THESIS

CULTIVAR-LEVEL VARIATION IN POLLINATOR ATTRACTION AND EFFECTIVENESS IN CHILE PEPPERS

Submitted by

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ABSTRACT

CULTIVAR-LEVEL VARIATION IN POLLINATOR ATTRACTION AND EFFECTIVENESS IN CHILE PEPPERS

Insect pollinators play a critical role in sustainable agriculture, enhancing crop yield and productivity. Their contributions, however, are commonly overlooked when growers select plant varieties to cultivate. Crop traits such as fruit production, disease resistance, and marketability are prioritized over attractiveness to pollinators, largely because cultivar-level differences in insect pollination and their relationship to yield are poorly documented. The goal of this research is to provide novel insights into the importance of cultivar selection in the context of pollination, encouraging a holistic and eco-friendly approach to farming that increases yield and profitability. The specific objectives of this study are to 1) quantify differences in pollinator attraction among fifteen chile pepper (*Capsicum annuum* L.) cultivars, 2) measure floral structures across cultivars to identify important plant traits that may correlate with pollinator attractiveness, and 3) determine whether variation in pollinator visitation affects yield. For this research, I conducted both field pollinator surveys and greenhouse pollination experiments to examine relationships between cultivar-level differences in pollinator visitation rates, floral morphology, and yield. Mean visits per flower per 15-minute observation period varied more than eight-fold across chile pepper cultivars, ranging from 0.049 visits per flower in Desperado to 0.397 visits per flower in Capperino. The number of flowers per plant was positively associated with floral visitation rate across the cultivars; 42% of the variation in visits per flower was explained by the number of

flowers per plant. To evaluate how floral morphology differed across cultivars, and how those traits might affect floral visitation, I measured corolla diameter, anther size, anther count, and style length from a subset of flowers from each cultivar. While all four morphological traits varied significantly across cultivars, none were correlated with floral visitation rate. For example, mean corolla diameter ranged from 13.65 mm to 21.86 mm across the cultivars but had no significant relationship with floral visitation rate. To estimate the effect of insect pollination on yield, I conducted flight cage experiments using six cultivars, in which half the plants from each cultivar were exposed to commercially reared bumblebees (*Bombus impatiens)*, and the remaining half were not. Average pepper mass was higher in bumblebee-pollinated plants for Charger (54%), Sweet Cherry (26%), and Capperino (12%). Average pepper mass was unaffected by bumblebee pollination for Big Jim, Mesilla, and Mosco. These findings suggest variation in the effect of insect-facilitated pollination on fruit mass across cultivars. In conclusion, pollinator attraction varies significantly among chile pepper cultivars—this variation is strongly influenced by the number of flowers per plant. The effect of insect pollination on yield, however, also varied across varieties. Growers can use these findings to improve their integrated pest and pollinator management (IPPM) strategies when managing their farms, as the yield in some cultivars appears to depend on pollinator visitation. Additionally, breeders can apply this research by selecting for increased flower count in future *C. annuum* cultivars.

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Introduction

Global food supplies are heavily reliant upon the ecosystem services provided by insects. Approximately 75% of cultivated crop species benefit from insect pollination; these pollinator-dependent crops represent ~35% of global crop production (Klein et al., 2007; Dicks et al., 2021). Growth of the human population is driving an ever-increasing demand for food, and flowering agricultural crops are being planted at an elevated rate to meet demand (van Dijk et al., 2021). As demand for pollination rises, environmental stressors including habitat loss, fragmentation, and agrochemicals contribute to pollinator population declines, potentially constraining future crop production (Potts et al., 2010; Rhodes, 2018). Effective pollination facilitates ovule fertilization within flowering plants, which enhances fruit size, quality and quantity (Samnegård et al., 2019) – traits that are desirable for agricultural productivity and marketability.

Studies that have documented the relationship between pollination efficiency and crop yield tend to focus on comparisons across crop species rather than variation among cultivars of the same crop (Greenop et al., 2023; Chabert et al., 2024; Harris & Ratnieks, 2026). Relatively few studies, however, have quantified the effects of cultivar identity on pollinator attraction and subsequent yield within the same crop species (Tscharntke et al., 2025). In a recent literature review, Harris and Ratnieks (2026) found that comparisons in pollinator attraction among varieties have been conducted for 25 crop species. Just over half of these studies found at least a two-fold difference in pollinator attraction. For example, Ceuppens et al. (2015) found a 2.05-fold difference in pollinator attraction among two varieties of strawberry and Garratt et al. (2016) found a 5.70-fold difference in pollinator attraction among four varieties of apple.

Variation in multiple floral traits may result in differences in pollinator attraction among varieties (Harris & Ratnieks, 2026). Flowering plants incentivize pollinator visitation with food rewards: pollen, which is rich in protein and lipids, and nectar, which is high in sugars (Nepi et al., 2018; Stephen et al., 2024), and these traits may vary among crop cultivars. For example, cultivars of pear and sunflower differ in the quantity of pollen produced and this variation is correlated with pollinator abundance (Quinet et al., 2016; Mallinger & Prasifka, 2017a). Likewise, cultivars of pear, sunflower, raspberry, and strawberry vary in nectar quantity and sugar concentration resulting in differences in pollinator visitation (Schmidt et al., 2015; Seo et al., 2019; Symington & Glover, 2024; Mallinger & Prasifka, 2017a). Plants also offer cues that attract pollinators to these rewards, including visual and olfactory stimuli. *Bombus terrestris* displayed an innate preference for genetic lines of *Vicia faba* with spotted flowers versus lines with non-spotted flowers (Bailes et al., 2023). Klatt et al. (2013) found that variation in floral VOC emissions influenced wild mason bee (*Osmia bicornis*) visitation across three strawberry cultivars (*Fragaria* × *ananassa*). Similarly, Zhang et al. (2025) used gas chromatography coupled with bumblebee (*Bombus lantschouensis*) choice tests in four tomato (*S. lycopersicum*) cultivars to find that bumblebees avoided the only cultivar with isophorone (a volatile ketone) in its floral scent profile. Flower density and floral morphology have also been shown to affect pollinator visitation among crop varieties (Wyatt, 1982). For example, Cromie et al. (2024) reported that flower density was an important predictor of pollinator visitation in 38 southern highbush blueberry (*Vaccinium corymbosum L.*) cultivars. Flower density has also been shown to affect pollinator attraction in red clover (Harris & Ratnieks, 2024), cowpea (Dingha et al., 2021), faba bean (Suso et al., 2001) and oilseed rape (Blažytė-Čereškienė et al., 2010). Flower morphology can also help explain differences in pollinator attraction among crop varieties.

Pollinator observations on 30 inbred lines showed that floret size was inversely associated with wild bee preference, with a reduction in floret length of 2 mm more than doubling pollinator activity (Portlas et al., 2018). In a study of four onion accessions, Soto et al. (2013) found that style length was negatively correlated with bee preference. These findings suggest that cultivar-level variation in pollinator attraction may be more widespread than previously believed.

Even fewer studies have documented variation among cultivars in the effect of insect pollination on yield (Tscharntke et al., 2025). A couple of studies have investigated differential effects of insect pollination on the yield of sunflowers. Mallinger and Prasifka (2017b), showed that across 15 sunflower hybrids, open pollination increased total seed mass by 26% on average compared with pollinator-excluded flowers. However, only five of the hybrids showed significant increases in total seed mass, ranging from 39 to 108%, while the other 10 hybrids showed no effect of insect pollination on yield (Mallinger & Prasifka, 2017b). DeGrandi-Hoffman and Chambers (2006) evaluated the effect of honey bee pollination on yield across ten cultivars and found no differences among the cultivars. Martin et al. (2019) quantified differences in bumblebee pollination and its effect on yield in three varieties of strawberries. They found that the presence of commercial bumblebees increased the amount of high commercial grade fruit produced by one variety by 25%. In contrast, no benefit of commercial bees on fruit quality was observed in the other two varieties. Likewise, Eeraerts et al. (2024) reported variation in pollination deficits across two cultivars of highbush blueberry, with one cultivar showing significant differences in berry weight between open pollination and hand pollination treatments, while the other did not. These inconsistent findings emphasize the need to further investigate the effects of pollination on yield across a broad range of cultivars.

Chile Peppers

Chile pepper (*Capsicum annuum* L., Solanaceae) is a warm season crop that grows optimally between 20–30°C and performs well in hot, arid climates when properly irrigated (Walters & Jha, 2016; Khaitov et al., 2019). The crop has an estimated annual global market value of USD 1.3 billion (Ali et al., 2025). Selective breeding has diversified this pepper species into a multitude of cultivars; there are approximately 3,400 documented accessions of *C. annuum* in the USDA germplasm bank (U.S. Department of Agriculture, 2017). These cultivars are grouped into agronomic types, such as cherry, New Mexican (many of which are Anaheim), jalapeño, and serrano—each of which differs in general fruit morphology, including shape, size, and color (Pickersgill, 1997; Barboza et al., 2022). Chile pepper pericarp (fruit wall) thickness also varies among cultivars and is agriculturally important, as it influences post-harvest water loss rates; fruits with thicker pericarp dehydrate more slowly, affecting marketability (Pessoa et al., 2023). In addition to being morphologically diverse, *C. annuum* also exhibits cultivar-level variation in disease resistance. An example of this is seen in alfalfa mosaic virus (AMV; *Bromoviridae*: *Alfamovirus*), an aphid-vectored, non-persistently transmitted virus that causes plant abnormalities and infects over 430 plant species, including *C. annuum* (Trucco et al., 2022). Upon inoculating 20 chile pepper cultivars (*Capsicum* spp.) with AMV, Amiri-Kazaz et al. (2025) found variation in symptom severity and disease incidence across cultivars. Some cultivars, including Mosco, showed significantly lower disease incidence and symptom severity than susceptible cultivars such as Joe Parker. Notably, Desperado exhibited relatively high disease incidence but was largely asymptomatic, suggesting that some cultivars are more tolerant to AMV than others (Amiri-Kazaz et al., 2025).

