

Wild Bee Visitation Rates Exceed Pollination Thresholds in Commercial *Cucurbita* Agroecosystems

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Abstract

Wild bees supply sufficient pollination in *Cucurbita* agroecosystems in certain settings; however, some growers continue to stock fields with managed pollinators due to uncertainties of temporal and spatial variation on pollination services supplied by wild bees. Here, we evaluate wild bee pollination activity in wholesale, commercial pumpkin fields over 3 yr. We identified 37 species of bees foraging in commercial pumpkin fields. Honey bees (*Apis mellifera* L. [Hymenoptera: Apidae]), squash bees (*Eucera (Peponapis)* Say, Dorchin [Hymenoptera: Apidae]), and bumble bees (*Bombus* spp., primarily *B. impatiens* Cresson [Hymenoptera: Apidae]) were the most active pollinator taxa, responsible for over 95% of all pollination visits. Preference for female flowers decreased as distance from field edge increased for several bee taxa. Visitation rates from one key pollinator was negatively affected by field size. Visitation rates for multiple taxa exhibited a curvilinear response as the growing season progressed and responded positively to increasing floral density. We synthesized existing literature to estimate minimum ‘pollination thresholds’ per taxa and determined that each of the most active pollinator taxa exceeded these thresholds independently. Under current conditions, renting honey bee hives may be superfluous in this system. These results can aid growers when executing pollination management strategies and further highlights the importance of monitoring and conserving wild pollinator populations.

Key words: agricultural entomology, crop pollination, pollination, social insects, vegetable entomology

Commercially produced pumpkins (*Cucurbita pepo pepo* L. [Cucurbitales: Cucurbitaceae]) are among the most pollinator-dependent crops worldwide (Klein et al. 2007). Pumpkins are monocious, with separate male (staminate) and female (pistillate) flowers blooming on the same plant. Male flowers produce a large, heavy pollen that must be vectored by insects to the sticky pistil in female flowers. When insect pollinators were excluded from female flowers, *C. pepo* plants yielded no fruit (Hoehn et al. 2008, Artz et al. 2011). Originally domesticated in Mexico between 5–10,000 yr ago (Smith 1997), pumpkins and other *Cucurbita* are now grown world-wide for both consumption and ornamentation. Demand for pumpkins has more than doubled since the 1980s. In the United States in 2017, pumpkin production was worth >\$185 million, with 70% of all production from seven states, including Pennsylvania, where the industry was worth over \$13 million (USDA NASS 2017a). Because this culturally and economically valuable crop is a completely reliant on insect-vectored pollination, fields are often supplemented with honey bees (*Apis mellifera* L. [Hymenoptera: Apidae]). Managed pollinators can be expensive: in 2017, the cost of renting honey bees in the Mid-Atlantic was \$76.20

per hive (USDA NASS 2017b; this can be higher in other regions and cropping systems) with guidelines recommending one hive per acre (Canon 2011, Orzelek et al. 2012). With almost 5,000 acres of pumpkins grown in PA in 2017, the cost of pollination alone could amount to nearly \$400,000 annually. With these expenses in mind, growers are eager for cost-saving alternatives, including pollination provided by wild bee populations.

Pumpkin Pollinators

Recent studies have highlighted several wild bee species foraging in pumpkin flowers worldwide. Wild species include the solitary *Cucurbita* specialists *Eucera (Peponapis)* Say, Dorchin (Hymenoptera: Apidae) and *Eucera (Xenoglossa)* Smith, Dorchin (Hymenoptera: Apidae) (‘squash bees’, a taxon that was newly revised by Dorchin et al. (2018) at the time of this publication), *Halictus* and *Lasiglossum* generalists (‘sweat bees’), and eusocial *Bombus* generalists (‘bumble bees’) (Julier and Roulston, 2009, Artz et al. 2011, Artz and Nault 2011, Cane et al. 2011, Petersen et al. 2013, Phillips and Gardiner 2015, Pfister et al. 2017). The community and the relative abundance of pollinating visits varied between

studies. This variation may be due in part to differences in the surrounding landscape or farm management practices, both of which has been shown to affect pollinator communities and abundances (Julier and Roulston 2009, Ullmann et al. 2016).

The potential value of a pollinator depends not only on their visitation abundance but also on their foraging preferences and pollination efficiency. Foraging preferences, likely dictated by resource needs of each bee taxa, will affect how frequently male and female flowers are visited. While only male flowers produce pollen, both male and female flowers produce nectar. Bees foraging for pollen, like female squash bees who collect pumpkin pollen to provision their nests (Hurd et al. 1971), may be more likely to visit male flowers. Alternatively, bees foraging for nectar may preferentially visit female flowers because of their large nectaries, as was the case for honey bees foraging in New York pumpkins (Artz and Nault, 2011, but see Pfister et al. 2017). Furthermore, previous studies provide a wide range of pollen deposition rates per bee taxa, but even the most conservative studies estimate that *Bombus* spp. deposit the most pumpkin pollen per visit, ranging from 3× (*A. mellifera*, *E. (Peponapis)*) to 75× (halictids and other small bees) that of other pollinators (Artz and Nault 2011, Pfister et al. 2017). Furthermore, the number of pollen grains needed for adequate pollination varies across *Cucurbita* species. Minimum requirements, i.e., ‘pollination thresholds’, have been mentioned for various cultivars worldwide. Phillips and Gardiner (2015) compared observed deposition to estimated required deposition to determine, which bees were providing sufficient pollination for *C. p. pepo* cv ‘Gladiator’ in Ohio. Pfister et al. 2017 used pollinator efficiency in tandem with plant fertilization requirements to calculate the minimum number of visits needed to achieve adequate pollination of *C. maxima* cv ‘hokkaido’ Duchesne (Cucurbitales: Cucurbitaceae) in Germany. However, ‘pollination thresholds’ based on visitation rates remains undefined for the most active pumpkin pollinators in the United States. Furthermore, no studies have compared native bee visitation rates to estimated ‘pollination thresholds’ to determine whether native bees are supplying sufficient pollination services.

Agricultural Objectives

In addition to pollinator attributes (visitation abundance, foraging preferences, pollination efficiency), production objectives influence pollination needs. In commercial agroecosystems, objectives depend largely on 1) the end use of pumpkin and 2) retail strategy. In the United States, ‘pie’ pumpkins are processed for consumption, whereas ‘face’ pumpkins are grown for ornamentation, often carved with faces during autumnal festivities. In Pennsylvania, >99% of pumpkins produced in 2016 were ‘Face pumpkins’ (USDA NASS 2017a). Face pumpkins reach consumers through two main retail strategies: direct market and wholesale. Direct market pumpkins are produced for pick-your-own operations and farm stands, where harvest occurs multiple times throughout October. In a wholesale system, pumpkins are harvested earlier (in early September), packed into standardized bins, and shipped to large retailers nationwide. Each field is typically harvested once, with agricultural objectives emphasizing synchronous production and fruit maturation, early in the fall season in large quantities. Because of the need for a relatively early harvest date, wholesale fields are often planted and bloom earlier than direct market fields. Therefore, the timing of pollination activity is critical. Temporal dynamics of species-specific visitation rates to pumpkin flowers across the growing season are currently unknown.

Because wholesale growers need large quantities, fields tend to be larger. Foraging strategies and ranges differ among bee taxa, and

therefore, bees may move through a patch of resources (i.e., fields of pumpkin flowers) differently. It is currently unknown if species-specific pollination activity is equally distributed across fields or concentrated at field edges. Additionally, larger fields will inevitably contain more flowers. Pumpkin plants produce large yellow-orange flowers that stand out against a backdrop of dark leafy green. Because of their location high up on the plant, male flowers may serve as bright advertisements to attract passing pollinators. A higher density of male flowers would create a more concentrated floral display and potentially attract greater forager abundances. However, if pollinator populations are limited, increased floral resources may dilute pollination services as the set number of pollinators disperse among the larger numbers of flowers. Pollinator response to *Cucurbita* floral density is understudied in commercial settings. Furthermore, its unknown if density of the more visible male flowers will affect visitation rates to female flowers.

Multiple studies have demonstrated that when pollinator visits are intentionally limited, there is a strong, positive relationship between bee visits and seed set for *Cucurbita pepo* (Artz and Nault 2011, Xie et al. 2016). However, seed set is only one component of fruit set, fruit retention, and harvestable yield (Stephenson 1981). *Cucurbita* plants may selectively invest resources to produce fewer fruit, concentrating on fruit fertilized under conditions of high pollen competition (Winsor et al. 1987). Artz and Nault 2011 demonstrated strong, positive relationships between the number of visits from specific bee species and the percentage of fruit set, and increased pollination activity has been linked with increased weight and yield (but see Peterson et al. 2013, where pollination activity did not influence weight in a commercial setting). Pollination also effects fruit shape, which is important for face-pumpkins, particularly in a wholesale setting, where a predetermined number of pumpkins are packed into standardized bins. Growers are aiming for a defined pumpkin diameter – pumpkins too small or too large are not harvested. These yield relationships remain understudied. The relationship between seed set and weight is unreported for *C. p. pepo* cv ‘Gladiator’ and the relationship between pumpkin weight, and shape (circumference and length) is also unreported.

