowenstein et al. 2014) and for crop species in particular, this diversity can be driven by the socio-economic status and cultural diversity of densely populated urban neighborhoods (Lubbe et al. 2010). Therefore, the pattern we documented could also be a function of social-ecological influences on urban plant community composition; while beyond the scope of this study, understanding the social-ecological forces that shape the urban plant community is a critical area for future research (Philpott et al. in revision). Overall, our findings provide additional evidence that urban gardens are likely acting as important foraging centers for pollinators and may be utilized to different degrees depending on landscape composition.

We also found that the number of herbaceous plant species in the gardens impacted several aspects of *B. vosnesenskii* pollen foraging. As we hypothesized, herbaceous plant species richness (a measurement including crops, ornamentals, and weedy species) in the urban gardens was positively

correlated with the proportion of pollen collected from within the garden, rather than from outside the garden. Past work has shown that bee abundance and diversity is higher in urban gardens with higher floral diversity (Ballare et al. 2019) especially when particularly attractive plant species are incorporated (Pawelek et al. 2009). In fact, one study of common bumble bees in Lüneburg, Germany found that bee persistence in urban landscapes was driven less by the degree of urbanization and more by plant species richness, diversity, and composition across urban greenspaces and gardens (Hulsmann et al. 2015). Other past studies also support our findings, showing that floral visitation rates (Ebeling et al. 2008) and pollinator persistence (Kleijn and Raemakers 2008) in a patch are correlated with patch plant diversity. This pattern may be particularly clear in urban ecosystems relative to nature preserves and farmland, given that pollinators may exhibit more generalist behaviors, foraging from a greater number of plant species in urban areas (Baldock et al. 2015). Interestingly, in our study system, the number of herbaceous plant species did not drive the diversity of pollen found in the bees' pollen loads; instead pollen load diversity was negatively related to garden size. Given that garden size did not correlate with herbaceous plant species in our study, and that previous work in this system has found that garden size does not predict bee composition (Plascencia and Philpott 2017), we hypothesize that larger garden size may simply represent larger patch size and but not greater floral resource availability. In particular, the pattern we found could be reflective of optimal foraging theory predictions where pollinators forage at fewer flowers in larger patches because they are attempting to maximize their rate of resource acquisition (Goulson 2000).

Interestingly, we found that the proportion of pollen collected from ornamental plants was positively correlated with herbaceous plant species richness, while the proportion of pollen collected from crop plants was negatively correlated with herbaceous plant species richness. Specifically, we found that *B. vosnesenskii* can forage primarily on crop species in some gardens, but if given more plant species options, they will shift to collecting pollen from more ornamental plant species. Lowenstein et al. (2019) similarly found that a number of ornamental plants were visited more often than other plant types, and Hennig and Ghazoul (2011) found that higher floral abundance and diversity can concentrate pollinators towards more attractive plant species. Overall, these patterns suggest that small differences in the diversity of plant species within a site can critically impact pollinator foraging. However, we note that these past studies and our own do not measure the impacts of such a shift on plant reproduction and therefore it remains a debate as to whether reductions in a single pollinator's plant fidelity may be outweighed by frequent pollinator visitation in terms of plant reproduction (Brosi and Briggs 2013; Geslin et al. 2013). Plant reproductive success relies on the robustness of pollinator networks (Brosi

2016), but in urban contexts these dynamics likely change as pollinator networks may be in constant flux in response to land-use change and resource inconsistency (Geslin et al. 2013). Indeed, Carvalheiro et al. (2012) and Blaauw and Isaacs (2014) found that small patches of non-crop flowers within large farms increase pollinator-dependent crop output, suggesting that increases in visitation due to greater flowering diversity may outweigh the negative reproductive impacts of heterospecific pollen deposition, depending on how these species are arranged spatially (Werrell et al. 2009). Other work conducted within our study system also indicates that pollinator density and diversity predict crop plant reproductive success, but this relationship depends on floral abundance and diversity in the gardens (Cohen et al., in press). Overall, these studies suggest that small decreases in crop-pollen collection within the more plant species-rich urban gardens may be outweighed by greater overall pollinator visitation at these sites, but further study is required to connect urban bee foraging patterns with urban plant reproductive success.

Finally, we ran a preference analysis which revealed that *B. vosnesenskii* displayed significant foraging preferences overall, where 6 of the top 10 most preferred species were non-crop species even though the majority of plant species in the gardens were crops. Specifically, 4 of the top 10 preferred plants were ornamentals, likely planted for aesthetics or biodiversity provision since they do not satisfy human sustenance needs. This preference pattern, which is analyzed on a per-bee basis, is consistent with general pollen load composition patterns across bees (45.7% ornamental species, 49.9% crop species, and 4.4% weed species) and considering that gardens are heavily skewed toward crop plant cover (21.7% ornamental cover, 60.7% crop cover, 17.6% weed cover). Although most of the ornamental species in our study gardens were not native to the region, and non-native flowers are believed to be less attractive forage for wild bees in the study region (Morandin and Kremen 2013), *B. vosnesenskii* does not display a strong preference for only wild native species (as seen in Jha et al. 2013; Saifuddin and Jha 2014; Harmon-Threatt et al. 2017). Indeed, one crop species *B. vosnesenskii* preferred relative to its availability in our study gardens was strawberry (*Fragaria x ananassa*). It is possible that this preference came out strongest, not necessarily because of the plant species' presence in our observed pollen loads relative to its availability in our gardens, but because of the presence of large-scale strawberry cultivation in the region, which could increase animal-mediated strawberry pollen carryover into the gardens. Beyond this species, *B. vosnesenskii* displayed a strong preference for *Eschscholzia californica*, or California poppy, and to a lesser extent perennial shrub *Eriogonum fasciculatum*, California buckwheat, which are both native to the region and have been cited as preferred foraging resource for bumble bees previously (Morandin and Kremen 2013; Harmon-Threatt et al. 2017). Both species are among several