In chile pepper, pollen, which is essential for crop reproduction, is also collected by pollinators as a food source (Chauhan & Imtinaro, 2024). Das et al. (2025) reported chile pepper (*Capsicum* spp.) producing approximately 47,200–59,700 pollen grains per flower, depending on cultivar. Nectar is also produced by *C. annuum* and contains fructose and glucose (Rabinowitch et al., 1993). Some evidence suggests that the frequency of floral visitation in chile pepper is influenced by nectar sugar content. Rabinowitch et al. (1993) documented a positive correlation between honey bee visits and nectar sugar quantity across seven genotypes of *C. annuum*.

Chile Peppers in Colorado

Chile pepper cultivar types have been selectively bred for different culinary applications, such as hot sauce, salsa, spices, and stuffing (Tripodi & Kumar, 2019; Barboza et al., 2022). These uses are important in Colorado, where chile pepper is a specialty crop worth approximately 2 million USD annually, grown on ~222 hectares statewide (Colorado State University Agricultural Biology, 2024). In southeast Colorado, where the weather is optimal for chile pepper production, many growers want to know if their chile peppers are receiving adequate insect pollination, and how to boost it if not. This research investigates which chile pepper cultivars attract the most pollinators and how that attraction affects yield.

Chile Pepper Flowers

Chile pepper flowers are hermaphroditic, enabling them to set viable fruit via self-pollination (Raw, 2000). Some studies, however, suggest that chile peppers benefit from insect pollination, and supplementation is frequently recommended in greenhouse-grown peppers. For example, Putra et al. (2016) reported a 66% increase in total fruit mass in insect-pollinated chile peppers. Similarly, a study conducted by Nasrin et al. (2021) reported heavier fruits and a higher

number of fruits per plant in open-pollinated chile peppers, resulting in ~10% higher total fruit mass compared to plants excluded from insect pollination via netting. In chile pepper flowers, anthers dehisce along longitudinal slits, allowing pollen to be accessible by a broad range of pollinator taxa (Barboza et al., 2022). In contrast, many other solanaceous crops, such as eggplant and tomato, have functionally poricidal anthers, in which pollen is restricted by an apical pore (Carrizo García et al., 2008; Campos et al., 2022). Poricidal anthers are specialized for pollen release via sonication—a behavior predominantly exhibited by bumblebees (*Bombus spp.*), making these crops often reliant on bumblebee pollination (Campos et al., 2022; Vallejo-Marín & Russell, 2024). These morphological differences in anther dehiscence are illustrated in Figure 1.

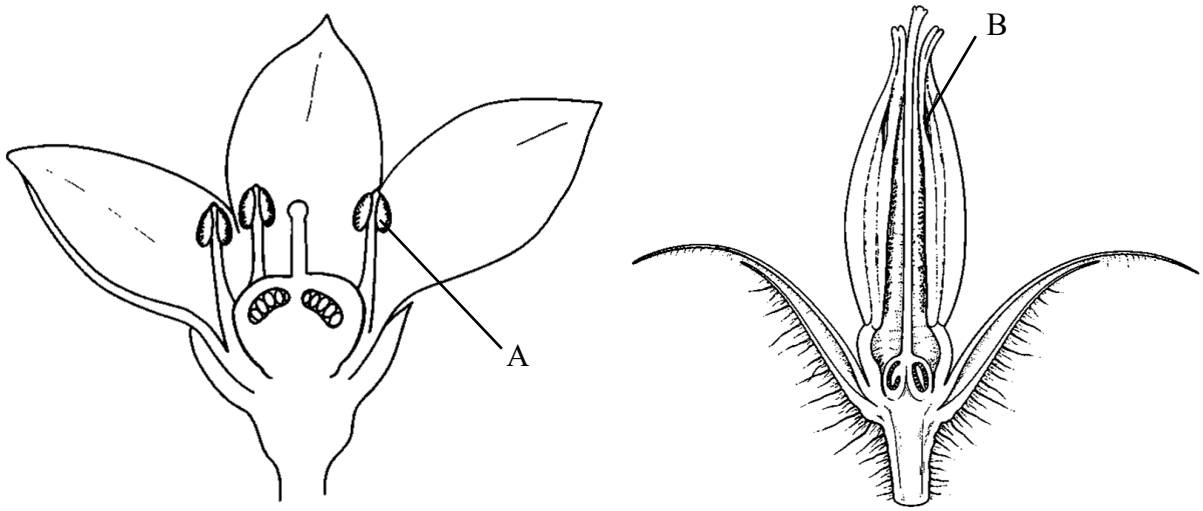

Figure 1. Visual representation of the longitudinally dehiscent anthers of a chile pepper (*C. annuum*) flower (A) and the poricidal anthers of a tomato (*Solanum lycopersicum*) with its restrictive apical pores (B). Images adapted from Rabinowitch et al. (1993; Fig. 1) and Free (1993, Fig. 184).

Pollinators

C. annuum flowers are commonly visited by a diverse set of bee species, including sweat bees (e.g. *Agapostemon, Lasioglossum*, and *Semiaerinus* spp., Halictidae), stingless bees

(*Tetragonula spp*., Apidae), honey bees (*Apis mellifera* L., Apidae), and bumblebees (*Bombus* spp., Apidae) (Raw, 2000; Putra et al., 2016; Aminatun et al., 2019; Nasrin et al., 2021; Chauhan & Imtinaro, 2024). For example, Chauhan & Imtinaro (2024) examined the effects of open pollination on yield in *C. annuum* and reported 11 insect species visiting the chile pepper flowers, including *Semiaerinus* sp., *Tetragonula spp.*, and syrphid flies. Their study found ~9% higher fruit set in chile pepper plants that were open-pollinated compared to plants excluded from pollination. Chauhan & Imtinaro (2024) did not report cultivar identity or indicate the use of multiple cultivars.

Although relatively few in number, these studies indicate that floral traits associated with pollinator visitation are likely to vary among many crop cultivars, and that the effect of insect pollination on yield is also likely to vary among cultivars. Thus, the primary objectives of this project are to (1) quantify floral visitation rates across 15 *Capsicum annuum* pepper cultivars, (2) measure floral traits to identify correlations with visitation, and (3) evaluate how differences in visitation across cultivars are associated with yield.

Materials and Methods

Cultivars and Seeding

Fifteen *C. annuum* cultivars were chosen based on their availability and popularity among chile pepper growers in Colorado. Most seeds were sourced from commercial distributors: Johnny's Selected Seeds (JSS; Winslow, Maine, USA), Pepper Joe's (PJ; Myrtle Beach, South Carolina, USA), and Holmes Seed Company (HSC; Canton, Ohio, USA). Seeds for Potosi, Pueblo Primrose, and Mosco were provided by the Colorado State University Arkansas Valley Research Center (AVRC; Rocky Ford, Colorado, USA).

The cultivars included in this study represent a broad range of pepper types, each with their own distinct characteristics, including cherry, New Mexican, serrano, jalapeño, and banana type peppers. Cherry peppers are characterized by their distinct spherical shape, relatively small size, and thick pericarp. Serrano and jalapeño type peppers are generally small and cylindrical, with moderately thick pericarp. New Mexican and banana peppers are typically larger, elongated, and have relatively thin pericarp.

Figure 2. Photos of each *C. annuum* cultivar, from the field. Photo credit: Jeff Davidson, CSU.

Table 1. Cultivar characteristics and sources. Days to harvest were obtained from descriptions provided by their respective seed suppliers. Typical harvest windows vary among cultivars, as some are harvested during green stages and others at full maturity (red). Cultivars are ordered alphabetically by type.

Cultivar	Type	Days to Harvest	Supplier
Fury	Banana	55–65	HSC
Sweet Sunset	Banana	80–89	PJ
Capperino	Cherry	80–89	JSS
Sweet Cherry	Cherry	70–79	PJ
Pueblo Primrose	Cherry (Ornamental)	70–79	AVRC
Jalapeño	Jalapeño	75–85	JSS
Big Jim	New Mexican	70–79	PJ
Charger	New Mexican	80–89	JSS
Desperado	New Mexican	60–70	HSC
Mesilla	New Mexican	62–72	HSC
Mirasol	New Mexican	80–89	PJ
Mosco	New Mexican	70–79	AVRC
Spitfire	New Mexican	80–89	JSS
Altiplano	Serrano	72–82	JSS
Potosi	Serrano	70–79	AVRC

Seeds from each of the chile pepper cultivars were sown in 2.5 × 2.5 cm plug trays and kept in a greenhouse to germinate. Trays were bottom watered daily, or twice a day if conditions were especially hot and dry. The seeding of each block's chile peppers was staggered by two weeks to extend the window of flower availability for observation throughout the growing season, as individual chile pepper flowers stay open for approximately 3–4 days following anthesis (Aleemullah et al., 2000). Block 1 seeding began March 24, 2025; Block 2 began April 7, 2025; and Block 3 began April 21, 2025. Cultivars with relatively faster germination periods (Potosi, Mesilla, Sweet Sunset, Big Jim, and Mosco) were seeded two days prior to the remaining cultivars (Fury, Desperado, Charger, Capperino, Jalapeño, Altiplano, Spitfire, Sweet

Cherry, Mirasol, Pueblo Primrose). Germination timing was determined from observations during the previous growing season's chile pepper experiments. All plants were transplanted to the field on May 23, 2025.

Field Experiment

96 *C. annuum* plants from each of the 15 cultivars were planted in a randomized complete block design in Otero County, Colorado, at the Arkansas Valley Research Center, (38.0387° N, 103.6930° W), United States. Three blocks were established, each containing four replicated rows of eight plants per cultivar. In each replicate, a single row from every cultivar was randomly arranged in three columns of five. Adjacent replicates were spaced approximately 1.8 m apart. Rows within each replicate were spaced 76 cm apart from each other. Plants within each row were separated by 30 cm. This design allowed researchers to simultaneously observe floral visitation from either side of the column. After the *C. annuum* plants were transplanted, liquid urea ammonium nitrate (UAN; 32-0-0) was applied once at 234 L/ha (99 kg N/ha), prior to transplanting. Weeds were removed by hand three times throughout the growing season.