In this study, we determine the community composition and dominance distribution of pollinators in commercial wholesale face-pumpkin agroecosystems over 3 yr in Pennsylvania. We measure visitation rates of the most common pollinators and determine if wild visitors are supplying sufficient visits per female flower to achieve optimal fertilization. We explore sources of variation impacting pollinator visitation rates, including flower sex, temporal dynamics across the growing season, spatial dynamics across larger pumpkin fields, and floral density. Finally, we explore relationships between visitation rates and pumpkin yield.

Methods

We conducted this study during pumpkin bloom relevant to commercial yield (16 July to 22 August) in 2 regions (Lancaster county, and Columbia and adjacent counties) of Pennsylvania in 2013, 2014, and 2015. In total, we sampled 24 commercial fields (2013, $n = 6$; 2014, $n = 8$; 2015, $n = 10$) ranging in area from 1.28 to 12.7 ha (6.25 ± 0.63 SE). Within each field, we designated four transects, 80- to 100-m long, located 0, 25, 50, and 100-m parallel from the field edge (Fig. 1). In most cases, field edge was adjacent to unmanaged or forested habitat. All plants were the cv ‘Gladiator’ in 22 of the 24 fields. Several *C. p. pepo* cv ‘Cannonball’ were in one field (field 7) in 2013, but only in a few measures per transect. In 2015, one field (field 21) was entirely *C. p. pepo* cv ‘Giant’ and was excluded from yield analyses.

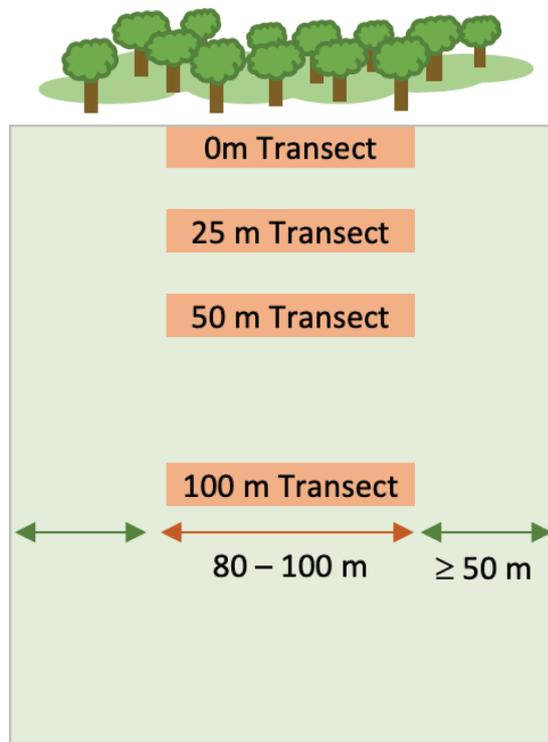


Fig. 1. Sampling diagram. Visitation, floral density and yield measures were collected along transects (rectangles) spaced 0, 25, 50 and 100 m from the field edge (forested). Transects were between 80- to 100-m long (middle arrow) with at least 50 m of field on either side (side arrows).

Sampling Procedures

Pollination Activity

Observers visited most fields (18 of 24) on 2 dates during bloom to observe bee visits to pumpkin flowers. Four fields were sampled only once, and two fields were sampled times times (sampling support detailed in [Supp Appendix A \[online only\]](#)). We sampled for pollination activity between 0630 and 1200 h EST when weather conditions were favorable for bee activity ($>15.5^{\circ}\text{C}$ with low-wind speeds). The sampling unit was the transect, and along each transect, we collected ≈ 60 independent measures ([Supp Appendix A \[online only\]](#)), which were averaged for a single value per transect. For each measure, we designated specific pumpkin flowers within a 1-m^2 area and recorded all bee visits to all flowers for 45 s. Designated flowers were defined as the available flowers in which an observer could confidently keep track of bee visits: across the entire study, 3.47 ± 0.02 SE flowers were observed per 45 s measure. Flower number, sex, and visits per bee morpho-taxa were recorded. Because not all observers could reliably identify bees to species in the field, bees were recorded as one of nine morpho-categories: honey bee (*Apis mellifera*), bumble bee (*Bombus* spp.), squash bee (*E. Peponapis*), large black bee, small black bee, and large striped bee, Small striped bee, green bee, and other (see [Table 1](#) for species associated for each morpho-taxa). A ‘visit’ was defined as any instance in which a bee came in contact with the reproductive portions of the flower (either stamen or pistil). These measures provided a rate of taxa-specific pollinator visits per flower sex per 45 s.

Bee Pollinator Survey

In between-individual visitation measures, we collected representative examples of each morpho-taxa that were actively foraging

on both stamens and pistils, using 20-ml scintillation vials placed over an actively foraging bee. Collected specimens were pinned and identified to species with assistance from experts. The species list was then compared with the number of visits contributed by each morpho-taxa to determine the dominance distribution of pollination activity. The taxa providing $>95\%$ of the visits were included in subsequent analyses.

Floral Density

In 22 of the 24 fields, we measured floral density for each transect on each sampling date after completing visitation observations. The number of male and female flowers in 1m^2 was recorded. Along each transect, we collected 10–60 (detailed in [Supp Appendix A \[online only\]](#)) floral density measures, which were averaged for a single value per transect.

Yield

We visited 18 of the 24 fields once after pumpkin maturation to collect yield metrics in advance of commercial harvesting (28 August to 26 September, sampling support detailed in [Supp Appendix A \[online only\]](#)). We collected five types of data: weight, circumference, length, seed set per pumpkin, and fruit per square meter. Along each transect, we randomly selected pumpkins to weigh and measure the circumference at the roundest part of the pumpkin ($n = 5$ per transect in 2013; $n = 20$ per transect in 2014 and 2015, resulting in 1,141 measures). Of the weighed pumpkins, we cut open 5 per transect from stem to calyx to measure the length, and in 2013 and 2014, we also collected, washed, dried, and counted all seeds, resulting in 250 measures of length and seed set. Additionally, in 2014 and 2015, fruit per square meter was measured 20 times along each transect (resulting in 1,038 measures) by counting the number of mature pumpkins in random 1-m^2 plots. Analyses were based on means per transect (72 transects for weight and circumference, and 52 transects for length, seed set, and fruit per square meter).

Analysis

We used JMP Pro, Version 14.3 (SAS Institute 2007, Cary, NC) to complete all analyses. Significance is at $\alpha = 0.05$ unless otherwise specified. All regressions were completed using ‘Fit Model’ with model personality ‘Standard Least Squares’, and emphases ‘Effect Leverage’. multivariate analysis of variance (MANOVA) was completed using ‘Fit Model’ with model personality ‘MANOVA’, response specified as ‘Identity’ and ‘Test each column tested separately also’ selected. Analyses of variance (ANOVAs) were completed using ‘Fit Y by X’. Visitation rate data were normalized using $\text{Log}_E(x + 0.01)$ transformations, based on results from Box-Cox Y tests (details in [Supp Appendix D \[online only\]](#)). Untransformed data are presented in all figures.

Flower Sex Foraging Preferences

To test for flower sex foraging preferences, we compared the distribution of male and female flowers observed to the distribution of male and female flower visits from each bee taxa separately. We considered spatial dynamics of flower sex preference by examining preferences for each distance from field edge. Comparisons were made using a Likelihood Ratio χ^2 test based on total visits per bee taxa, summed across all sampling dates for each transect, implemented with the contingency analysis function in JMP Pro. Because there were 12 independent tests (3 bee taxa \times 4 distances from field edge), significance is found at $\alpha = 0.004$ after Bonferroni corrections.

Table 1. Comprehensive list of all bee species collected from *Cucurbita pepo pepo* cv 'Gladiator' flowers including the morpho-taxa terminology used during visitation observations

