

# Pollination service to urban agriculture in San Francisco, CA

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Published online: 14 January 2015  
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**Abstract** Urban agriculture can increase the sustainability of cities by reducing their ecological footprint, conserving biodiversity, and improving quality of life in a city. Given the environmental, economic and social value of urban agriculture, it is important to understand the ecosystem services that sustain it. We experimentally investigated how pollination by wild bees affects tomato production on 16 urban agriculture sites in San Francisco, CA. By comparing four pollination service indicators (fruit set, fruit mass, yield, and seed set) in four pollination treatments (open, artificial-self, artificial-cross, control), we were able to determine that tomatoes pollinated by wild bees significantly outperform the control in terms of all four pollination service indicators measured. Furthermore, the results of this study indicate that urban areas can support adequate pollination service to urban agriculture, regardless of garden size, garden age, or proportion of impervious surface in the surrounding matrix, and that floral resource density is a major factor influencing pollination service.

**Keywords** Pollination services · Urban ecology · Urban agriculture

## Introduction

Despite their inherent density of people and infrastructure, cities have significant potential for producing food. It is estimated that globally 15–20 % of food is produced in or near urban environments (Armar-Klemesu 2000), with over 800,000,000 actively engaged urban farmers worldwide (Smit et al. 2001). Urban agriculture is particularly important in developing countries (van Veenhuizen 2000), and is increasing in industrialized nations (Lawson 2005). Although many urban agriculture crops benefit from bee pollination (Klein et al. 2007), little is known about pollination service to urban agriculture (Matteson and Langellotto 2009). This study assesses pollination service to urban agriculture in San Francisco, CA, and identifies potential local and landscape variables affecting that service.

Urban agriculture can increase the sustainability of cities by reducing their ecological footprint (van Delft and McDonald 1998) or the total land, water and energy required to meet material consumption and waste discharge of a defined population (Wackernagel and Rees

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1996). Urbanization is associated with increased reliance on industrial agriculture and resource depletion, pollution and habitat destruction because cities consume large quantities of food transported from remote regions (SAFE Alliance 1994; Smit et al. 2001). Urban agriculture improves urban sustainability by producing food closer to where it is consumed, which conserves biodiversity (Smith et al. 2006), reduces the carbon footprint of agricultural products (Smit et al. 2001), and improves quality of life in the city by increasing food security and improving nutrition in urban “food deserts” (Mougeot 1994; Smit et al. 2001). Given the environmental, economic and social value of urban agriculture, it is important to understand the ecosystem services that sustain it.

Inadequate pollination service is a potential limitation to the production of urban agriculture. Although managed hives of honeybees (*Apis mellifera*) are the primary pollinator taxon in rural agriculture, pollination in urban agriculture is more dependent on numerous species of wild bees (Matteson and Langellotto 2009). Previous studies have shown that urban environments have lower bee abundance and diversity than surrounding areas (Ahrné et al. 2009; Matteson et al. 2008), and therefore may have poor pollination service (Ahrné et al. 2009). These studies also show that proximity to wildland influences bee abundance and diversity, which suggests that the landscape context of an urban garden may influence its pollination service (Greenleaf and Kremen 2006; Ahrné et al. 2009; Matteson and Langellotto 2010).

In this study, we investigate the role of wild bees in providing pollination service to urban agriculture in San Francisco, CA. We ask: (1) Are tomato plants in San Francisco pollination service limited? (2) Which local variables influence pollination service? (3) Which landscape variables influence pollination service?

## Methods

### Study sites

We established 18 study sites in urban gardens in the city of San Francisco, California, a densely populated metropolis on the west coast of the United States. The city’s steep topography and peninsular geography result in a mosaic of intensely developed urban areas, suburban neighborhoods and open spaces. San Francisco has a typical Mediterranean climate with mild wet winters and dry summers. Study sites were chosen at random from a list of over 200 school and community garden sites found in San Francisco.

### Study plants

To track wild bee pollination service, we used the SunGold variety of cherry tomato (*Solanum lycopersicum*). This variety has been shown to benefit from animal pollination because it has a stigma that projects beyond the anther cone, hindering self-pollination (Greenleaf and Kremen 2006). Tomato pollen is generally only accessible to bees that use buzz pollination, requiring the specialized movement of flight muscles to sonicate the flower to release pollen from the poricidal anthers (Buchmann 1983). Tomato flowers produce no nectar so, honeybees, incapable of sonication to obtain pollen, rarely visit the flowers when other floral resources are present (Free 1963, 1993; King and Buchmann 2003). Thus, non-*Apis* bees are the primary tomato pollinators (Higo et al. 2004). This experiment, therefore, measures pollination service provided by the subset of local wild bees capable of sonication, primarily bumblebees.