Pollinator Survey

Floral visitation surveys were conducted between July 2 and August 6, 2025. Immediately prior to each observation period, the number of flowers on each plant was counted to estimate the number of visits per flower. Field surveys were conducted with two researchers positioned on opposite sides of a single column of plants (5 rows of 8 plants) at a time, for 15-minute intervals, between 8:00 AM and 12:00 PM (sensu Rabinowitch et al., 1993; Fijen & Kleijn, 2017). Twenty observation periods were conducted per cultivar during the growing season. Each plant in Block 1 was observed once during the growing season, while plants in

Blocks 2 and 3 were observed twice during the growing season. This sampling design maximized the number of observations of plants within each cultivar, rather than repeated observations of individual plants. Throughout each observation period, all floral visitors and their respective taxa were tallied for each individual chile pepper plant. Representative floral visitor specimens were sampled and identified to genus when possible, using dichotomous keys and other taxonomic resources (Miranda et al., 2013; Skevington et al., 2019; Carril & Wilson, 2023). The visit per flower metric was calculated as the number of floral visits recorded during each 15-minute observation period divided by the number of open flowers on that plant; this metric controls for differences in flower number across plants. Floral visitors were defined as insects that directly contacted the adaxial surface of the corolla of a chile pepper flower for any duration. Following each observation period, the two researchers rotated to the adjacent eastward column of chile pepper plants for the next observation period, effectively randomizing the time of day for floral visitation observations across the cultivars due to the randomized complete block design.

Floral Measurements

Once all plants in Block 1 had been observed, 15 flowers, sampled from at least five plants per cultivar, were randomly picked for floral trait measurements. Block 1 was then excluded from further pollinator observations because floral abundance had been altered. The fifteen flowers from each cultivar were used to measure the following floral traits: corolla diameter, anther length, anther width, anther count, and style length. Because anthers are irregular in shape, anther size index was used to approximate anther size and was calculated as maximum anther length × maximum anther width. Style length was measured from the top of the ovary to the tip of the stigma. Each of these morphological traits were measured using a digital

handheld caliper. Plants that had flowers picked were not observed in pollinator activity surveys again.

Enclosed Bumblebee Pollination Experiment

To estimate the effect of bumblebee pollination on yield, 19 seeds from Charger and Mesilla were sown in plug trays and placed into a germination chamber on August 23, 2024; these cultivars were chosen based on their relatively high floral visitation observed in preliminary trials during the previous growing season. On September 20, seedlings were transplanted into 10-cm pots, maintained in insect-netted enclosures inside a greenhouse. On October 25, three of the plants from each cultivar (n = 3 per cultivar) were arranged outdoors on flat grass in a 2.44 × 1.22 × 1.83 m mesh cage. A commercially sourced *Bombus impatiens* colony was situated in the center of the cage (Natupol®, Koppert Biological Systems, Howell, MI, USA). *B. impatiens* was used because commercially reared colonies are available and are used in greenhouse pepper production (Shipp et al., 1994). Between 1:30–3:00 PM, three researchers observed the plants to assess pollinator activity. At 1:30 PM, 15 bees were released from the colony, and at 2:15 PM an additional 15 bees were released (total = 30 bees). Following the pollination treatment, all chile pepper plants were returned to the insect-netted enclosures inside the greenhouse until fruits reached maturity. Yield metrics began on December 2, when the first peppers began to change color; fruit mass was recorded for both insect-pollinated chile pepper plants and pollinator-excluded plants.

To further investigate the effects of bumblebee pollination on yield across chile pepper cultivars, a second pollination experiment was initiated in December 2025 using similar methods to the 2024 experiment. On December 12, thirty seeds from each of the following cultivars were sown in plug trays and placed into a germination chamber: Big Jim, Capperino, Mosco, Mesilla,

and Sweet Cherry. These cultivars were chosen based on their differences in floral visitation during the 2025 field experiment. On January 8, seedlings were transplanted into 3.8-L pots and maintained inside a greenhouse under Barrina T8 42-W LED grow lights.

A single cultivar was evaluated at a time. Beginning March 4, as Capperino flowers began to bloom, 15 Capperino plants were arranged on a bench inside a bio-controlled greenhouse. Each plant was separated by ~25 cm inside a 2.44 × 1.22 × 1.83 m mesh cage. A commercially sourced *B. impatiens* colony was situated in the center of the cage (Natupol®, Koppert Biological Systems, Howell, MI, USA). Before bees were released, hemp string was used to tie a small knot on the stem of three flowers from each plant to track flowers that were open during the treatment period. After flowers were marked, twelve bees were released from the colony at 9:00 AM and foraged freely until 1:00 PM; researchers observed the plants to confirm pollinator activity. Following the pollination treatment, all chile pepper plants were returned to the primary greenhouse bench. The following day, the remaining 15 Capperino plants were placed in the mesh cage in the bio-controlled greenhouse for the same duration, without exposure to *B. impatiens*. The same hemp string procedure was used for these pollinator-excluded plants to track flowers consistently between treatments. This process was repeated on March 11 for Mesilla, March 17 for Sweet Cherry, March 25 for Big Jim, and March 30 for Mosco.

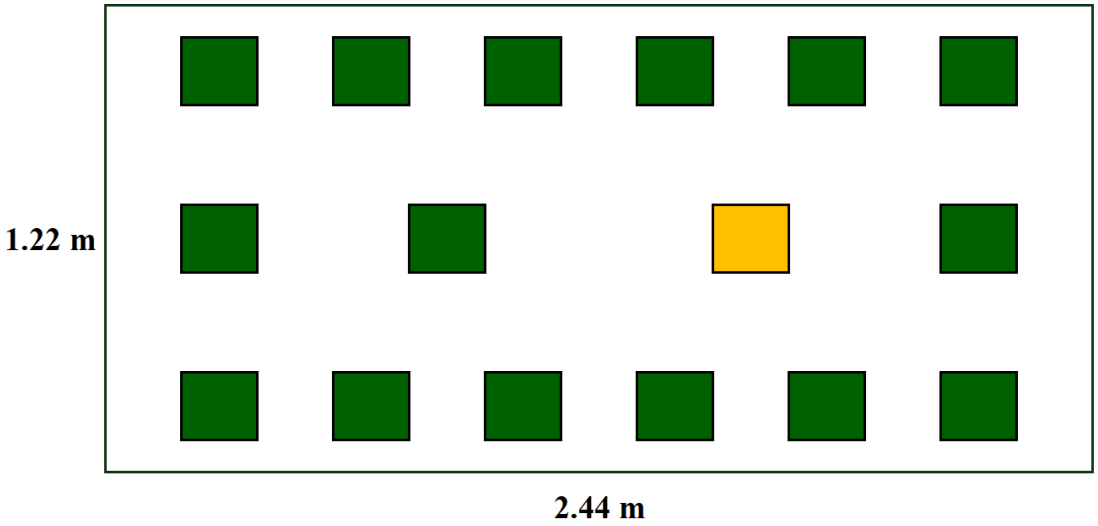

Figure 3. Top-down view of the arrangement of the chile pepper plants and *B. impatiens* colony inside the mesh flight cage used for the greenhouse pollination experiment. Green squares represent individual plants, and the yellow square represents the bee colony. Adjacent plants were spaced approximately 25 cm apart.

To test the effect of *B. impatiens* pollination on fruit number and fruit mass within cultivars, I counted the total number of fruits on each pollinated and pollinator-excluded plant when peppers began to change color, approximately 1.5 months after *B. impatiens* exposure. I also weighed three peppers from each plant within three days of harvest. Capperino plants were harvested on April 17, Mesilla on April 21, Sweet Cherry on April 27, Big Jim on May 12, and Mosco on May 13.

Data Analysis

Statistical analyses in this study were conducted using R version 4.5.0 (R Core Team, 2025). Variation in floral count among cultivars was analyzed using raw visitation data and a one-way ANOVA. Cultivar-level variation in visits per flower was analyzed using ANCOVA, with cultivar as the main factor and number of flowers as a covariate. Cultivar-level variation in

corolla diameter, anther size index, anther count, and style length was analyzed using separate one-way ANOVAs. Separate linear regressions were used to examine whether flower count, corolla diameter, anther size index, anther count, and style length predicted variation in visits per flower. Pollinator composition across cultivars was analyzed using a chi-square test. I conducted separate linear regressions to assess the relationship between the proportion of Lasioglossum visits and each of the measured floral traits. Because floral visitor taxon proportions add up to 100% within each cultivar, proportions were not treated as independent measures. For the linear regression analyses, the proportion of Lasioglossum visits was arcsine-square-root transformed. This taxon was used because it was the dominant floral visitor across all cultivars. Differences in fruit number and fruit mass between pollinated and pollinator-excluded plants were analyzed using two-sample t-tests. A two-way ANOVA was used to test whether the effect of *B. impatiens* exposure on fruit mass differed across cultivars, including cultivar, pollination treatment, and their interaction. A linear regression was used to test whether field visits per flower across the six cultivars used in the enclosed pollination experiment were associated with differences in fruit mass following *B. impatiens* exposure.

Results

Table 2. Mean visits per flower per 15-minute observation period (± 95% CI), mean flowers per plant, and residual visits per flower from the regression of visits per flower on mean flowers per plant. Sample size (n) indicates the number of plant-level observations included across the pollinator survey. Plants without open flowers were excluded from these analyses. Cultivars are ordered by descending mean visits per flower observed in the pollinator survey, from top to bottom.