Taxa	N	Morpho-taxa	Year	Field
Total: 4 families, 15 genera, 37 species	844	9	3	30
Apidae (7 genera, 13 species)				
<i>Apis mellifera</i> Linnaeus, 1758	147	<i>A. mellifera</i>	2013, 2014, 2015	All*
<i>Bombus bimaculatus</i> Cresson, 1863	4	<i>Bombus</i> spp.	2013, 2014, 2015	3, 14, 22
<i>Bombus fervidus</i> Fabricius, 1798	5	<i>Bombus</i> spp.	2013	8
<i>Bombus griseocollis</i> De Geer, 1773	9	<i>Bombus</i> spp.	2013, 2015	8, 22, 23, 32
<i>Bombus impatiens</i> Cresson, 1863	349	<i>Bombus</i> spp.	2013, 2014, 2015	All
<i>Bombus terricola</i> Kirby, 1837	3	<i>Bombus</i> spp.	2014	14
<i>Bombus vagans</i> Smith, 1854	2	<i>Bombus</i> spp.	2013	4, 6
<i>Ceratina calcarata</i> Robertson, 1900	1	Small Black	2013	7
<i>Ceratina dupla</i> Say, 1837	1	Small Black	2013	7
<i>Melissodes bimaculatus</i> Lepeletier, 1825	10	Large Black Bee	2013, 2014	3, 7, 8, 13, 33
<i>Eucera (Peponapis) pruinosa</i> Dorchin, 2018	164	<i>E. (Peponapis)</i>	2013, 2014, 2015	All*
<i>Triepeolus remigatus</i> Fabricius, 1804	4	Large Striped	2013	7
<i>Xylocopa virginica</i> Linnaeus, 1771	1	Other	2015	33
Halictidae (6 genera, 22 species)				
<i>Agapostemon virescens</i> Fabricius, 1775	4	Green	2013	6, 7
<i>Augochlora pura</i> Say 1837	60	Green	2013, 2014, 2015	All except 5, 8, 17, 23, 24
<i>Augochlora aurata</i> Smith, 1853	10	Green	2013, 2014, 2015	5, 7, 15, 22, 23
<i>Augochloropsis metallica</i> Fabricius, 1793	1	Green	2013	6
<i>Halictus ligatus</i> Say, 1837	1	Small Striped	2013	3
<i>Halictus rubicundus</i> Christ, 1791	1	Small Striped	2013	5
<i>Lasioglossum albipenne</i> Robertson, 1890	1	Small Black	2014	15
<i>Lasioglossum bruneri</i> Crawford, 1902	2	Small Black	2013, 2015	5, 33
<i>Lasioglossum ephialtum</i> Gibbs, 2010	4	Small Black	2015	22
<i>Lasioglossum hitchensi</i> Gibbs, 2012	4	Small Black	2013, 2014, 2015	7, 14, 22
<i>Lasioglossum illinoense</i> Robertson, 1892	1	Small Black	2013	7
<i>Lasioglossum imitatum</i> Smith, 1853	5	Small Black	2015	23, 32, 33
<i>Lasioglossum laevisimum</i> Smith, 1853	1	Small Black	2014	13
<i>Lasioglossum lineatulum</i> Crawford, 1906	1	Small Black	2014	14
<i>Lasioglossum obscurum</i> Robertson, 1892	1	Small Black	2014	12
<i>Lasioglossum paradmirandum</i> Knerer & Atwood, 1966	4	Small Black	2015	22, 23
<i>Lasioglossum pilosum</i> Smith, 1853	16	Small Black	2013, 2014, 2015	3, 4, 6, 13, 21, 23, 24, 32
<i>Lasioglossum truncatum</i> Robertson, 1901	2	Small Black	2014	13, 33
<i>Lasioglossum versans</i> Lovell, 1905	1	Small Black	2013	3
<i>Lasioglossum versatum</i> Robertson, 1902	7	Small Black	2013, 2014, 2015	3, 6, 15, 22, 31
<i>Lasioglossum weemsi</i> Mitchell, 1960	6	Small Black	2013, 2014, 2015	4, 15, 22, 23, 25
<i>Lasioglossum zephyrum</i> Smith, 1853	8	Small Black	2013, 2014	7, 8, 12, 31
Colletidae (1 genus, 1 species)				
<i>Hylaeus annulatus</i> Linnaeus, 1758	2	Small Black	2013	6
Megachilidae (1 genus, 1 species)				
<i>Megachile brevis</i> Say, 1837	1	Large Striped	2013	5

*Not collected at every field, but reliable visitation data indicates species presence in all fields.

Factors Influencing Visitation Rates

We used an overall model to examine the effect of categorical (bee taxa and flower sex) and continuous (field area, distance from field edge, day of year, and male flower floral density per square meter) variables on visitation rates. We included two- and three-way interactions between categorical variables and each continuous variable. We used an overall regression model examining just the fixed effects as well as an overall mixed model including year, region, and field as random effects. Both provided similar results and because the overall regression model provides an *R*-squared value indicating the amount of variation explained by the model, we report results for the regression model in the text (mixed model results in [Supp Appendix B \[online only\]](#)). Removing nonsignificant terms from the overall regression only

increased the value of the *F*-statistic, and therefore, we report the model including only significant terms.

We examined significant two-way interactions between categorical variables (bee taxa and flower sex) with a two-way ANOVA. When three-way interactions were significant, we partitioned visitation rates by flower sex and evaluated the effect of continuous variables for each bee taxa separately using regression. When two-way interactions involving continuous variables were significant, we first combined visitation rates across the nonsignificant categorical variable and then partitioned visitation rates by the significant categorical variable to examine the effect of continuous variables on each subset of data. When significant continuous variables did not interact with any categorical variable, we combined visitation rates across bee taxa and flower sex to examine the effect of continuous variables with regression.

Pollination Thresholds

We synthesized literature to determine the number of required visits per female flower lifetime for optimal *Cucurbita* pollination for the most active bee taxa in our study. To be as conservative as possible, we then used the highest number of visits required to achieve pollination reported for each taxa. Required visits were converted to visitation rates (visits per flower per 45 s) to reflect the unit of visitation rates measured in our study. Because pumpkin flowers are open a minimum of ~4 h on a single day (Tepedino 1981), pollinators have a minimum of 14,400 s (4 h × 3,600 s/h) to deliver the maximum necessary visits within a female flower's lifetime. Therefore, the 'visitation rate threshold' per taxa can be calculated as

$$\frac{\text{Necessary visits per flower}}{14,400 \text{ s}} \times 45 \text{ s} = \text{Necessary visitation rate}$$

To determine whether current visitation rates meet or exceed pollination thresholds, we compared mean female flower visitation rates observed during this study with the calculated 'visitation rate threshold' for each bee taxa.

Yield

Before averaging by transect, we calculated the mean, standard error, and range of each yield metric. We examined the effect of year on each yield metric using ANOVA, followed by pairwise comparisons of means using Tukey tests. We evaluated the relationship between seed set and pumpkin weight using regression. We measured the strength of linear relationships between the weight, circumference and length per pumpkin using Pearson's correlation implemented through 'Correlations Multivariate' in JMP Pro with significance reported at $\alpha = 0.01$. We used MANOVA to test for relationships between yield metrics and visitation rates of the three dominant bee taxa (*Bombus*, *Apis*, and *Eucera*) to each flower sex, using averaged yield metrics by transect within each field. Bee taxa that contributed significant effects were further examined with simple linear regression.

Results

Pollinator Community Composition

From a total of 844 collected specimens, 37 bee species were identified from 15 genera within 4 families (Table 1). The majority (78%) belonged to three species from the Apidae family: *Bombus impatiens* Cresson (Hymenoptera: Apidae) ($n = 349$, 41%), *Eucera (Peponapis)* ($n = 164$, 19%), and *Apis mellifera* ($n = 147$, 17%). While the majority of *Bombus* specimens were *B. impatiens* (94%), five additional species were encountered. To maintain accuracy, the term '*Bombus* spp.' is used in subsequent analyses. Most other collected pollinators were small green or black sweat bees. Most green sweat bees were a single species, *Augochlora pura*, while the small black bees were a mix of species, many from the *Lasioglossum* genus (Table 1).

Pollinator Activity Distribution

Over the course of the study, 10,436 visitation measures were taken (60 measures per transect × 4 transects per field × 2 dates per field × 24 fields – missing data) for a total observation time of ~130 h (45 s × 10,436 measures). After calculating an average per transect for each date for each field, analyses were performed on a sample size of 182 transects (4 transects per date × 2 dates per field × 24 fields – missing data). Between 68 and 553 male flowers were observed per transect (189.9 ± 7.12 SE) and 0–53 female flowers were observed per transect (8.9 ± 0.65 SE).

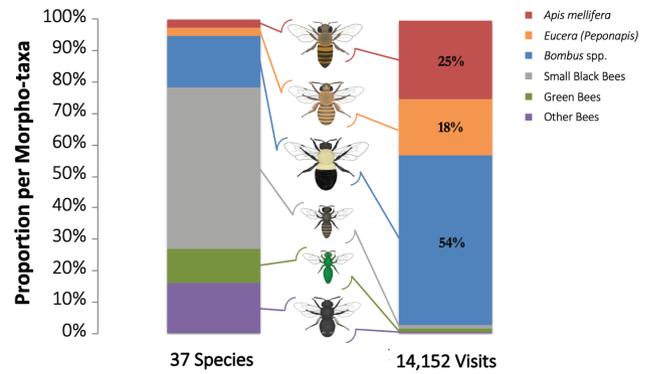


Fig. 2. Comparison of pollinator community composition and dominance distribution of pollination activity for the six morpho-taxa included in our study. While *A. mellifera*, *E. (Peponapis)* and *Bombus* spp. only accounted for 8 of the 37 species, they supplied 97% of all pollination visits. See Table 1 for bee species included in each morpho-taxon.

We recorded 14,152 bee visits to pumpkin flowers. Three taxa were responsible for 97% of all visits: *Bombus* spp. ($n = 7,690$, 54%), *A. mellifera* ($n = 3,482$, 25%), and *E. (Peponapis)* ($n = 2,577$, 18%) (Fig. 2). Small black and green sweat bees combined were responsible for 2.3% of all visits ($n = 332$), with all other visitors providing just 0.5% of pollination activity. Because *A. mellifera*, *Bombus* spp. and *E. (Peponapis)* were the most common pollinators in this study, subsequent analyses focus primarily on these three species.