The plants were purchased at uniform age from a local grower/nursery (Annie’s Annuals, Richmond, CA) to standardize their variety, cohort, and treatment. The

plants were transplanted into 5-gallon pots and kept in a pollinator-free greenhouse until the experiment began.

### Experimental design

We adapted the experimental design described by Greenleaf and Kremen (2006). Each plant had four experimental inflorescences, one for each of the four treatments: open pollination, artificial-cross pollination, artificial-self pollination, and control. Treatment labels were attached far below the inflorescences to prevent the labels from affecting normal bee visitation (Kearns and Inouye 1993). Pollinator exclusion bags constructed from bridal veil material were placed over the inflorescences of the three treatments other than open pollination before the plants were taken outside of the pollinator-free greenhouse (Kearns and Inouye 1993). The pollinator exclusion bags permitted airflow around the flowers and allowed wind to move the inflorescences (Kearns and Inouye 1993). The pollinator exclusion bag was the only treatment for the control. We treated the artificial-self and artificial-cross pollination treatments every other day as the flowers bloomed. The anther cones of the artificial-self pollination flowers were sonicated with a middle C tuning fork to mimic floral sonication provided by bees (Greenleaf and Kremen 2006). This method of sonication produced a visible ejection of pollen and resulted in a visible deposit of pollen on the anthers. The stigmas of artificial-cross pollination flowers were dipped in pollen collected from other plants. This pollen was sonicated from the non-experimental flowers of on-site replicate tomato plants, collected on a clean petri dish and used immediately. Treatments were continued until every inflorescence had ten flowers in bloom in order to minimize any effect variation in inflorescence size might have on fruit production.

Plants were delivered to the study sites on June 1st and 2nd, 2012. Three plants were set up as replicates at each site. The experimental dates were chosen based on the time period in which every plant had buds beginning to open on at least four inflorescences during the local tomato-growing season. After 2 weeks of the above treatments, we returned the plants to the greenhouse and removed the pollinator exclusion bags before the flowers senesced in order to minimize differences in fruit development conditions. Plants were provided with regular water and fertilizer in a greenhouse to eliminate variation due to nutrient resource limitation.

We began the experiment with four inflorescences on each plant, one for each treatment, and three plants at each of the 18 sites. One site was excluded from the study due to an aphid infestation and another was lost to wind damage. We measured only the fruits produced by the first ten flowers in bloom on each inflorescence, resulting in  $n=480$  for each of the four treatments.

### Pollination service

Tomatoes were picked at the same stage of ripeness as when picked by local farmers (deep orange-gold color). We collected data on four pollination service indicators: fruit set, average fruit mass, average yield mass, and seed set. We calculated fruit set by dividing the number of developed fruits by the number of flowers and multiplying by 100 to determine the percentage of flowers to mature into fruit. We measured the mass of each fruit using a digital scale to determine average fruit mass and average yield mass. While Greenleaf and Kremen (2006) used volume as a proxy to gauge seed set, we decided to use mass rather than volume because mass can be accurately measured more easily and does not vary with ripeness whereas volume does (Ho and Hewitt 1986). We counted the seeds of one randomly selected tomato per inflorescence from each plant to determine seed set.

## Local and landscape variables

We calculated the proportion of impervious surface area (i.e., roads and rooftops) within a 1 km radius of each site using 2006 National Land Cover Database (NLCD) Percent Developed Impervious Surface imagery in ArcMap 10.1. This value provided a measure of the proportion of land incapable of providing either nesting or floral resources to wild bees within foraging range of each site (Gathmann and Tscharntke 2002; McFrederick and LeBuhn 2004; Greenleaf et al. 2007). We visually estimated abundance of flowers in bloom in each site at the time of the study, using a logarithmic scale to estimate flower abundance, i.e., 1, 10, 100, 1000, flowers per plot (McFrederick and LeBuhn 2004). We calculated floral resource density by dividing flower abundance by site area. Site managers provided garden age (years in cultivation), and Baker Beach Software provided average temperatures of the San Francisco microclimates in which each site was located during the time period of the study as recorded by Weather Underground.