Cultivar	Mean Visits per Flower	Residual Visits per Flower	Mean Flowers per Plant	n
Capperino	0.397 ± 0.111	+0.123	5.01 ± 0.62	140
Mesilla	0.320 ± 0.157	+0.116	4.02 ± 0.60	104
Altiplano	0.291 ± 0.107	−0.005	5.31 ± 0.75	134
Pueblo Primrose	0.290 ± 0.102	−0.042	5.82 ± 0.75	130
Potosi	0.288 ± 0.106	+0.036	4.69 ± 0.70	121
Jalapeño	0.242 ± 0.163	+0.118	2.90 ± 0.35	114
Spitfire	0.202 ± 0.104	+0.056	3.21 ± 0.44	101
Charger	0.164 ± 0.098	+0.054	2.71 ± 0.42	91
Mosco	0.133 ± 0.084	−0.005	3.10 ± 0.48	97
Sweet Sunset	0.126 ± 0.070	−0.013	3.12 ± 0.48	100
Fury	0.122 ± 0.052	−0.034	3.36 ± 0.51	107
Mirasol	0.067 ± 0.048	−0.068	3.06 ± 0.51	110
Sweet Cherry	0.060 ± 0.038	−0.166	4.34 ± 0.64	110
Big Jim	0.058 ± 0.032	−0.111	3.54 ± 0.49	102
Desperado	0.049 ± 0.033	−0.058	2.67 ± 0.38	99

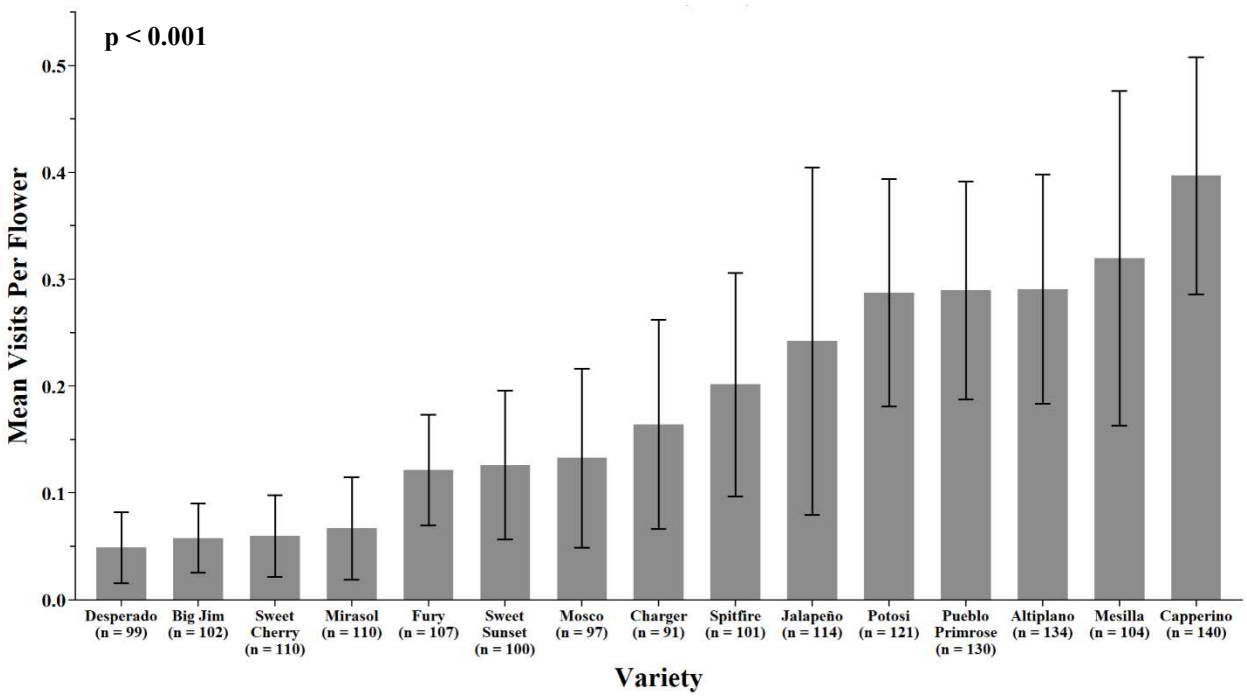

Figure 4. Mean visits per flower per 15-minute observation period (± 95% CI) across the 15 *C. annuum* cultivars.

The number of flowers per plant varied significantly among the cultivars (one-way ANOVA: $F_{14,1644} = 12.59$, $p < 0.001$; Table 2). Visits per flower, which controls for flower count, varied significantly across the 15 C. annuum cultivars (ANCOVA: $F_{14,1644} = 5.41$, $p < 0.001$; Fig. 4; Table 2). Over an eight-fold difference between the least attractive and most attractive cultivars was observed, from 0.049 ± 0.033 visits per flower in Desperado to 0.397 ± 0.111 visits per flower in Capperino (Table 2). In addition to Capperino, several other cultivars showed relatively high visitation rates, including Mesilla (visits per flower = 0.320 ± 0.157), Altiplano (visits per flower = 0.291 ± 0.107), and Pueblo Primrose (visits per flower = 0.290 ± 0.102) (Table 2). Conversely, multiple cultivars exhibited relatively low visitation rates, comparable to Desperado, including Big Jim (visits per flower = 0.058 ± 0.032), Sweet Cherry (visits per flower = 0.060 ±

0.038), and Mirasol (visits per flower = 0.067 ± 0.048) (Table 2). Plants without flowers at the time of observation were excluded from this analysis.

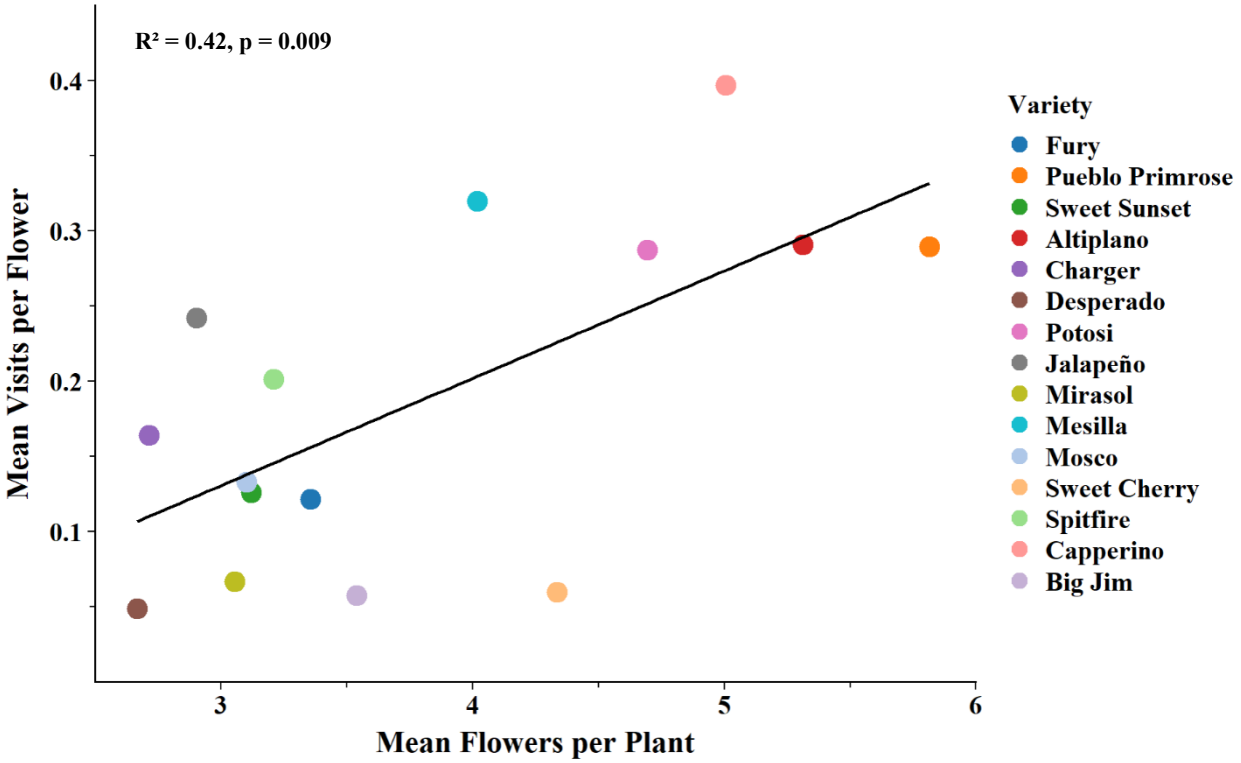

Figure 5. Mean visits per flower versus mean flowers per plant across the 15 *C. annuum* cultivars. Points represent cultivar-level means, and the solid line represents the fitted linear regression model.

Visitation rates were positively correlated with the number of flowers per plant across *C. annuum* cultivars ($\beta = 0.071$, $R^2 = 0.42$, $p = 0.009$; Fig. 5). Forty-two percent of the variation in mean visits per flower was explained by the number of flowers per plant. Several cultivars deviated from this relationship by more than ±0.1 visits per flower (Table 2). These deviations suggest some cultivars receive substantially more or less visitation than their number of flowers would predict; cultivars with positive residuals relative to the regression line include Capperino (+0.123 visits per flower), Mesilla (+0.116 visits per flower), and Jalapeño (+0.118 visits per flower) (Table 2). Negative residuals relative to the regression line include Big Jim (−0.111 visits per flower) and Sweet Cherry (−0.166 visits per flower) (Table 2).

Table 3. Mean floral metric data. Corolla diameter (mm ± 95% CI), anther count (per flower), anther size index (anther length × width; mm^2 ± 95% CI), and style length (mm). Cultivars are ordered by descending mean corolla diameter, from top to bottom.