Flower Sex Foraging Preferences

In total, 36,192 were observed, 95.51% of which were male ($n = 34,566$) and 4.49% of which were female ($n = 1,626$). Distance from field edge did not influence the distribution of male and female flowers observed ($\chi^2 = 1.37$, $P = 0.72$). The proportion of *A. mellifera* visits to female flowers was significantly greater than the proportion of female flowers observed for every distance from field edge (Fig. 3, 0 m: $\chi^2 = 349.1$, $P < 0.0001$; 25 m: $\chi^2 = 281.38$, $P < 0.0001$; 50 m: $\chi^2 = 173.1$, $P < 0.0001$, 100 m: $\chi^2 = 111.8$, $P < 0.0001$), but as distance from edge increased, proportion of *A. mellifera* female flower visits decreased from 22.5% at 0 m to 14.9% at 100 m from the edge. The proportion of *Bombus* spp. visits to female flowers also decreased as distance from field edge increased (0 m: 9%, 100 m: 4.5%) and female flower visits were only significantly greater than female flowers observed at 0, 25 and 50 m from field edge (Fig. 3, 0 m: $\chi^2 = 57.5$, $P < 0.0001$; 25 m: $\chi^2 = 12.7$, $P = 0.0004$; 50 m: $\chi^2 = 12.3$, $P < 0.0005$; 100 m: $\chi^2 = 0.003$, $P = 0.96$). The distribution of male and female flower visits for *E. (Peponapis)* never differed from the distribution of male and female flowers observed (Fig. 3, 0 m: $\chi^2 = 0.04$, $P = 0.84$; 25 m: $\chi^2 = 2.1$, $P = 0.15$; 50 m: $\chi^2 = 0.003$, $P = 0.96$; 100 m: $\chi^2 = 0.45$, $P = 0.48$).

Spatial, Temporal, and Floral Resource Effects on Visitation Rates

Bee taxa, flower sex, field area, distance from field edge, day of year, and male flower floral density all influenced visitation rates, either independently or when interacting with other factors (Table 2, $F = 21.86$; $df = 18$, 956; $P < 0.001$; $R^2 = 0.29$).

The interaction between bee taxa and flower sex in the overall model (Table 2), was supported with a two-way ANOVA on visitation rates, which showed significant effects of bee taxa, flower sex, and their interaction on visitation rates (Fig. 4, $F = 25.8$; $df = 5$,

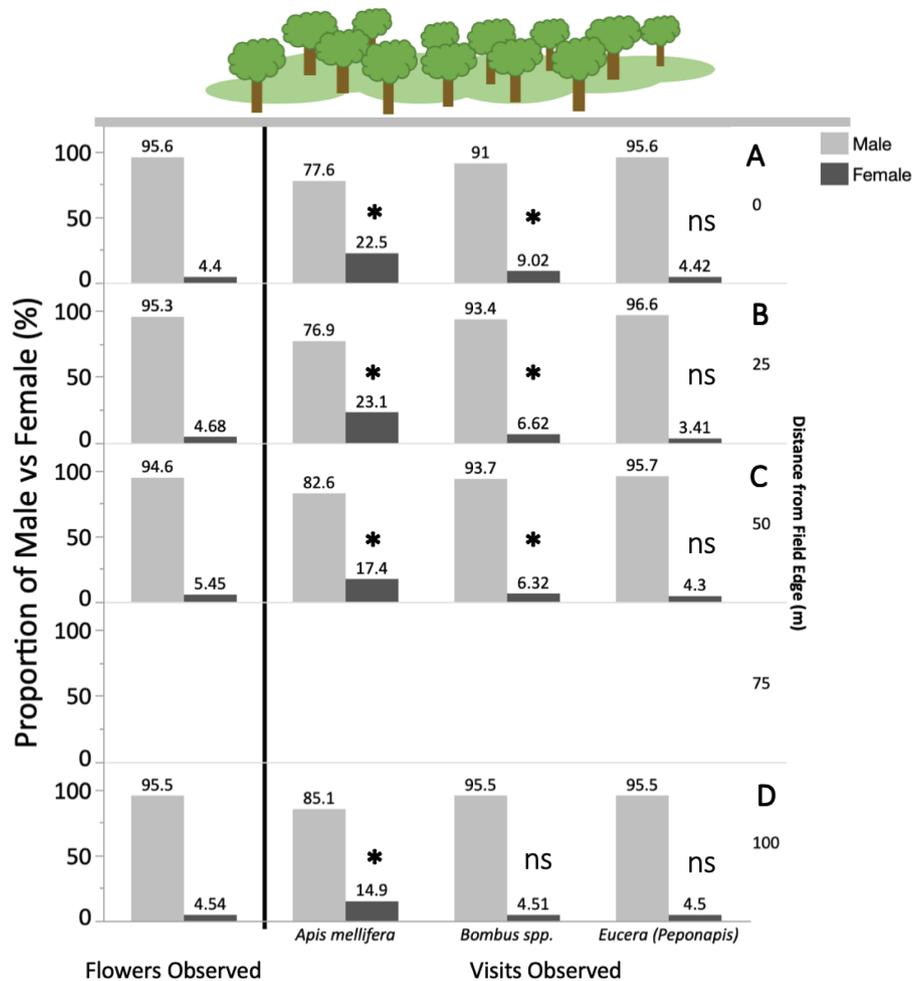


Fig. 3. For each distance from field edge (A) 0 m, (B) 25 m, (C) 50 m, and (D) 100 m, the distribution of male and female flowers observed (left of black line) is compared with the distribution of male and female flowers visits for *Apis mellifera*, *Bombus* spp., and *Eucera (Peponapis)* (right of the black line). Male flowers observed and male flower visits are light gray while female flowers observed and female flower visits are dark gray. After Bonferroni corrections, the proportion of female flowers visits is significantly higher than the proportion of female flowers observed when $P < 0.004$, indicated by an * for each taxa at each distance from field edge (m).

1029; $P < 0.0001$). On female flowers, visitation rates were highest for *A. mellifera*, followed by *Bombus*, and were lowest for *E. (Peponapis)*. On male flowers, however, visitation rates were highest for *Bombus*, and similar for *A. mellifera* and *E. (Peponapis)*.

Because of the three-way interaction between flower sex, bee taxa, and male flower floral density (Table 2), we examined the effects of floral density on visitation rates for each bee taxa to each flower sex separately. *Eucera (Peponapis)* visitation rates to male and female flowers, and *Bombus* spp. visitation rates to female flowers, were independent from male flower floral density ($P > 0.73, 0.38, 0.48$, respectively). However, male flower floral density had a positive relationship with *A. mellifera* visitation rates to both female (Fig. 5A, $F = 33.48$; $df = 1, 151$; $P < 0.0001$; $R^2 = 0.18$), and male flowers (Fig. 5B, $F = 42.16$; $df = 1, 170$; $P < 0.0001$; $R^2 = 0.19$) and as well as *Bombus* spp. visits to male flowers (Fig. 5C, $F = 35.63$; $df = 1, 170$; $P < 0.0001$; $R^2 = 0.09$).

Field area influenced visitation rates, but in different patterns for different bee taxa (e.g., bee taxa interacted with field area, Table 2); therefore, we examined the effect of field area on visitation rates for each bee taxa separately, using visitation rates pooled for both male and female flowers. *Apis mellifera* and *E. (Peponapis)* visitation

rates were independent from field area ($P > 0.28, 0.88$, respectively). However, although the relationship was weak, *Bombus* spp. visitation rates declined with increasing field area (Fig. 6, $F = 7.23$, $df = 1, 180$; $P = 0.0079$; $R^2 = 0.04$).

Not surprisingly, visitation rates varied seasonally, but it did so in different patterns for the different taxa, resulting in a two-way interaction between bee taxa and day of year (Table 2). We examined the effect of day of year on visitation rates for each bee taxa separately, again using rates combined from male and female flowers. *Eucera (Peponapis)* visitation rates were independent from day of year ($P > 0.52$). In contrast, as the season progressed, *A. mellifera* and *Bombus* spp visitation rates both exhibited a curvilinear response with significant quadratic terms (*A. mellifera*: Fig. 7A, $F = 18.89$; $df = 2, 179$; $P < 0.0001$; $R^2 = 0.17$; *Bombus* spp: Fig. 7 B, $F = 47.3$, $df = 2, 179$; $P < 0.0001$; $R^2 = 0.35$).

Distance from field edge was significant in the overall model and did not interact with either flower sex or bee taxa (Table 2). We pooled visitation rates across flower sex and bee taxa. Distance from field edge has a weak, negative relationship with visitation rates, only significant at $\alpha = 0.1$ (Fig. 8, $F = 2.72$; $df = 1, 180$; $P = 0.1$; $R^2 = 0.02$).