## Data analysis

To determine whether wild bees contribute to production in San Francisco urban agriculture, we first pooled the sites and compared the four treatments using within-subjects analysis of variance (ANOVA) and Bonferroni adjustments for multiple comparisons for each of the four response variables: fruit set, average fruit mass, average yield mass, and seed set. This also tested two (non-mutually exclusive) mechanisms by which bees could increase crop production: bees increase production by increasing self-pollination through sonication; and bees increase production by facilitating cross-pollination (Greenleaf and Kremen 2006). All data were analyzed using SPSS ver 21 (2012).

To determine which local and landscape factors affect pollination service, we used forward stepwise multiple regression with the following independent variables: proportion of impervious surface in the surrounding matrix, floral resource density, site age, site size, and mean temperature. We checked all variables for normality using skewness and kurtosis values. Floral resource density and site size were log transformed and site age and temperature were square root transformed. We conducted four separate analyses for each of the four pollination service indicators: fruit set, average fruit mass, average yield mass, and seed set. In order to ensure that our response variables represented pollination service differences, we calculated the percentage by which open treatments benefited relative to the control. To accomplish this we subtracted the control from the open treatment and divided this by the control and multiplied by 100 for each pollination service indicator at each site  $[(\text{open}-\text{control})/\text{control} * 100]$ .

## Results

For the experiment as a whole, 972 of the 1920 flowers included in the experiment matured into fruit. The open pollination treatment had significantly higher fruit set, average fruit mass, average yield mass, and seed set than the control. The open pollination treatment had higher fruit set than either of the artificial pollination treatments, but these pairs did not differ significantly in terms of average fruit mass, average yield mass, or seed set. Artificial pollination treatments were statistically similar to each other for all pollination service indicators, and were significantly higher than the control for all pollination service indicators except fruit set.

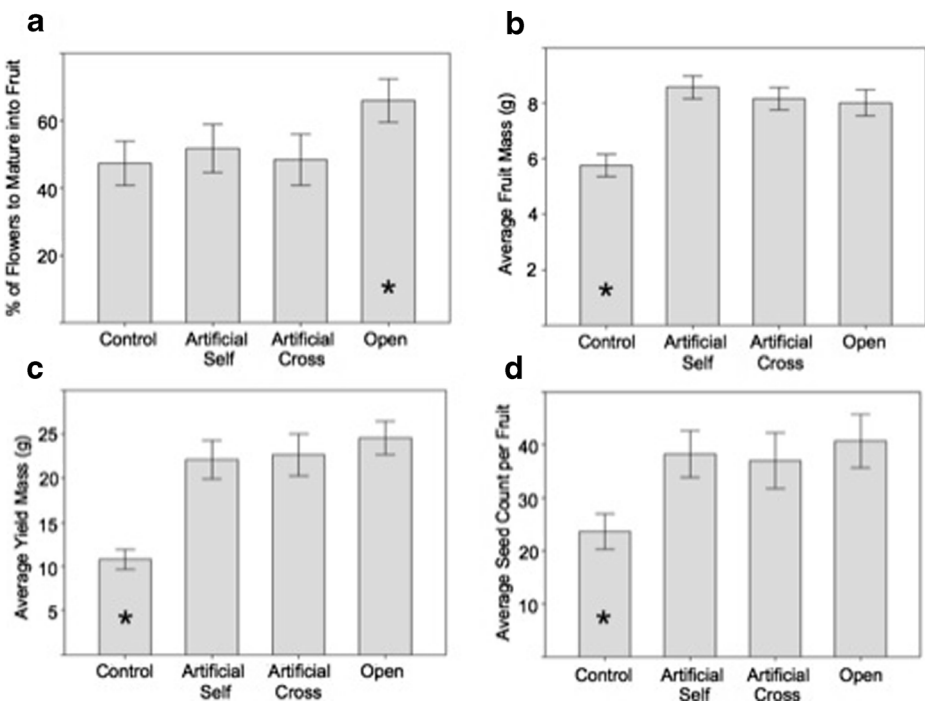
Open pollination treatments had significantly higher fruit set than did artificial-cross pollination, artificial-self pollinated and control treatments ( $F_{(3,43)}=9.285$ ,  $p<0.0005$ ,

Fig. 1a). Tomatoes in the open pollination treatments had a significantly greater average fruit mass than tomatoes from the control ( $F_{(3,39)}=54.397$ ,  $p<0.0005$ , Fig. 1b). The open pollination treatments produced a significantly higher average yield mass than the control ( $F_{(3,39)}=18.307$ ,  $p<0.0005$ , Fig. 1c). Tomatoes in the open pollination treatments had significantly more seeds on average than the control ( $F_{(3,39)}=65.591$ ,  $p<0.0005$ , Fig. 1d).