Cultivar	Corolla Diameter (mm)	Anther Size Index (mm^2)	Anther Count	Style Length (mm)	Anthers (n)	Flowers (n)
Mesilla	21.86 ± 1.84	5.56 ± 0.64	6.20	4.34	93	15
Big Jim	21.33 ± 0.96	4.11 ± 0.50	6.07	4.94	91	15
Spitfire	20.76 ± 0.93	4.03 ± 0.69	6.67	5.32	100	15
Charger	20.08 ± 1.15	4.35 ± 0.52	6.00	4.68	90	15
Desperado	19.79 ± 1.34	4.78 ± 0.58	5.53	4.54	83	15
Capperino	19.46 ± 1.14	3.47 ± 0.33	5.73	4.53	86	15
Mosco	19.13 ± 0.89	4.10 ± 0.38	5.33	3.98	80	15
Sweet Cherry	19.12 ± 1.04	4.39 ± 0.38	5.88	4.40	94	16
Mirasol	18.77 ± 1.21	4.46 ± 0.79	5.47	3.63	82	15
Sweet Sunset	18.61 ± 1.18	4.75 ± 0.62	5.53	4.56	83	15
Potosi	17.70 ± 1.53	3.30 ± 0.46	5.67	4.32	85	15
Altiplano	17.48 ± 1.85	4.08 ± 0.56	5.53	4.18	83	15
Fury	17.38 ± 1.56	3.85 ± 0.73	5.93	4.30	89	15
Jalapeño	16.64 ± 1.31	4.15 ± 0.57	5.67	3.75	85	15
Pueblo Primrose	13.65 ± 1.12	3.44 ± 0.39	5.27	4.21	79	15

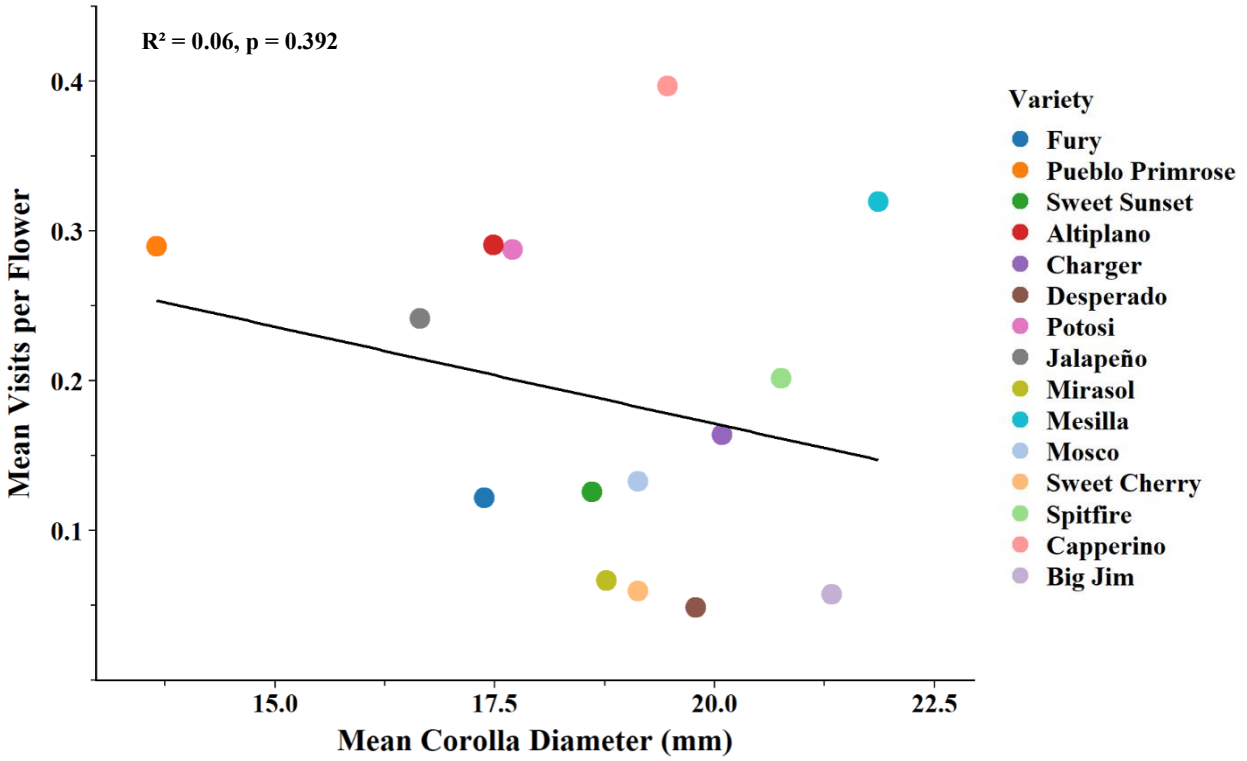

Figure 6. Mean visits per flower versus mean corolla diameter across the 15 *C. annuum* cultivars. Points represent cultivar-level means, and the solid line represents the fitted linear regression model.

Corolla diameter significantly differed across the cultivars, ranging from 13.65 mm in Pueblo Primrose to 21.86 mm in Mesilla (ANOVA: $F_{14,210} = 11.07$, $p < 0.001$; Table 3). However, there was no significant relationship between corolla diameter and visits per flower ($\beta = -0.013$, $R^2 = 0.06$, $p = 0.392$; Fig. 6). Some cultivars with large flowers received relatively low floral visitation, while others with similarly large flowers showed relatively high visitation (Fig. 6). For example, Big Jim had a mean corolla diameter of 21.33 ± 0.96 and 0.058 ± 0.032 visits per flower, while Mesilla had a mean corolla diameter of 21.86 ± 1.84 and 0.320 ± 0.157 visits per flower (Tables 2 and 3). Notably, the cultivar with the smallest flowers, Pueblo Primrose (mean corolla diameter = 13.65 ± 1.12), showed relatively high pollinator visitation (visits per flower = 0.290 ± 0.102) (Fig. 6; Tables 2 and 3).

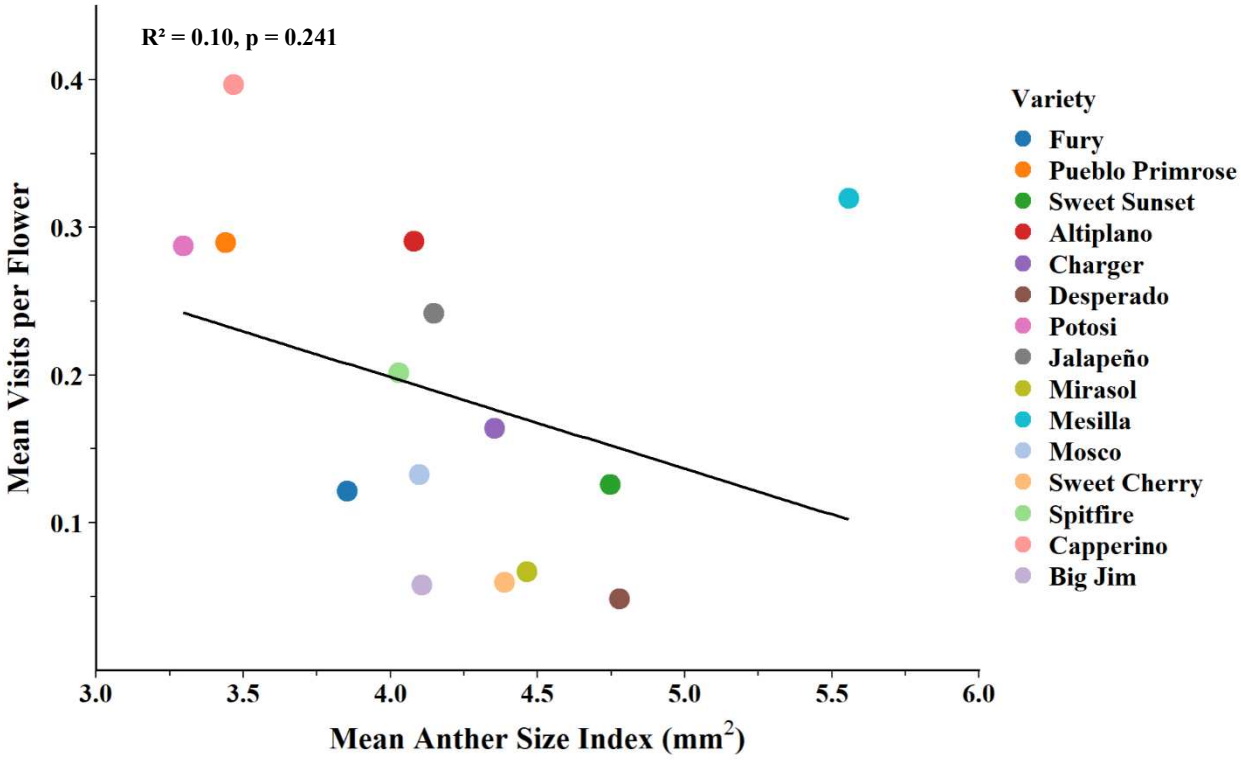

Figure 7. Mean visits per flower versus anther size index across the 15 *C. annuum* cultivars. Points represent cultivar-level means, and the solid line represents the fitted linear regression model.

Anther size index varied significantly across the *C. annuum* cultivars (ANOVA: $F_{14,211} = 4.95$, $p < 0.001$; Table 3). Mean anther size index was not a significant predictor of pollinator visits per flower ($\beta = -0.062$, $R^2 = 0.10$, $p = 0.241$; Fig. 7). Relatively high floral visitation was observed in cultivars on both high and low ends of the anther size index (Fig. 7). For example, Mesilla, with the highest anther size index (5.56 ± 0.64), received 0.320 ± 0.157 visits per flower, while Potosi, with the lowest anther size index (3.30 ± 0.46), received 0.288 ± 0.106 visits per flower (Tables 2 and 3). Additionally, Desperado, with 0.049 ± 0.033 visits per flower, had the second highest anther size index (4.78 ± 0.58), while Capperino had the highest visits per flower (0.397 ± 0.111) and was among the lowest anther size index cultivars (3.47 ± 0.33) (Tables 2 and 3).

Additionally, anther count and style length were examined to assess their relationship with floral visitation; these measurements were taken from the same flowers used to quantify the previous floral traits. Anther count varied significantly across the 15 *C. annuum* cultivars (ANOVA: $F_{14,211} = 6.29$, $p < 0.001$; Table 3), but mean anther count did not predict visits per flower ($R^2 < 0.001$, $p = 0.85$). Similarly, style length varied significantly across the 15 *C. annuum* cultivars (ANOVA: $F_{14,209} = 2.65$, $p = 0.0014$; Table 3), but mean style length did not predict visits per flower ($R^2 < 0.001$, $p = 0.70$).