Table 2. Overall regression model testing the effect of bee taxa, flower sex, field area, day of year, distance-from-field-edge, and male flower floral density on visitation rates (bee visits/flower/45 s) in commercial pumpkin agroecosystems

Source/variable	df	Estimate	F	P	R
Overall model	18		21.86	<0.0001	0.29
Bee taxa	2		51.36	<0.0001	
Flower sex [^]	1		0.01	0.943	
Field area [^]	1	-0.012	0.64	0.4255	
Distance-from-field-edge	1	-0.005	14.64	0.0001	
Day of year	1	0.017	13.96	0.0002	
Male flower floral density per m2	1	0.19	59.39	<0.0001	
Bee taxa*Flower sex	2		23.91	<0.0001	
Bee taxa*Field area	2		4.47	0.0117	
Bee taxa*Day of year	2		56.58	<0.0001	
Bee taxa*Male flower floral density per m2	2		17.51	<0.0001	
Flower sex*Male flower floral density per m2	1		0.01	0.9315	
Flower sex*Bee taxa*Male flower floral density per m2	2		4.06	0.0175	

[^]Non-significant factors are significant in higher level interaction terms

Bold indicates significance at alpha = 0.05. Parameter estimates included for continuous variables. Non-significant interactions terms not shown.

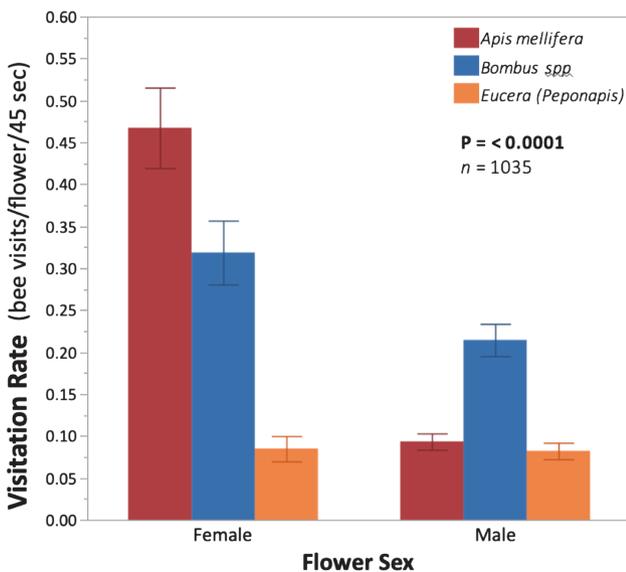


Fig. 4. Bee taxa and Flower sex significantly affected mean visitation rates (visits/flower/45 s) to pumpkin flowers. (All test statistics based on transformed data; $F = 25.8$; $df = 5, 1029$; $P < 0.0001$). Error bars are 1 SE from the mean.

Pollination Thresholds

Literature synthesis revealed a range of values (both within and among specific taxa) for necessary pollinator visits to achieve adequate *Cucurbita* yield (Table 3). We used the maximum visits published to set the most conservative ‘Total Visits Threshold’ for each species: 16 required visits for *A. mellifera*, 8 required visits for *B. impatiens*, and 16 for *E. (Peponapis)* (Table 3). In this study, each female flower received a mean total of ≈ 282.5 visits from all pollinators (male flower visits detailed in Supp Appendix C [online only]). Each species independently provided 1.7 \times to 12.75 \times of required pollination services, exceeding ‘pollination thresholds’ (Table 3).

Visitation Rates and Yield Metrics

Most yield metrics were stable across years: there were no differences in yearly means for fruit per square meter ($F = 0.01$; $df = 2$,

1036; $P = 0.94$), seed set ($F = 3.2$; $df = 1, 248$; $P = 0.07$), or length ($F = 0.26$; $df = 1, 247$; $P = 0.61$). Weight ($F = 87.4$; $df = 1, 1138$; $P \leq 0.0001$) and circumference ($F = 87.9$, $df = 2, 1138$; $P \leq 0.0001$), however, did vary among years. Weight was affected by seed set (Fig. 9, $F = 68.6$, $df = 1, 242$; $P < 0.0001$; $R^2 = 0.22$). These measurements per pumpkins were often correlated: weight was strongly correlated with circumference ($r = 0.92$, $P < 0.0001$) and length ($r = 0.78$, $P < 0.0001$), and length with circumference ($r = 0.75$, $P < 0.0001$). Because of these strong correlations among fruit measurements, only weight, the variable most often reported in NASS summary statistics and related papers, along with fruit per square meter and seed set, was selected for analysis of how visitation rate affected yield. Across all fields and years, visitation rates of the community of the three dominant bee taxa (*Bombus*, *Apis*, and *Eucera*) significantly influenced the yield metrics (fruit per square meter, weight, and seeds; MANOVA, Wilks’ Lambda = 0.179; $F = 3.04$; $df = 18, 65$; $P = 0.0005$). However, when considering each bee taxa and flower sex within this multivariate analysis of all yield metrics, the only visitation rates that retained significance were *Bombus* spp. visitation rate to female flowers retained significance ($F = 5.18$; $df = 3, 23$; $P = 0.007$) and *E. (Peponapis)* visitation rate to male flowers ($F = 3.8$; $df = 3, 23$; $P = 0.023$). Regression of *Bombus* spp. visitation rate female flowers for each yield metric separately resulted in significance only for weight (Fig. 10, $F = 6.49$; $df = 1, 68$; $P = 0.013$, $R^2 = 0.087$). Regression of *E. (Peponapis)* visitation rate to male flowers for each yield metric separately resulted in significance only for fruit per square meter (Fig. 11, $F = 9.54$; $df = 1, 50$; $P = 0.0033$, $R^2 = 0.16$)

Discussion

Pollinator Community Composition

Commercial *Cucurbita* agroecosystems in Pennsylvania supported a surprisingly high diversity of bee species ($n = 37$; Table 1); although most were not significantly contributing to pollination services based on the highly skewed dominance distribution (Fig. 2). On average, 7 species were found at each field, but species richness almost doubled at field 7 (13 species). Field 7, in Lancaster, PA, has a long history of no till agriculture and cover cropping (S. Groff, personal communication), which may support pollinators and account for the increase in species richness (Ullmann et al. 2016). Similar to previous studies, the three most abundant pollinators were *A. mellifera*, *B. impatiens*, and

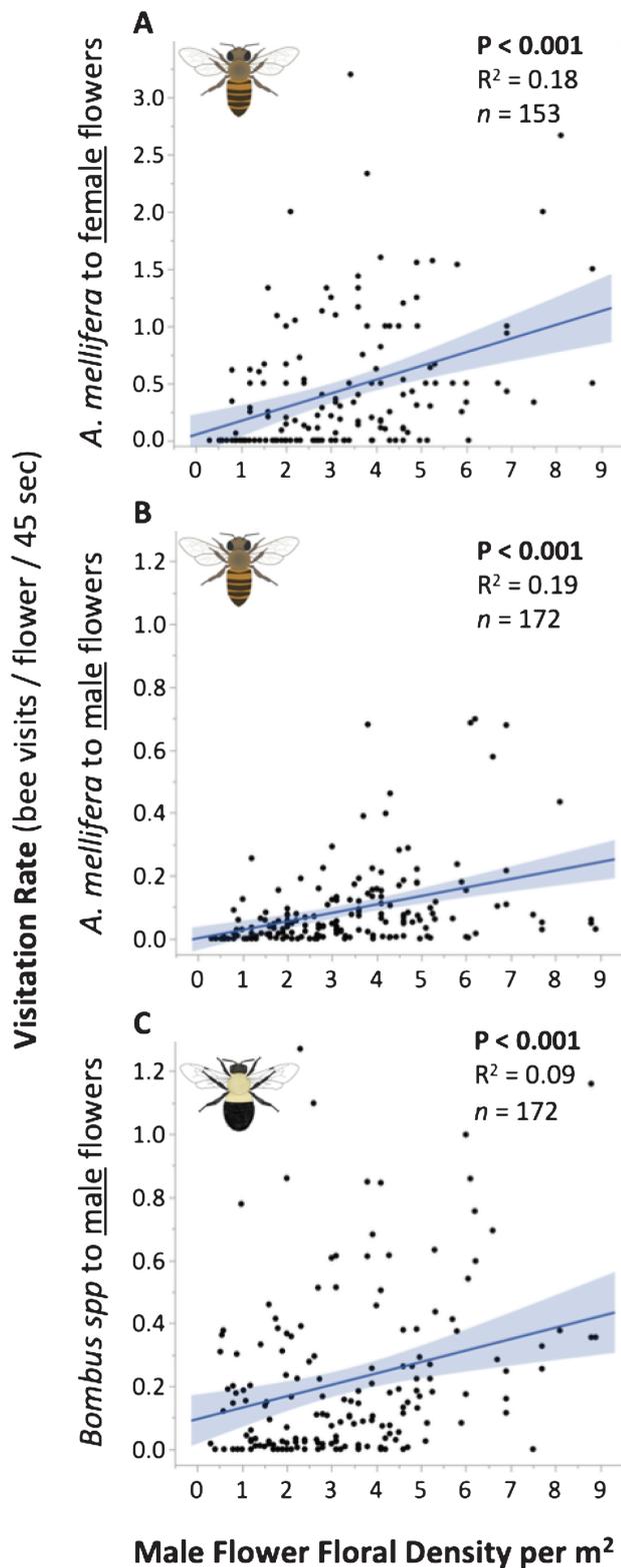


Fig. 5. Male flower floral density per m^2 positively affected *A. mellifera* visitation rates to (A) female and (B) male flowers, as well as (C) *Bombus* spp. visitation rates to male flowers. Each point represents a single mean per transect. The x-axis is uniform for all graphs. The y-axis is uniform per flower sex. The shaded region represents a 95% CI surrounding the regression line of fit (P and R^2 values based on $\text{Log}_e(Y+0.01)$).