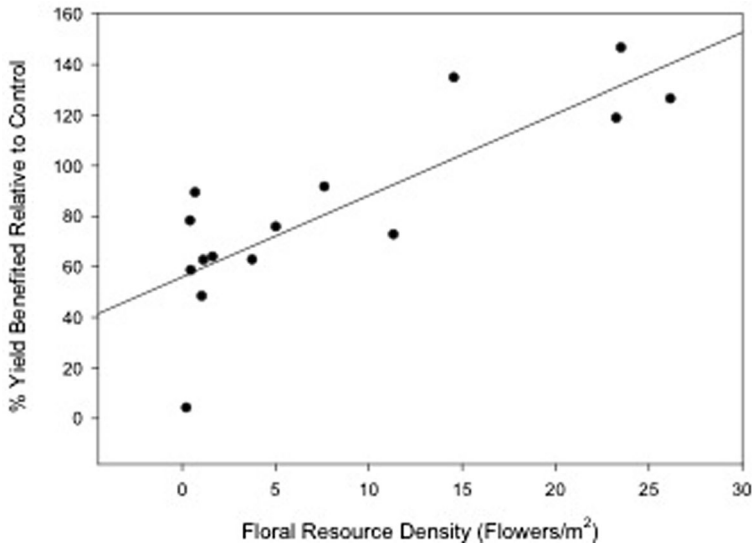
Tomato average yield mass is positively correlated with floral resource density. The overall forward stepwise multiple regression of average yield mass with the five independent variables was highly significant ( $F_{(1,15)}=14.771$ ,  $p=.002$ ,  $R^2=.513$ , Fig. 2), with log floral resource density being the only independent variable entering into the model. None of the independent variables entered into the overall forward multiple regressions of fruit set, average fruit mass or seed set. Garden sites in this study ranged from 1 to 22 years in cultivation, with a mean of 6 years. Site size ranged from 25 to 1100 m<sup>2</sup> with a mean area of 310 m<sup>2</sup>. Proportion of impervious surface in the surrounding matrix ranged from 42 to 91 % with a mean of 61 %. Average temperatures at each site during the study period ranged from 11 to 16 °C.

## Discussion

The results of this study indicate that urban areas can support adequate pollination service by wild bees to support urban agriculture. Floral resource density is associated with increases in



**Fig. 1** a-d. Bee pollination increases tomato fruit set (a), average fruit mass (b), average yield mass (c), and seed set (d). Means and standard error bars are shown for each of the four pollination service indicators measured. Open pollination treatments were visited by bees; artificially pollinated flowers had insect visitors excluded and were pollinated by hand with the aid of a tuning fork; all visitors were excluded from the control flowers. Treatments labeled with an asterisk were significantly different at a 95 % confidence interval



**Fig. 2** Tomato average yield mass significantly positively correlated ( $R^2=0.513$ ) with floral resource density

pollination service. It was the only local or landscape variable tested that had a significant effect on pollination service. Our data suggest that wild bees enhance urban agriculture production by means of floral sonication and cross-pollination, regardless of proportion of impervious surface in the surrounding matrix, garden size, garden age, or average temperature.

#### Pollination service

The open pollination treatments significantly outperformed the control for all four pollination service indicators, and outperformed both artificial-self and artificial-cross pollination treatments in terms of fruit set, demonstrating that tomatoes grown in this urban environment receive adequate pollination service. Morandin et al. (2001) reported 100 % tomato fruit set with sufficient pollination in a greenhouse environment with controlled climate conditions. However, poor tomato pollen viability has been reported at temperatures below 10 °C (Charles and Harris 1972), thus fertilization and fruit set do not necessarily result from pollination in environments such as San Francisco where the nighttime temperature commonly drops below 10 °C, even in summer. This means fruit set is a proxy rather than a direct measure of pollination service, and we cannot define adequate pollination service as 100 % fruit set. Greenleaf and Kremen (2006), in an experiment very similar in design to ours but using commercially grown tomatoes in a rural setting reported an open pollination treatment fruit set value of 60 %, comparable to our result of 66 %.

Although tomatoes are a relatively small subset of urban agriculture in San Francisco, they are not pollinated by honeybees, but by multiple generalist wild bee genera (Greenleaf and Kremen 2006), suggesting adequate pollination to tomatoes is an indication of pollination service by wild bees to a broader set of agricultural plants. Previous research has found wild bees pollinate between 42 and 80 % of the 100 most important staple crops (Klein et al. 2007; Buchmann and Nabhan 1996). These data suggest that urban areas can support adequate pollination service to urban agriculture.