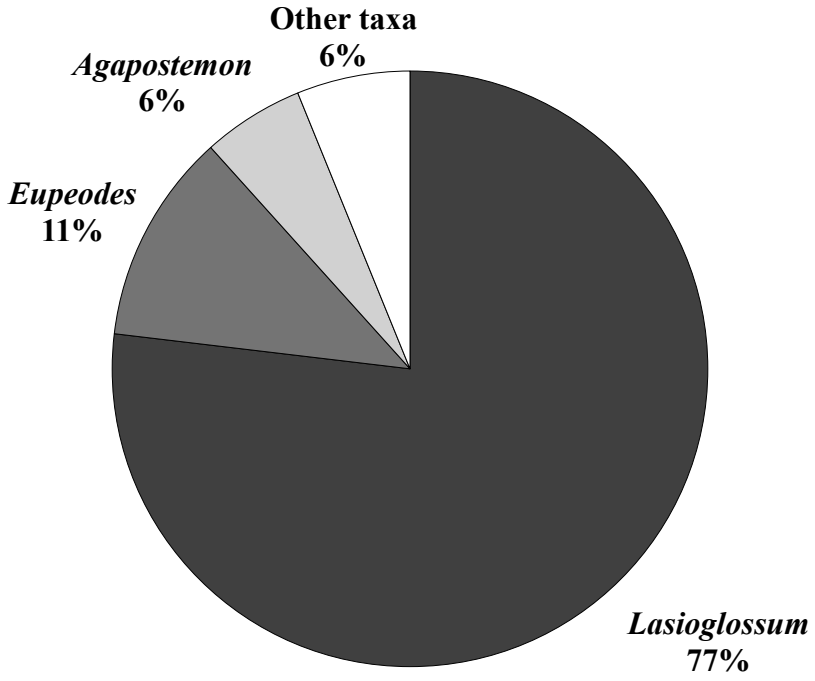

Figure 8. Total composition of pollinators observed across all 15 *C. annuum* cultivars during the field experiment. 943 floral visits were recorded throughout the growing season.

Pollinator taxa visiting chile pepper flowers included halictid bees, primarily *Lasioglossum* spp. (725 visits; 77%) and *Agapostemon* spp. (52 visits; 6%), along with syrphid flies, *Eupeodes* spp. (108 visits; 11%) (Fig. 8). The remaining floral visits (6%; 58 visits) were

made by various unidentified moth, fly, wasp, and beetle taxa (Fig. 8). No honey bees (*Apis mellifera*) or bumblebees (Bombus spp.) were observed during pollinator surveys.

Table 4. Percent composition of floral visitor taxa across the *C. annuum* cultivars. Cultivars are ordered by descending mean visits per flower observed in the pollinator survey, from top to bottom.

Cultivar	*Lasioglossum* (%)	*Eupeodes* (%)	*Agapostemon* (%)	Other Taxa (%)	Total Visits
Capperino	84.3	5.8	2.6	7.3	191
Mesilla	75.6	10.3	6.4	7.7	78
Altiplano	78.3	14.2	4.2	3.3	120
Pueblo Primrose	75.8	14.8	1.3	8.1	149
Potosi	76.0	4.8	13.5	5.8	104
Jalapeño	75.5	2.0	6.1	16.3	49
Spitfire	70.0	20.0	5.0	5.0	40
Charger	92.6	3.7	0.0	3.7	27
Mosco	54.3	37.1	0.0	8.6	35
Sweet Sunset	67.7	0.0	32.3	0.0	31
Fury	85.7	7.1	7.1	0.0	42
Mirasol	60.9	26.1	8.7	4.3	23
Sweet Cherry	59.1	31.8	4.5	4.5	22
Big Jim	73.7	26.3	0.0	0.0	19
Desperado	92.3	7.7	0.0	0.0	13

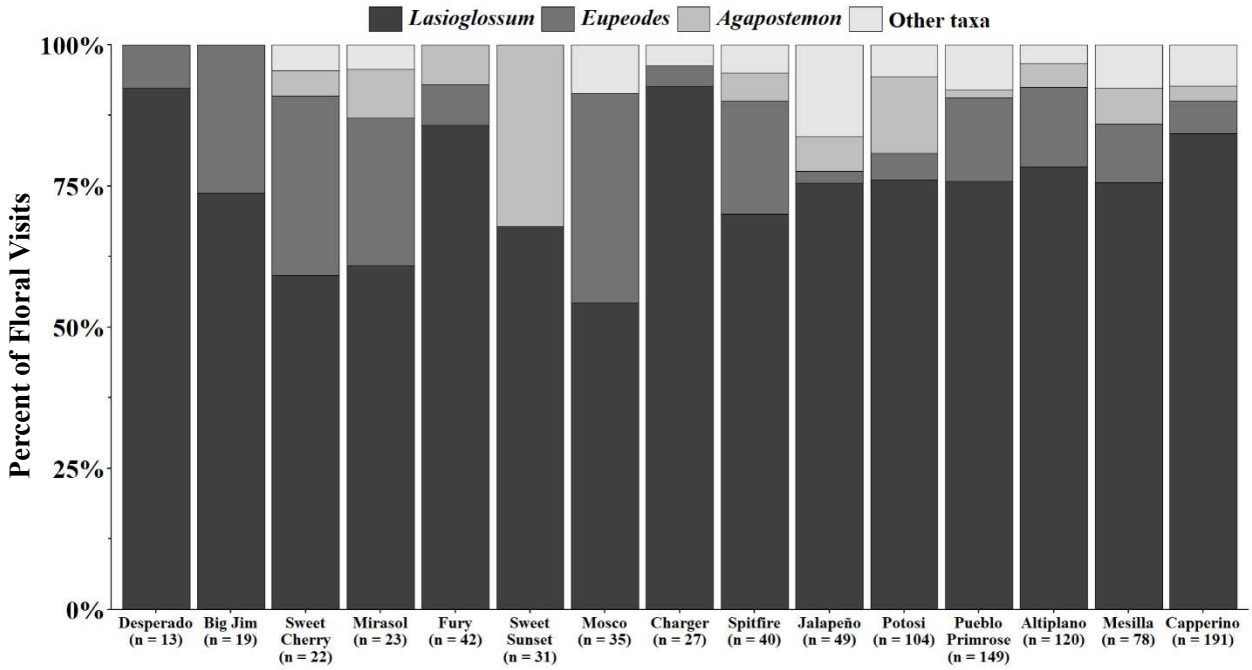

Figure 9. Stacked bar chart representing the percentage composition of floral visitor taxa across the 15 *C. annuum* cultivars (n = total floral visits). Cultivars are sorted from lowest to highest visits per flower, from left to right.

Floral visitor composition varied significantly across the cultivars (chi-square test: χ^2 = 152.64, df = 42, $p < 0.001$; Fig. 9; Table 4). *Lasioglossum* bees were the dominant floral visitors across all the chile pepper cultivars, with a relatively high proportion observed in Charger (25 visits, 92.6%), Desperado (12 visits, 92.3%), Fury (36 visits, 85.7%), and Capperino (161 visits, 84.3%) (Table 4). Additionally, cultivars with relatively high proportions of *Eupeodes* visits include Mosco (13 visits, 37.1%), Sweet Cherry (7 visits, 31.8%), Mirasol (6 visits, 26.3%), and Big Jim (5 visits, 26.3%) (Table 4). *Agapostemon* visited most but not all cultivars; Sweet Sunset showed the highest proportion of *Agapostemon* visits (10 visits, 32.3%), followed by Potosi (14 visits, 13.5%) (Table 4).

Table 5. Associations between floral traits and the proportion of floral visits made by Lasioglossum across the 15 *C. annuum* cultivars. Statistics are from separate linear regressions, using arcsine-square-root transformed Lasioglossum visit proportion as the response variable.

Variable	R^2	Slope (β)	p
Flower count	0.003	−0.008	0.839
Corolla diameter	<0.001	0.001	0.941
Anther size index	0.002	−0.010	0.880
Anther count	0.018	0.049	0.638
Style length	0.078	0.089	0.314

None of the floral traits measured in the present study predicted the proportion of floral visits made by *Lasioglossum* bees across the 15 *C. annuum* cultivars. *Lasioglossum* was the dominant floral visitor taxon observed, but no significant associations were observed between its proportional visitation and flower count, corolla diameter, anther size index, anther count, or style length ($p \geq 0.314$; Table 5). All linear regression models explained little variation in the proportion of visits made by *Lasioglossum* ($R^2 \leq 0.078$; Table 5).

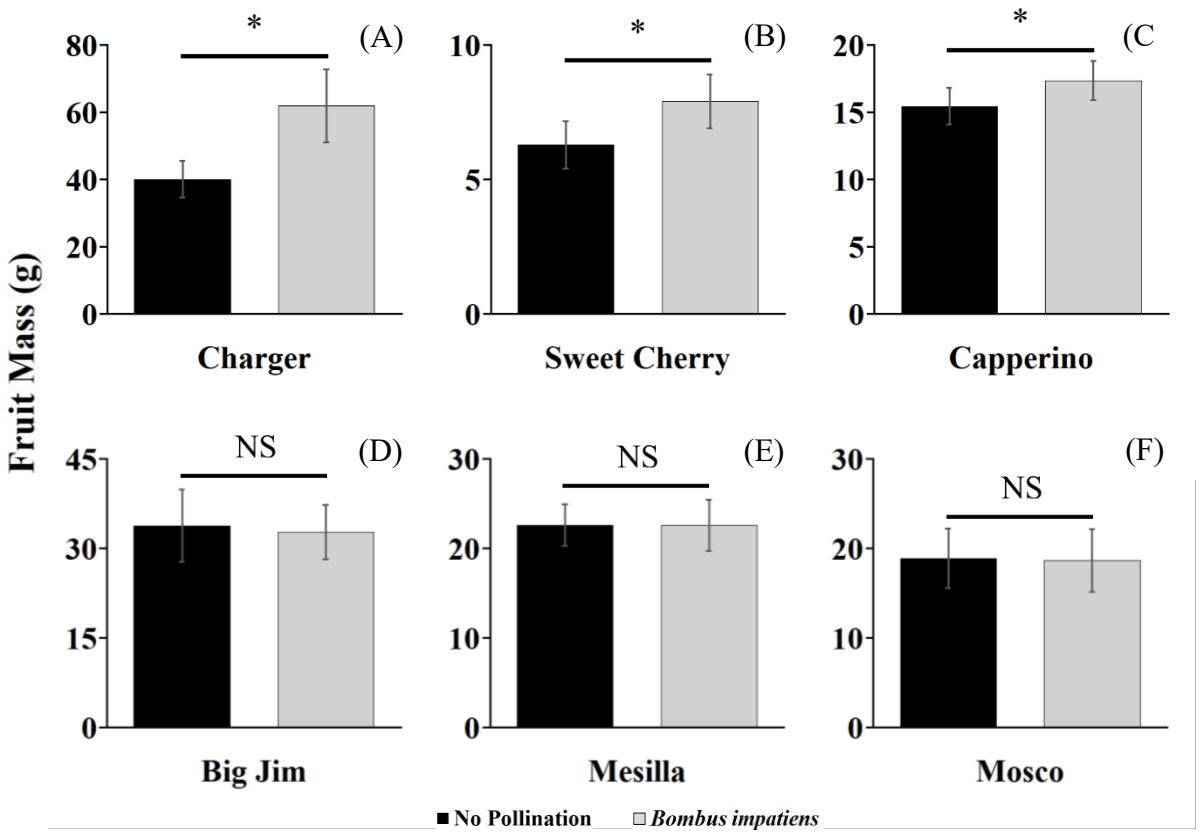

Figure 10. Enclosed pollination experiment results for Big Jim, Capperino, Charger, Sweet Cherry, Mesilla, and Mosco. Black bars represent mean fruit mass in pollinator-excluded plants, while gray bars represent plants exposed to bumblebee pollination (*B. impatiens*). Error bars represent 95% confidence intervals. * indicates a significant difference ($p \leq 0.05$), NS indicates no significant difference ($p > 0.05$).