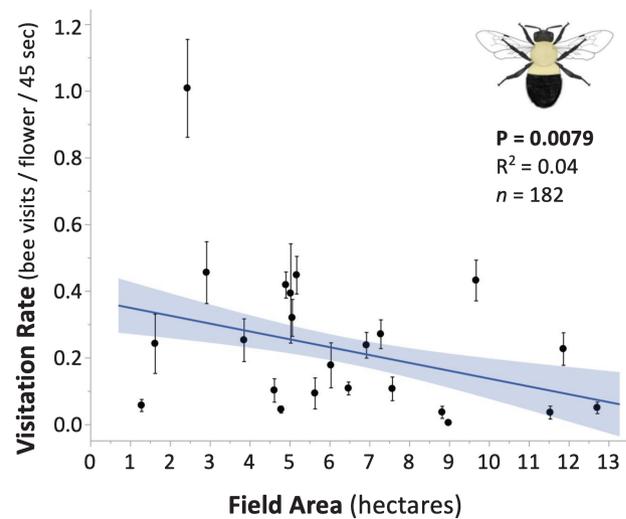


Fig. 6. Pumpkin field area negatively affected *Bombus* spp. visitation rates in commercial pumpkin fields. Each point represents the mean visitation rate for a given field area with error bars indicating 1 SE. The shaded region (blue) represents a 95% CI surrounding the regression line of fit (P and R^2 values based on $\text{Log}_e(Y+0.01)$).

E. (Peponapis) (Julier and Roulston 2009, Artz et al. 2011, Petersen et al. 2013, Phillips and Gardiner 2015). These were also among the largest in body size and thus expected to transfer more pollen per visit than the smaller species, such as the many *Lasioglossum* that we documented. Most previous studies have reported only a single *Bombus* species: *B. impatiens*, whereas we collected five additional species, albeit in low quantities. Several *Bombus* species collected are considered ‘uncommon’ including, *B. fervidus* Fabricius (Hymenoptera: Apidae) and *B. terricola* Kirby (Hymenoptera: Apidae), the latter of which is thought to be in decline throughout its range (Colla et al. 2011). At one site, we also collected *Tripeolus remigatus* Fabricius (Hymenoptera: Apidae), a kleptoparasite of *E. (Peponapis)* (Table 1). Within an ecological context, the presence of kleptoparasites indicates that primary consumer populations are robust enough to support a tertiary trophic level. In our case, the presence of *T. remigatus* suggests robust *E. (Peponapis)* populations.

Flower Sex Preferences and Spatial Patterns of Pollination Services

Similar to previous studies, we found that the proportion of *A. mellifera* and *Bombus* spp. visits to female flowers was 5× to 3× and up to 2× higher than the proportion of female flowers observed, respectively (Fig. 3A–D). Preference for female flowers supports the hypothesis that *A. mellifera* and *Bombus* spp. foragers were primarily nectar collecting (as reported in Artz et al. 2011), because female flowers have larger nectaries with greater volumes of and, under certain settings, a more concentrated nectar than male flowers. Nectar and pollen collecting behaviors were not measured in our study; nevertheless, most observers reported that both *A. mellifera* and *Bombus* spp. foragers were primarily nectar collecting when visiting either sex of pumpkin flowers, and *Bombus* spp. foragers were occasionally observed brushing pollen from their bodies, leaving behind bright bursts of orange pollen on the dark green pumpkin leaves. Pollen foraging may be limited due to fitness costs associated

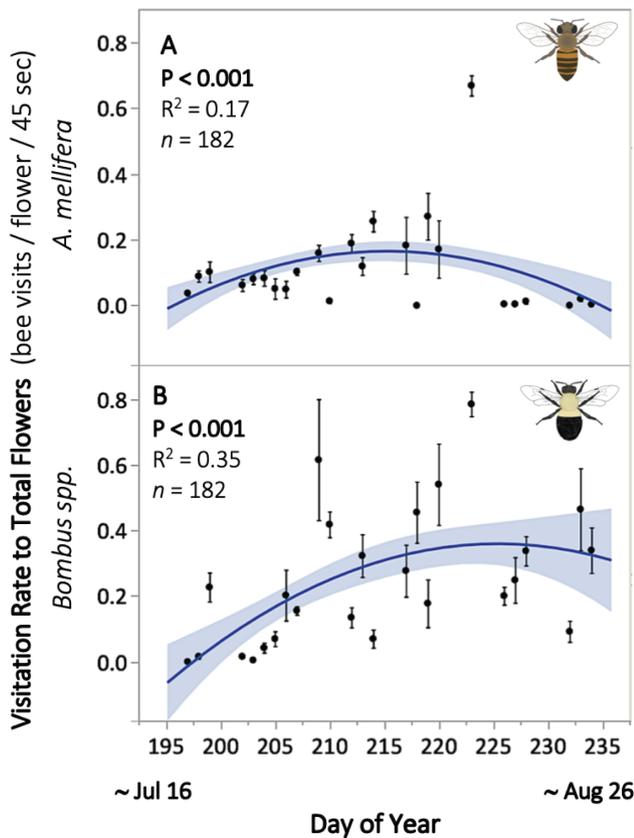


Figure 7. Visitation rates from (A) *A. mellifera* and (B) *Bombus* spp. exhibited a curvilinear response throughout the pumpkin floral bloom period. Data are summarized as a mean visitation rate for each day, surrounded by error bars indicating 1 SE. The shaded region (blue) represents a 95% CI surrounding the regression line of fit (P and R^2 based on $\text{Log}_e(Y + 0.01)$).

with consuming pumpkin pollen. In microcolony experiments, *B. impatiens* workers did ingest pumpkin pollen, but they lost weight compared with workers fed other diets (Treanore et al. 2019), perhaps due to toxic secondary plant compounds in pollen (Palmer-Young et al. 2019) or poor nutritional quality (Vaudo et al. 2016, Treanore et al. 2019).

However, we did find that preference for female flowers was affected by spatial patterns: as distance from field edge increased, preference for female flowers decreased for both pollinators (Fig. 3). This could be due in large part to plant structure and flower placement. Female flowers, located close to the ground, can be obscured by leafy vegetation. Pumpkin plants tend to get more lush and vegetative as distance from field edge increases – which could conceal female flowers and make female flower foraging more energy intensive. We noticed *Bombus* spp. foragers flying awkwardly through dense foliage, often bumping into spiky pumpkin stems when trying to reach flowers among thick vegetation. The much more numerous and easily accessible male flowers may have provided adequate nectar resources.

Unlike the other two taxa, *E. (Peponapis)* did not exhibit a flower sex preference (Fig. 3), possibly due to competition. Xie et al. (2016) found that bees foraging in *C. pepo* took longer to enter a flower after it was visited by individuals of a different species, compared with individuals of the same species, and Artz et al. (2011) reported *E. (Peponapis)* avoided entering flowers with other bee species. Also, flower sex preferences for *E. (Peponapis)* may depend on the sex of the *E. (Peponapis)* forager. *Eucera (Peponapis)* is a solitary pollinator and both male and

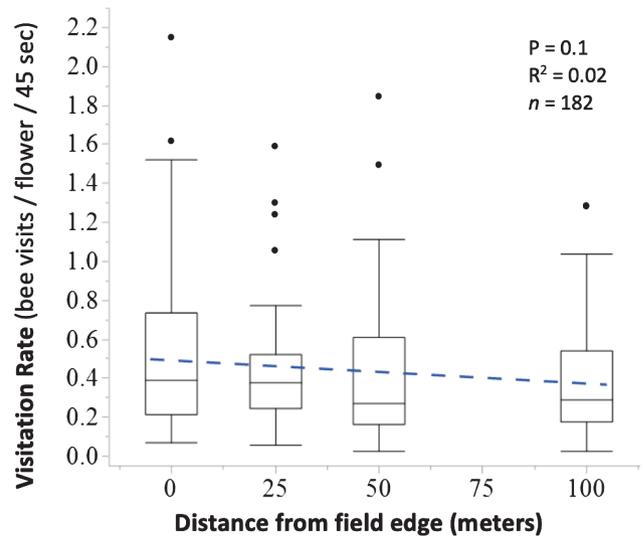


Fig. 8. Distance from field edge has a weak, negative relationship with visitation rates ($\alpha = 0.1$). Visitation rates are summarized for four distances as boxplots. The dotted line represents the nonsignificant line of fit for the regression (P and R^2 based on $\text{Log}_e(Y + 0.01)$).

females forage in pumpkin flowers. With no nests to provision, males are unlikely to be using pollen resources, but females use both nectar and pollen. Future studies should consider *E. (Peponapis)* male and female foragers separately when evaluating flower sex preference.