California natives that are being targeted by many local bee conservation planting programs, as their reward offerings appear to be more attractive to native bumble bees than honeybees (Kremen et al. 2002). Other ornamentals we found that *B. vosnesenskii* preferred include snapdragons and roses, exotics introduced to the area that are well-known for being 'bee-friendly' and particularly suited to bumble bee pollination (Odell et al. 1999; Frankie et al. 2005). Additionally, *B. vosnesenskii* preferred two *Brassicaceae* species, wild mustard and wild radish, which are both prevalent and naturalized agricultural weeds that are nectar and pollen sources for a variety of pollinators (Sahli and Conner 2007). Overall, our preference results align with other studies that have found that urban bee communities may increase their diet breadth when placed under biotic pressure to forage on exotic and introduced species within urban landscapes (Cane 2005). Outside of urban systems, bumble bee species that are able to survive land use changes are often those able to switch their preferences toward floral resources in the altered landscape, where their new diets reflect changes in plant community composition, such as the increasing presence of non-native plants in altered landscapes (Kleijn and Raemakers 2008; Burkle et al. 2013; MacIvor et al. 2014). Based on these studies, *B. vosnesenskii* appears to be a species capable of such foraging shifts in the face of increasing land-use change.

Conclusions

We show that gardens across even the most urbanized landscapes function as crucial resource centers for *B. vosnesenskii* and that resource collection depends critically on both local garden vegetation management and landscape composition. Therefore, our work resonates with other studies that have indicated that effectively supporting healthy pollinator communities across urban landscapes requires thoughtfully designed and abundant greenspaces, especially in the mostly densely urban portions of cities (Braker et al. 2014). Because urban gardens may be one of the few habitats where urban-dwelling bees can forage, adding elements to these gardens that better support their biology will be critical; this includes supplementing crop plantings with a higher proportion and particularly a higher diversity of ornamental plant species and allowing for some flowering weeds to persist. Gardeners may also see secondary benefits from such planting schemes, as many studies have found that supplemental non-crop, native wildflower plantings can attract a higher diversity of insect visitors at higher visitation rates, which can help increase plant seed set and crop reproductive output (Carvalheiro et al. 2012; Blaauw and Isaacs 2014). Additionally, because a high number of popular fruit and vegetable crops have been found to be obligately outcrossing, and thus more dependent on animal-mediated pollination to set fruit at all (Klein et al.

2006; Matteson and Langellotto 2009), gardeners may see increases in the number of successfully fruiting crop species if they can successfully attract a variety and abundance of pollinators to their plots. For example, by cultivating a wide variety of ornamentals and native flowers to supplement their crop gardens, it is likely that gardeners will increase the temporal window for which floral forage is available in their gardens, as many of these plant species display varying, but predictable phenologies to which native bees are often accustomed (Hernandez et al. 2009). Additionally, weeds are known to be important sustenance for pollinators in altered and agricultural landscapes (e.g., Requier et al. 2015); given that some weeds may pose a management challenge for gardeners, gardeners could evaluate this tradeoff and choose to forego weed removal specifically when there is low general floral resource availability. Establishing an urban garden as a consistent and early resource epicenter may help pollinators develop spatial memories of these resource locations (Cartar 2004; Burns 2005) and can possibly ensure that urban gardeners will receive their pollination services throughout the growing season (Pawelek et al. 2009).

By expanding the way urban gardens are perceived, from isolated patches primarily intended to meet human sustenance needs, to permeable refugia that dually support both food production and urban biodiversity, these gardens can address the food resource needs of both humans and foraging animals. In regard to *B. vosnesenskii*, this species is a highly effective pollinator that is a critical actor in the maintenance of genetic connectivity for native and ornamental plant populations, many of which are also obligately outcrossing and need pollinator-assisted pollen distribution to set seed and produce healthy offspring (Cane 2005). Additionally, because urbanized landscapes may act as a filter for bee communities (Banaszak-Cibicka and Żmihorski 2012), the diets of bee species that persist in these environments, like *B. vosnesenskii,* need to be considered for the maintenance of healthy bee populations in these resource-limited environments (Ahrné et al. 2009; Vaudo et al. 2015). Further, gardeners and conservationists who cultivate plants according to *B. vosnesenskii's* preferences are likely to capture the preferences of many other wild pollinator species found in cities, as they also often display preferences for highly attractive ornamentals (Lowenstein et al. 2019). In growing cities, there is a movement to increase the cultivation of native plant species for pollinator conservation (Southon et al. 2017); we posit that efforts to commit space and resources for non-crop species may be further supported if such implementations are promoted by city or state incentives or if the proposed enhancements are oriented along the garden edge or pathway, limiting competition with human food production goals. Overall, we echo Turo and Gardiner (2019) in proposing that urban gardens be considered

critical conservation spaces and the people who plant them as key stakeholders in the discussion around urban planning and pollinator conservation, now and into the future.

Data availability Will be made available on the DRYAD repository upon publication.

Compliance with ethical standards

Conflict of interest We have no conflicts of interest to report.

Ethics approval Our research did not require any ethics approvals.

Consent to participate Our research did not involve human subjects.

Consent for publication Urban Ecosystems has our permission to publish this work.

Code availability Will be made available on GitHub upon publication.

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