Mean fruit mass from Charger plants exposed to bumblebee pollination was 54% higher than plants excluded from pollinators (pollinated n = 4; excluded n = 27; two-sample t-test: t = 5.04, df = 7.39, p = 0.001; Fig. 10). Bumblebee-pollinated Charger plants had a mean fruit mass of 61.90 ± 10.88 g, while pollinator-excluded Charger plants produced chile peppers that were 40.10 ± 5.45 g. Similarly, mean fruit mass was significantly higher in Sweet Cherry plants exposed to bumblebee pollination (pollinated: n = 45; excluded: n = 45; t = 2.46, df = 86.5, p = 0.01; Fig. 10). Bumblebee-pollinated Sweet Cherry plants had a mean fruit mass of 7.91 ± 1.00 g, while pollinator-excluded Sweet Cherry plants produced chile peppers with a mean mass of 6.28 ± 0.88 g (Fig. 10). *B. impatiens* exposure increased mean fruit mass by 26% in Sweet

Cherry. Mean fruit mass from Capperino plants exposed to bumblebee pollination significantly differed from Capperino plants that were excluded from pollinators (pollinated n = 45; excluded n = 45; t = 1.92, df = 87.7, p = 0.05; Fig. 10). Bumblebee-pollinated Capperino plants had a mean fruit mass of 17.30 ± 1.45 g, while pollinator-excluded Capperino plants produced chile peppers with a mean mass of 15.40 ± 1.37 g.

In contrast, bumblebee pollination did not significantly affect fruit mass in Mesilla plants (pollinated n = 50; excluded n = 72; two-sample t-test: t = −0.008, df = 104, p = 0.9; Fig. 10). Bumblebee-pollinated Mesilla plants had a mean fruit mass of 22.60 ± 2.83 g, while pollinator-excluded Mesilla plants set chile peppers that were 22.60 ± 2.29 g (Fig. 10). Similarly, bumblebee exposure did not significantly affect fruit mass in Big Jim (pollinated: n = 41, 32.80 ± 4.57 g; excluded: n = 32, 33.80 ± 6.08 g; t = −0.287, df = 61.2, p = 0.7), or Mosco (pollinated: n = 21, 18.60 ± 3.50 g; excluded: n = 21, 18.90 ± 3.34 g; t = −0.108, df = 39.9, p = 0.9; Fig. 10).

Fruit number did not significantly differ between pollinated and pollinator-excluded plants within any cultivar. Specifically, total fruit number did not significantly differ in Big Jim (t = 0.06, df = 19.80, p = 0.949), Capperino (t = 0.77, df = 24.57, p = 0.450), Mesilla (t = 1.64, df = 25.56, p = 0.112), Mosco (t = 1.53, df = 11.86, p = 0.152), or Sweet Cherry (t = 1.31, df = 27.95, p = 0.200). While fruit mass significantly differed between pollinated and pollinator-excluded Sweet Cherry plants, fruit number remained statistically similar within all cultivars.

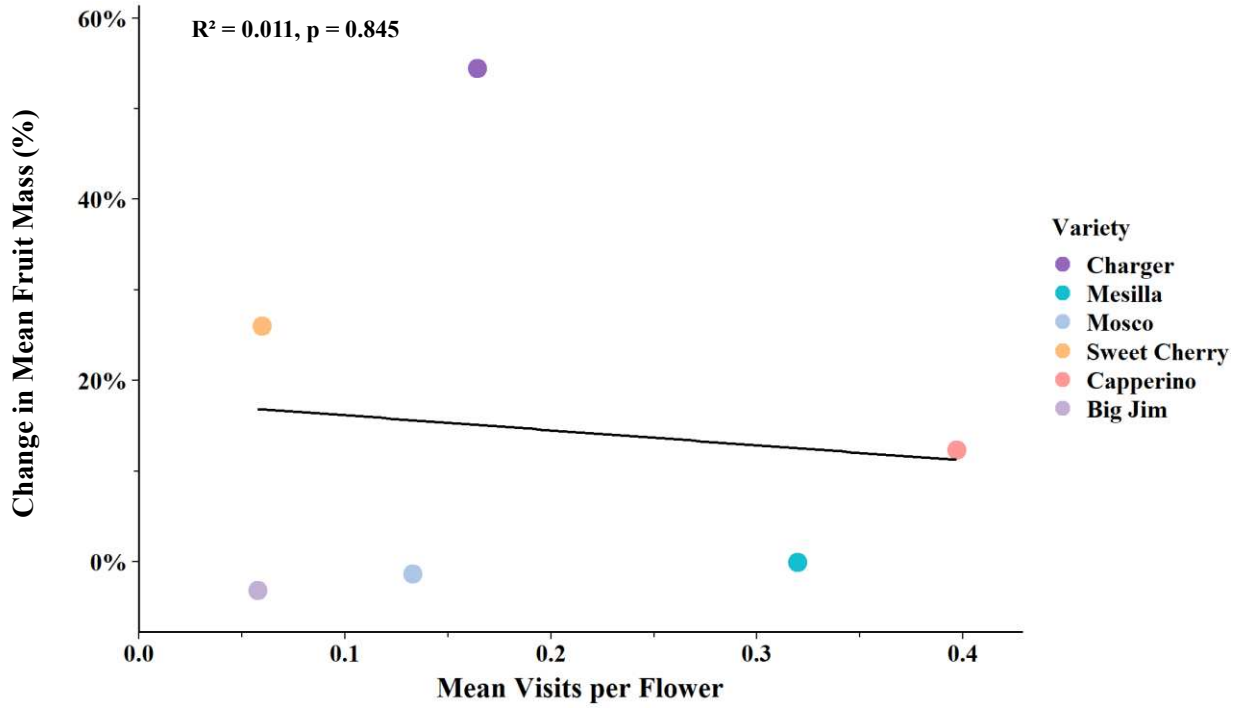

Figure 11. Mean visits per flower versus change in mean fruit mass percentage following *B. impatiens* exposure across the six *C. annuum* cultivars included in both enclosed bumblebee pollination experiments. Points represent cultivar-level means, and the solid line represents the fitted linear regression model.

The effect of *B. impatiens* exposure on mean fruit mass differed significantly across the six cultivars (two-way ANOVA: $F_{5,436} = 3.69$, $p = 0.003$). However, there was no significant relationship between mean visits per flower and percent change in mean fruit mass ($\beta = -16.6$, $R^2 = 0.011$, $p = 0.845$; Fig. 11). Charger, with an intermediate mean visits per flower relative to these six cultivars, exhibited the greatest positive change in mean fruit mass following *B. impatiens* exposure (+54.4 ± 25.3%), followed by Sweet Cherry (+26.0 ± 21.0%) and Capperino (+12.3 ± 12.8%). In contrast, Big Jim, with the lowest visits per flower among these six cultivars, exhibited limited change in mean fruit mass (−3.2 ± 22.1%), as did Mosco (−1.3 ± 24.8%) and Mesilla (−0.1 ± 16.0%).

Discussion

My results reflect significant variation in pollinator visitation across the fifteen chile pepper cultivars. The most visited *C. annuum* cultivar was Capperino (visits per flower: 0.397), a cherry-type cultivar with a relatively high number of flowers per plant. Capperino flowers had over an eight-fold higher level of attraction than the least attractive cultivar, Desperado (visits per flower: 0.049). This magnitude of variation in floral visitation is comparable to existing chile pepper pollination studies; Rabinowitch et al. (1993) conducted a study in Rehovot, Israel, reporting variation in honey bee (*A. mellifera*) visitation rates across seven *C. annuum* genotypes, ranging from approximately 0.05 to 0.45 visits per flower per 15-minute observation period across genotypes (Rabinowitch et al., 1993). Additionally, Browning et al. (2023) investigated insect pollinator visitation across 24 cultivars of ornamental flowers, including marigold (*Tagetes erecta and T. patula*), bidens (*Bidens ferulifolia and B. aurea*), and portulaca (*Portulaca oleracea and P. grandiflora*). In their two-year study, they found highly significant variation in pollinator visitation across cultivars within each flower type; approximately 5-fold in marigold, 24-fold in bidens, and 7-fold in portulaca. Together, these results indicate substantial variation in floral visitation at the cultivar level.

In contrast, Courcelles et al. (2013) examined variation in floral visitation among four cultivars of the highbush blueberry crop (*V. corymbosum*). Floral visitation in their study varied by a range of approximately two-fold. The most attractive blueberry cultivar, Duke, had a mean visitation of 20.1 honey bees and bumblebees per 10-minute sampling period (2.01 visits per minute), while Draper had a mean of 8.5 visits (0.85 visits per minute). Although not reported numerically, Courcelles et al. (2013) noted that fruit set appeared to correlate with visitation rate; Duke, the most attractive of the four blueberry cultivars, exhibited the highest relative fruit set.

Overall, these findings suggest that cultivar-level variation in floral visitation is an intrinsic attribute of flowering plants, including crops. This variation may be an important consideration for crop breeding programs with the aim of improving crop performance.