Overall, we found that visitation rates decreased as distance from the field edge increased; however, it was not a strong relationship (Fig. 8). Even with these spatial dynamics and foraging preferences at play, female flowers 100 m from the edge were visited at a relatively high rate (0.7 ± 0.11 SE bee per flower per 45 s). If decreasing visitation rates, particularly for female flowers, continues at distances >100 m from the edge, there could be a negative effect on production in certain field layouts. Any square field larger than 4 ha (200×200 m) or circle fields larger than 3.14 ha (100-m radius) could begin to experience yield issues toward the center. Cultivation practices in Pennsylvania, however, often follow contours in hilly landscapes, resulting in a large edge-to-area ratio. This agricultural practice, typically implemented by farmers for soil conservation goals, may be helping ensure pollination services in our agroecosystems. Future studies could map pollinator activity throughout entire fields (Fleischer et al. 1999) to gain a better understanding of taxa-specific movement through large floral resources and to predict where pollination services might be lacking within a field.

Temporal Dynamics of Pollination Services

Visitation rates across the season varied differently for each bee taxa. *A. mellifera* visitation rates peaked mid-season and were highest during the timeframe in which growers typically rent commercial hives (Fig. 7A), suggesting that most foragers were from managed, as opposed to feral, colonies, at or near a given field. *Bombus* spp. visitation rates, in contrast, increased throughout the season leveling out at the end of sampling (Fig. 7B), a pattern similar to Julier and Roulston (2009). Our grower collaborators did not stock commercial bumble bees. Instead, all *Bombus* spp. visitation rates were supplied by wild populations. The greatest number of *Bombus* colonies will be in early spring when over-wintering queens emerge and found colonies. Over time, colonies will fail due to lack of resources, parasitism, predation or disease and thus throughout the season, colony

Table 3. Visitation rate thresholds calculated using necessary number of pollinator visits per taxa to achieve optimal *Cucurbita* yield, synthesized from multiple studies

Pollinator Taxa	Citation	<i>Cucurbita</i> type	Fertilized ovarioles	Total pollen required	Pollen deposition per visit	Total visits threshold	Visitation rate threshold	Visitation rate observed	Total visits estimated
<i>Apis mellifera</i>	Nicodemo et al. 2009	<i>C. maxima</i> cv 'Exposição'	-	-	-	16	0.05 (1 every 15 min)	0.467 ± 0.05 (1 every 1m 36 s)	~150
	Vidal et al. 2010	<i>C. pepo</i> cv 'Howden'	500	1253 + 484	53 – 250e	12			
	Pfister, 2017	<i>C. maxima</i> cv 'hokkaido'	500	2500	582 ± 752e 260m	11			
<i>Bombus terrestris</i> , <i>lucorum</i> and <i>cryptarum</i>	Artz and Nault, 2011	<i>C. pepo</i> cv 'Mystic'	400–500	~1,360	70e	> 8			
<i>Bombus impatiens</i>	Pfister, 2017	<i>C. maxima</i> cv 'hokkaido'	500	2500	3368 ± 2473e 864m	2			
	Artz & Nault, 2011	<i>C. pepo</i> cv 'Mystic'	400–500	~1,360	170e	4–8	0.025 (1 every 30 min)	0.32 ± 0.04 (1 every 2 m 21 s)	~102
<i>Eucera (Peponapis)</i>	Cane et al. 2011	Variety of squash and zucchini	~ 225	-	-	7			
	Artz & Nault, 2011	<i>C. pepo</i> 'Mystic'	400–500	~ 1,360	~70e	> 8	0.05* (1 every 15 min)	0.0848 ± 0.02 (1 every 8 m 52 s)	~27
<i>Lasioglossum</i>	Pfister, 2017	<i>C. maxima</i> 'hokkaido'	500	2500	45 ± 76e 16 m	123			

'-' indicates data type not collected. Fertilized ovarioles indicate the necessary number to achieve optimal fruit set or weight; Total Pollen Required indicates the necessary number of grains deposited to fertilize ovarioles; Pollen Dep. per Visit indicates the average number of grains deposited during a single visit by each pollinator taxa, established through empirical observations (e) or modeling (m); Total Visits Threshold indicates the number of visits to each female flower needed to deposit sufficient pollen for optimal yield, with the maximum per taxa bolded; Visitation Rate Threshold indicates the necessary number of bee visits to a female flower every 45s to achieve the required number of visits within the 4 h flower lifetime with a calculated time interval between visits included below in parenthesis; visitation rate observed is the average bee visits to a female flower every 45 s documented in this study; total visits estimated is the calculated number of visits per female flower for each taxa, assuming a steady visitation rate across the 4 h flower lifetime.

*While there is no clear consensus from the literature regarding necessary visits for *E. (Peponapis)*, Artz and Nault 2011 found that *E. (Peponapis)* and *A. mellifera* deposited similar amounts of pollen per visit and that both species needed >8 visits, therefore, we used the conservatively high *A. mellifera* 'Total visits Threshold' of 16 from Nicodemo et al. 2009 to calculate the 'Visitation Rate Threshold' for *E. (Peponapis)*.

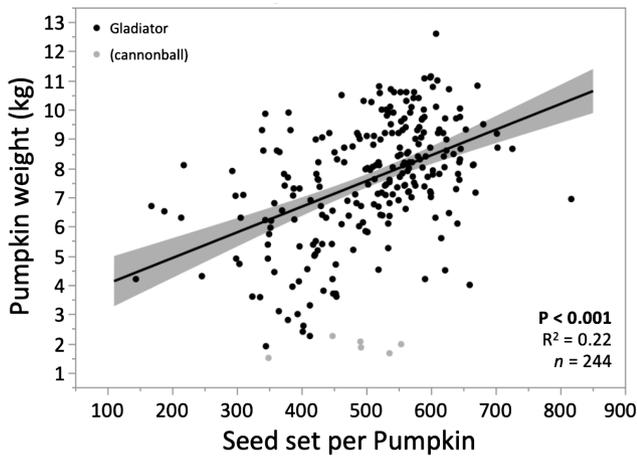


Figure 9. Seed set effects weight per *Cucurbita pepo* cv 'Gladiator' pumpkin. Each point represents a single pumpkin. *C. pepo* cv 'Cannonball' pumpkins are displayed (gray) but not included in analysis. Line of fit is surrounded by a shaded region representing 95% CIs.

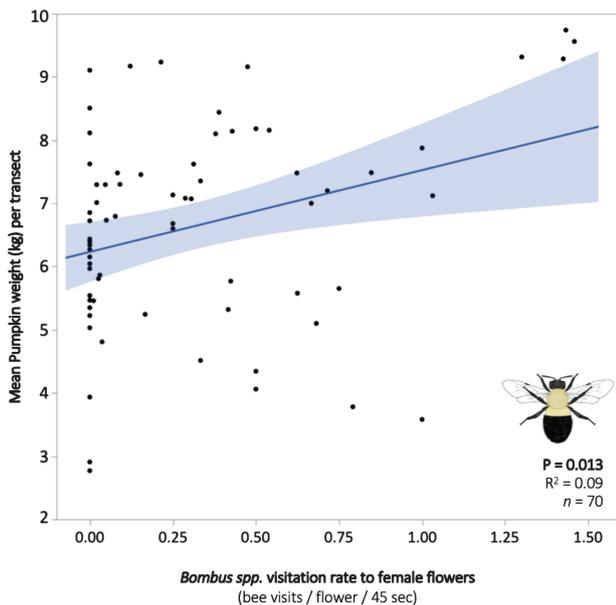


Fig. 10. Pumpkin weight was positively affected by *Bombus* spp. visitation rate to female flowers. Each point represents a single transect. The shaded region (blue) represents a 95% CI surrounding the regression line of fit (P and R^2 based on $\text{Log}_e(Y + 0.01)$).

numbers inevitably decrease (Goulson 2010). However, the colonies that persist grow in size as the queen continuously lays eggs and additional workers emerge. *Bombus impatiens*, the most common *Bombus* species in our study, is estimated to contain between 25 and 450 workers, the largest of which were reported later in the season (Plath 1934). Therefore, we believe that *Bombus* spp. visitation rates increased throughout the season due to the increasing colony size, rather than increasing numbers of colonies. If *Bombus* foragers originate from a few large colonies, pollination services could be vulnerable to the loss of a few key colonies. Future studies should estimate the abundance of common *Bombus* spp. colonies in this region to better understand the reliability of native pollinators. Seasonal patterns within the ~1 mo of bloom most relevant to wholesale production systems were not discernable for *E. (Peponapis)*.