Both the artificial-self and artificial-cross pollination treatments significantly outperformed the control and did not differ from the open-pollination treatment in terms of average fruit mass, average yield mass and seed set. This suggests that our artificial pollination treatments were successful. However, in the case of fruit set, the open-pollination treatments outperformed the artificial-self and artificial-cross pollination treatments, which did not differ from the control. One possible explanation is that the bees delivered more pollen grains to each stigma, possibly through repeated visits, although this difference is not reflected in terms of average fruit mass, average yield mass, or seed set. Another possible explanation is that the bees visited the flowers earlier in the day, allowing more time for fertilization to occur before temperatures dropped at night, reducing pollen viability. It was logistically impossible to artificially pollinate all the flowers at each of the 18 sites early in the day, and many were not artificially pollinated until afternoon. Future research is needed to investigate the effects of timing and temperature fluctuations on successful fertilization and fruit set resulting from artificial pollination.

Artificial-self and artificial-cross pollination treatments did not differ from each other for any of the four pollination service indicators, and both outperformed the control in terms of average fruit mass, average yield mass and seed set, indicating both sonication and cross-pollination are mechanisms by which wild bees may increase tomato production. These results were surprising because the SunGold variety of cherry tomato is an F1 hybrid produced by crossing two inbred parent lines, meaning all individuals should be relatively genetically uniform, suggesting limited benefit from cross-pollination (Greenleaf and Kremen 2006).

#### Local variables

Pollination service positively correlated with site floral resource density, likely not a direct effect of flowers on pollination of tomatoes, but an indirect effect of increased abundance of bees or increased visitation rates. Previous studies have established the positive connection between floral abundance (Matteson and Langellotto 2010) and diversity (Potts et al. 2003; Frankie et al. 2005; Kearns and Oliveras 2009) and bee abundance and diversity, but the connection between pollination service and floral resource density has not previously been shown. This finding is important because, while total floral abundance may depend on site size, floral resource density does not. Gardens in urban areas are often spatially limited, and this data suggests that gardens with high floral resource density are attractive enough to foraging bees to experience enhanced pollination service regardless of size.

Garden size and garden age had no effect on pollination service. These measures were evaluated because space and time for local bee colonization might influence pollination service. However, all garden sites were extensively cultivated, with very little unmanaged, undisturbed area. Previous studies have found negative correlations between level of garden management and bumblebee species richness (Smith et al. 2006). Unmanaged areas are important because there are fewer disturbances to nesting bees (Matteson and Langellotto 2010). It is possible that any benefit to pollination service resulting from local bee colonization was absent because the sites were too managed for bees to colonize.

#### Landscape variables

To our surprise, proportion of impervious surface in the surrounding matrix did not have a significant effect on pollination service. Study sites had a relatively large proportion of impervious surface in the surrounding matrix, and these results suggest that the urban green areas distributed throughout San Francisco provide sufficient bee habitat to support pollination

service. Previous research has shown that urban green areas can function to provide habitat for many bee species (McFrederick and LeBuhn 2004; Ahrné et al. 2009), and our data supports this. However, the available land use dataset analyzed did not allow for differentiation between pervious surfaces unlikely to serve as habitat (mowed lawns and mulched areas) and more hospitable areas. Further research is needed to improve methods of estimating potential bee habitat and determine the necessary extent and distribution of habitat required to support pollination service to urban agriculture.

Average site temperature did not correlate with pollination service. Warmer temperatures are known to increase bee activity levels (Kilkenny and Galloway 2008), and sunlight has been found to positively correlate with bee species richness and abundance (Matteson and Langellotto 2010). Poor tomato pollen viability has been found at temperatures below 10 °C (Charles and Harris 1972). Perhaps our findings owe to the fact that the available average temperature dataset included nighttime temperatures, likely providing a poor representation of the temperature range during the time of day in which bees forage.

Wild bee populations vary seasonally and annually (Greenleaf and Kremen 2006), so in order to ensure adequate pollination service to urban agriculture it is necessary to maintain a community of bees rather than just one species (Kremen et al. 2002). Furthermore, urban centers vary greatly in terms of extent, distribution and type of open space. This study raises questions about which genera are providing pollination service, and what exactly constitutes suitable habitat. Urban planning and land management techniques that maximize both species richness and abundance are necessary if we are to maintain pollination service for the future.

**Acknowledgments** This study was supported by the NSF TREE Fellowship. We thank E. Connor, and V.T. Parker. We also thank ECOSF School Farm, San Francisco Bee-Cause, and all the land managers and gardeners who volunteered their time and land.

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