The variation in floral visitation observed across the *C. annuum* cultivars in the present study is consistent with findings from other crop systems. For example, Harris and Ratnieks (2026) reviewed 52 studies that examined floral visitation rates across various crop accessions and found that 27 reported at least a two-fold difference in floral visitation between the most and least attractive accessions. Their review included multiple studies that analyzed floral visitation on a per-flower basis, similar to the present *C. annuum* pollination study. Among these, Gaffney et al. (2020) reported an 8.96-fold difference in visitation across 17 accessions of carrot (*Daucus carota*). This finding is closely aligned with the present study, which revealed over an eight-fold difference across 15 *C. annuum* cultivars, providing further evidence that strong cultivar-level variation in floral visitation is present in multiple crop systems.

I used a linear regression to assess whether flower count influenced this variation in floral visitation; it revealed that some cultivars received substantially different levels of floral visitation than the number of flowers alone would predict (Fig. 5). The R^2 value from this linear regression of flower number and visits per flower indicates that 42% of the variation in floral visitation is explained by the number of flowers per chile pepper plant. This finding is in line with existing research that indicates how differences in floral count influence pollinator attraction. For example, a study in Inner Mongolia, China investigated pollinator visitation in the Korshinsk pea shrub (*Caragana korshinskii*). They found that pollinator visits (per flower) were positively associated with the number of open flowers in both natural and managed populations of *C. korshinskii* ($R^2 = 0.738$ in natural populations; $R^2 = 0.922$ in managed populations; Chen &

Zhao, 2019). However, their study used a single genotype, which represents a general ecological response to increased flower count, whereas the present study observes variation in floral visitation rates on the cultivar level.

Similar relationships between flower count and visitation are also seen in blueberry; Cromie et al. (2024**)** reported that floral traits, including number of flowers, influence floral visitation across 38 genotypes of southern highbush blueberry (*V. corymbosum*). In their study, flower density was identified as a major driver of variation in honey bee visitation across genotypes. They used a random forest model that incorporated flower density along with other floral traits to predict floral visitation, reporting predictive abilities between 0.54 and 0.66 across pollinator taxa (Cromie et al., 2024). Visitation rates, however, were not consistently associated with fruit set across years. While flower count explains some of the variation in visitation among the chile pepper cultivars in the present study, a substantial amount of unexplained variation remains. These results, along with the floral visitation trends in the present study, indicate that flower count influences pollinator visitation at the cultivar level. However, substantial unexplained variation in pollinator visitation remains, much of which may be associated with other plant traits.

Many of the floral traits varied significantly across the 15 chile pepper cultivars in the present study, including corolla diameter, which ranged from 13.65 mm in Pueblo Primrose to 21.86 mm in Mesilla (ANOVA: $F_{14,210} = 11.07$, $p < 0.001$). Surprisingly, no significant association was found between the differences in corolla diameter and cultivar-level visits per flower ($p = 0.392$). Corolla diameter appeared to have no correlation with floral visitation rates across the 15 *C. annuum* cultivars (Fig. 6). This finding was inconsistent with observations in existing solanaceous crop studies; Mukhopadhyay et al. (2026) reported floral diameter as the

strongest predictor of visitation patterns across wild bee taxa (including *Lasioglossum* spp.) in eggplant (*Solanum melongena).* Among the floral traits measured, floral diameter accounted for 38.18% of the explained variation in their bee-flower interaction model. Other floral traits also contributed to the variation estimated by their model: style length, anther length, and anther width. Interestingly, Portlas et al. (2018) reported a negative relationship between flower size (measured as floret length) and pollinator visitation in cultivated sunflower (*Helianthus annuus* L.) ($R^2 = 0.52$). The authors suggested that floral rewards such as pollen and nectar content may explain the residual variation in bee visits, but noted these traits are often difficult to measure. Collectively, these findings suggest that flower size can influence floral visitation in cultivated crops, but its effect likely varies across crop systems.

In the present study, I measured several floral structures in chile pepper that relate to floral rewards and plant reproduction: anther size index (anther length × anther width), anther count, and style length. While each of these traits varied significantly across the 15 *C. annuum* cultivars, none predicted cultivar-level variation in visits per flower. The lack of association between these floral traits and pollinator visitation may indicate that anther dimensions, anther count, and style length did not explain variation in floral visitation across the *C. annuum* cultivars. Some evidence, however, suggests this trend does not extend to all solanaceous plants. Mukhopadhyay et al. (2026) reported that, in eggplant (*S. melongena*), anther length, anther width, and style length contributed 22.73%, 10.91%, and 27.27% of the explained variation in their bee-flower interaction model, respectively. While this comparison supports the relevance of anther dimensions and style length in the context of pollinator visitation, Mukhopadhyay et al. (2026) did not assess anther count. These results suggest that the influence of floral reproductive structures on pollinator visitation may vary across crop systems.

Additionally, while not examined in the present study, floral food rewards such as nectar volume may influence pollinator visitation in chile pepper. For example, Rabinowitch et al. (1993) reported a five- to six-fold difference in nectar volume across seven *C. annuum* genotypes, and honey bee visitation positively correlated with sugar quantity (r = 0.62–0.73). Their chile peppers were grown near a honey bee yard; however, honey bees were absent in the present study, in which flowers were primarily visited by halictid bees and syrphid flies. This discrepancy suggests pollinator community composition may also influence floral visitation rates in chile pepper—a possible consideration for growers who use managed bee populations.

Throughout the field season, *Lasioglossum* bees were the dominant floral visitors across all *C. annuum* cultivars, accounting for 77% of total visitation (Figs. 8 and 9). This dominance was followed by *Eupeodes* hoverflies (11%), *Agapostemon* bees (6%), and other unidentified taxa (6%) (Fig. 8). The proportion of these floral visitor taxa varied significantly across cultivars, suggesting cultivar identity may influence which pollinators visit them (Fig. 9). In the context of chile pepper pollination, it is important to note that *C. annuum* flowers have longitudinally dehiscent anthers, allowing pollen to be accessed by a broad range of floral visitors, including generalist pollinators (Fig. 1). Pollinator communities vary across crop systems and biogeographical regions (Kleijn et al., 2015). Some evidence suggests that variation in pollinator identity can influence fruit set. For example, Vicens and Bosch (2000) showed that pollinator identity can affect pollination efficacy in Red Delicious apples (*Malus domestica*). They compared fruit and seed set after flowers received a single visit from either a megachilid bee (*Osmia cornuta*) or a honey bee (*A. mellifera*). *O. cornuta* exhibited high levels of stigma contact (97.7% of visits), resulting in 27.4% fruit set, while only 4.8% of the flowers set fruit after being visited by *A. mellifera*, which exhibited relatively low stigma contact (32.7% of visits) (Vicens

and Bosch, 2000; Tables 1 and 3). It is important to note that *A. mellifera* were observed primarily foraging for nectar, while *O. cornuta* were observed collecting pollen and nectar simultaneously. These data suggest that foraging behavior among floral visitors can play a role in pollination efficacy, and that growers may benefit from managing their farms to support greater pollinator diversity.

Determining the number of visits per flower that optimizes yield across chile pepper cultivars is complex, as pollination efficacy depends on multiple factors, including floral phenology, visitation duration, and visitation frequency (Stephenson, 1981; Aizen & Harder, 2007). In the present study, I examined the effect of bumblebee pollination on yield across *C. annuum* cultivars by exposing flowering chile pepper plants to *B. impatiens* and comparing their yield to plants of the same cultivars that were excluded from pollination. I found significantly higher mean fruit mass in pollinated Charger and Sweet Cherry plants (Figs. 10 and 11). The other four cultivars, however, did not produce significantly heavier fruit when their flowers were exposed to *B. impatiens* (Figs. 10 and 11). Additionally, fruit number did not differ significantly between pollinated and pollinator-excluded plants within any cultivar. These data suggest that insect-facilitated pollination may increase fruit mass in some cultivars, while having little effect on fruit number in any cultivar.

While chile pepper flowers are capable of self-pollination, my findings are comparable to previous studies that suggest chile pepper yield can be influenced by pollination. For example, using two *C. annuum cultivars*, Carr and Davidar (2015) conducted a study in southern India and reported 72% fruit set in open-pollinated *C. annuum* compared to 36% in flowers that were excluded from pollinators via mesh bags. Across 297 chile pepper plants, they reported a mean floral visitation rate of 11.7 honey bee visits per hour. Visitation estimates were based on

observations of one or two freshly opened flowers at a time for 5-minute intervals (Carr & Davidar, 2015). Mean floral visitation rates in the present study were substantially lower: when standardized from 15-minute intervals to an hourly scale, chile pepper flowers received 0.79 visits per hour on average across all 15 cultivars. This discrepancy highlights the variability of pollinator visitation in *C. annuum* across geographic regions, which is likely influenced by pollinator identity and environmental conditions (Kleijn et al., 2015). Collectively, these findings suggest that pollinator visitation and pollinator-mediated yield responses vary across chile pepper cultivars.

In the present study, *B. impatiens* exposure increased mean fruit mass in three of the six cultivars by at least 12.3% compared to pollinator-excluded chile peppers. However, there was little to no effect of bee exposure in the remaining three cultivars. Charger exhibited the greatest boost in mean fruit mass, increasing by 54% following the *B. impatiens* treatment. This level of fruit mass increase is comparable to other *C. annuum* pollination studies. For example, Soli et al. (2020) reported 66.5% higher fruit mass in open-pollinated *C. annuum* compared to bagged plants. Similarly, Putra et al. (2016) reported 66.46% higher fruit mass in *C. annuum* plants pollinated by *T. laeviceps* compared to wind pollination. However, both of these studies used a single cultivar, while the present study used six cultivars and found that fruit mass increases following pollination treatment varied among them. Our findings indicate that some cultivars may benefit more than others from insect-facilitated pollination and highlight the need for future studies to compare the effects of pollination on yield across a broad range of cultivars.

Given the remaining unexplained variation in visitation across the 15 *C. annuum* cultivars, future research on chile pepper pollination should focus on variation in floral volatile organic compound composition across chile pepper cultivars, as this is known to affect floral

attraction in other crop systems, including strawberry (Klatt et al., 2013). Future research should also focus on how food rewards such as nectar volume and pollen availability vary across cultivars, as these may also be important considerations in the context of pollinator visitation (Rabinowitch et al., 1993; Raw, 2000). Additional floral traits, such as floral reflectance and color, may also influence pollinator visitation in flowering plants and should be considered in future chile pepper pollination studies (Schiestl & Johnson, 2013).

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