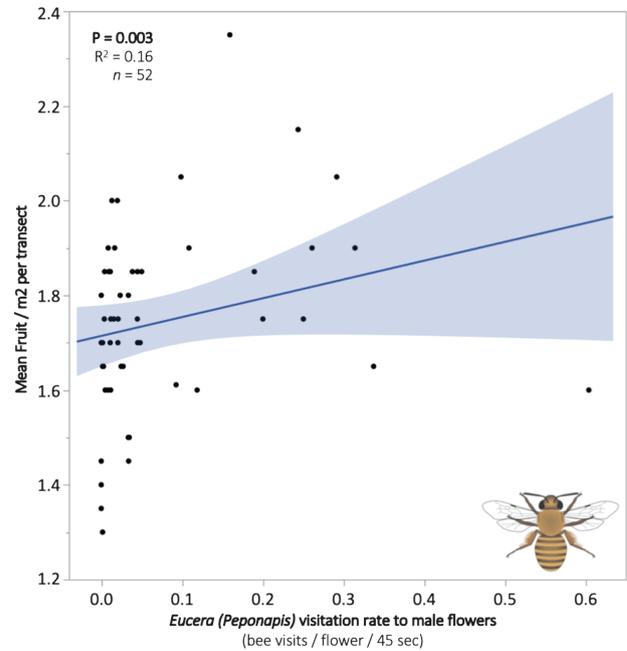


Fig. 11. Fruit per square meter was positively affected by *Eucera (Peponapis)* visitation rate to male flowers. Each point represents a single transect. The shaded region (blue) represents a 95% CI surrounding the regression line of fit (P and R^2 based on $\text{Log}_e(Y + 0.01)$).

Pollinator Response to Floral Resources

Both *A. mellifera* and *Bombus* spp. visitation rates increased with increasing male flower floral density (Fig. 5). This suggests *C. p. pepo* blooms act as a mass floral resource and attracts bee foragers (Westphal et al. 2003). Furthermore, it is interesting that male flower floral density also increased *A. mellifera* visitation rates to female flowers (Fig. 5). The idea of 'spillover' has often been studied in plant–pollinator interactions, where increased visitation rates to an attractive resource may cause insects to 'spill-over' into surrounding resources. In agricultural settings, planting wildflowers next to crops to increase crop pollination has been met with varying success. It is possible that pumpkin plants are employing a similar 'spill-over' strategy to increase visitation to female flowers with large displays of male flowers.

Increased visitation rates in response to increasing floral densities also suggests that pollinator populations in our current agroecosystems are large enough to keep up and even increase visitation rates in the face of additional flowers, as opposed to becoming diluted, suggesting an exciting possibility for native *Bombus* spp. populations to provide necessary levels of pollination services. *Eucera (Peponapis)* response to floral density was inconsistent in these larger, wholesale production fields.

Implications for Agricultural Production

Based on previous studies, we estimated that a female *Cucurbita* flower needs ~13.3 visits to achieve adequate pollination, given the pollination efficiency of our most active bee taxa (Table 3). If we assume a constant visitation rate during a 4-h window of a female flower being open, we estimate that each female flower received ~280 visits in a single morning (Table 3) to almost 20× what is required! A single female flower would have been visited ~150 times by *A. mellifera*, ~102 times by *Bombus* spp., and ~27 times by *E. (Peponapis)* (Table 3). Furthermore, we may have underestimated visitation rate by *E. (Peponapis)*, which tend to initiate activity very early in the morning.

Table 4. Overall and yearly means \pm SE for pumpkin yield metrics

Yield Metric	Overall	2013	2014	2015
Fruit per square meter <i>n</i> = 1,038	1.74 \pm 0.02 (1–5)	-	1.74 \pm 0.03	1.74 \pm 0.03
Weight (kg) <i>n</i> = 1,141	6.6 \pm 0.06 (1.5–13)	6.8 \pm 0.2 (A)	7.21 \pm 0.08 (A)	5.5 \pm 0.1 (B)
Circumference (cm) <i>n</i> = 1,141	87.5 \pm 0.33 (45.7–116.8)	86.5 \pm 1.1 (B)	91.1 \pm 0.4 (A)	82.1 \pm 0.53 (C)
Seed set <i>n</i> = 250	505.8 \pm 6.8 (144–817)	490.9 \pm 10.7	515.8 \pm 8.7	-
Length (cm) <i>n</i> = 249	25.7 \pm 0.2 (13.5–33)	24.8 \pm 0.3	25.6 \pm 0.27	-

The overall range is presented in parenthesis. Yearly means labeled with different letters per row are significantly different.
– indicates when data were not collected for a given year.

Although we recognize that visitation rates and style receptivity is not constant for the full time the flower is open, our data suggest that wild pollinators combined are providing the necessary pollination services for commercial pumpkins in Pennsylvania, potentially 15 \times the required visitation rate. Further work should consider site (e.g., farm)-specific variation, and how that might affect this conclusion. Excessive pollination services in *Cucurbita* agroecosystems have been reported previously. Phillips and Gardiner (2015) found female flowers received double the necessary pollen grains for *C. p. pepo* cv ‘Gladiator’ in Ohio, most of which was deposited before 800 EST. Pfister et al. (2017) used modeling to determine that only 11 and 7% of *Bombus* spp. and *A. mellifera* pollination activity, respectively, was necessary to adequately pollinate *C. maxima* cv ‘Hokkaido’ in Germany. Julier and Roulston (2009) reported 5.5 *E. (Peponapis)* and 3.1 *B. impatiens* foragers visiting *Cucurbita* flowers every minute. Additional studies have reported a single female flower receiving >100 *A. mellifera* visits, ~19 *Bombus* spp. visits, and ~5.5 *E. (Peponapis)* visits in a lifetime (Artz and Nault 2011, Pfister et al. 2017). Even so, pollination services supplied by wild bees in our study appear to be greater than surrounding areas. These differences could be artificial; simply a result of variation in the way different studies measured pollination services. For example, in our study, a single pollinator could supply multiple visits if it alighted and re-landed on the same flower. However, we believe our results represent actual differences in visitation rates, with our system experiencing substantially more visits (~5 \times) from wild bees than other systems because of larger wild bee populations. The cultivar used in our study, *C. p. pepo* cv ‘Gladiator’, produces a larger pumpkin than used in other studies (‘Mystic’ and ‘Hokkaido’) and therefore may also have larger flowers, able to accommodate more bees simultaneously or supply more resources per flower. Pennsylvania is also one of the leading states in no-till pumpkin agriculture (along with leading in no-till of many other crops), which has the potential to support much larger *E. (Peponapis)* populations (Shuler et al. 2005, Julier and Roulston 2009, Ullmann et al. 2016). Although many studies report intense wild bee activity, our work should encourage efforts to conduct context-specific research, even in closely related systems.

Our yield data supports the hypothesis that on average, current pollination services are sufficient to meet agricultural production objectives. Growers in our system are aiming for one to two pumpkins per square meter (B. Campbell, personal communication). On average, plants produced closer to 2 pumpkins per m² (1.74 \pm 0.03), and ranged up to 5 (Table 4), which was positively affected by *E. (Peponapis)* visits to male flowers (Fig. 11). Our growers were also able to produce pumpkins of sufficient size and weight. When growing

C. p. pepo cv ‘Gladiator’ for the wholesale market, growers are aiming for a diameter of 10–12 in. (25–30 cm), which requires a circumference of 78.5–94.5 cm. Pumpkins in our study met this objective with an average circumference of 87.5 \pm 0.33 cm (Table 4). Circumference was strongly correlated with weight (Table 4), which was positively affected by *Bombus* spp. visits to female flowers (Fig. 10). Seed set, fruit per square meter and pumpkin weight were related to the pooled visitation rates of the three dominant bee taxa. Interestingly, we were only able to distinguish positive relationships between wild bee visitation rates and yield metrics. Furthermore, we can anecdotally report that one grower collaborator decreased honey bee stocking rates from 1 to 0.5 hives per acre based on our preliminary results, and saw no negative effects on yield (B. Campbell, personal communication). Petersen et al. (2013) found no increases in visitation rates or yield when stocking pumpkin fields with managed bees in New York, and Julier and Roulston (2009) found native bee pollination activity was sufficient to pollinate *C. pepo* in Maryland and northern Virginia.

Conclusions

Although 37 bee species utilized resources in pumpkin fields, three taxa provided 97% of all visits. Managed *A. mellifera* accounted for roughly half (approximately every 1 m 36 s), *Bombus* spp. for one-third (approximately every 2 m 21 s), and *E. (Peponapis)* roughly 10% (approximately every 8 m 52 s) of the female flower visitation rates. Both managed *A. mellifera* and wild *Bombus* spp. demonstrated a preference for female flowers and responded positively to increasing floral resources. *Bombus* spp., (who deposit 3 \times –6 \times pollen grains per visit compared to *A. mellifera*), are likely providing a more valuable pollination services with less visits. On average *Bombus* spp. and *E. (Peponapis)* provided 12.75 \times and 1.7 \times , respectively, the necessary pollination services. Renting honey bee hives may be superfluous in this system. However, *Bombus* spp. visitation rates decreased as fields got larger and their preference for female flowers dropped as distance from field edge increased, suggesting that pollination from native bees may be limited in larger fields. Growers can test the sufficiency of native pollinators during the critical pollination time period (~55 d before harvest, depending on cultivar), by observing bee visits in female flowers. Assuming a 4-h bloom, if female flowers receive at least 1 *Bombus* spp. every 30 min or 1 *E. (Peponapis)* every 16 min, growers can expect that yield is not limited by pollination. Our results suggest that native bee populations can supply sufficient pollination services in commercial *Cucurbita* agroecosystems in Pennsylvania. Future studies should be aimed at understanding the abundance and resilience of native bee populations in this region to offer

growers a better sense of security when it comes to relying solely on native pollinators.

Supplementary Data

Supplementary data are available at *Journal of Economic Entomology* online.

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