Field design can affect cross-pollination and crop yield in strawberry (*Fragaria* x *ananassa* D.)

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Abstract

The distance travelled by pollinators between successive flower visits can affect the quality of pollen transferred among plants. In cropping environments, especially monoculture systems, pollinators that travel between plants or rows may increase cross-pollination and consequently crop yield. However, the most commonly utilized crop pollinator, *Apis mellifera* L., tends to forage consecutively on nearest-neighbouring plants within rows. The level of cross-pollination can be further restricted in crops that are propagated by cloning. When a clonal variety is planted over large areas, the potential for outcrossed pollen deposition would be limited, regardless of pollinator flight distances. To investigate how pollinator movement and varietal diversity interact to affect crop pollination, we conducted an experiment with wild and honey bees in single- and multiple-variety strawberry fields. We hypothesized that the amount of cross-pollination provided by wild bees in multiple-variety strawberry fields would be greater than in single-variety fields, and greater than that provided by honey bees in either field type. We found that, indeed, flowers visited by wild bees produced larger strawberries than those visited by honey bees in multiple-variety plots, but only in the more self-incompatible of the two strawberry varieties tested. Strawberries resulting from honey bee pollination were of similar size regardless of the number of varieties planted in the field. Our results show that

certain multiple-variety strawberry fields can benefit from the irregular foraging patterns of some solitary bee species, leading to increased cross-pollination and crop yield. Strawberry growers could take advantage of this effect by planting multiple varieties in close proximity and by supporting wild bee populations on farms.

1 Introduction

In pursuit of pollen and nectar, flower visitors dictate both the quantity and quality of pollen transferred between animal-pollinated plants (Lloyd and Schoen, 1992; Harder and Barrett, 1996). The pollen-transfer efficiency of crop pollinators is an important consideration for agricultural production as animal pollination is needed to maximize fruit and seed set for 70% of our main food crops (Klein et al., 2007). Of these crops, approximately 10% depend fully on animals to deposit outcrossed (or allogamous) pollen from other plants to set fruit, while the remainder have mixed-mating systems and can reproduce by both cross- and self-pollination. However, cross-pollination generally increases offspring fitness in mixed-mating systems (Darwin, 1876; Charlesworth and Charlesworth, 1987), and insect-pollination has been found to increase fruit yield or quality over self-pollination in crops such as cranberry (Sarracino and Vorsa 199; Cane et al., 1996), strawberry (Klatt et al. 2014; Weitzke et al. 2018), oilseed rape (Bommarco et al. 2012), tomato (Morandin et al. 2001; de Melo e Silva Neto et al. 2013), and hot and sweet peppers (Raw, 2000; Serrano and Guerra-Sanz, 2006). In self-compatible plants, outcrossed fruits tend to have more—and more vigorous—seeds, which can have a competitive advantage in obtaining maternal resources over inbred seeds (reviewed by Stephenson 1981). Metaxenia is also a proposed mechanism driving enhanced fruit production in some self-compatible plants. Metaxenia refers to the influence of foreign pollen (typically from another variety) on the characteristics of the plant maternal tissues (Swingle, 1928). Xenic effects have been found in crosses between certain varieties of apple, blueberry, raspberry (reviewed by Denny, 1992) and strawberry (de Oliveira et al. 1983).

The probability that a pollinator transfers outcrossed pollen between plants depends on a complex set of variables including the size and configuration of the plant population, and the foraging behaviours of pollinators (Levin and Kerster, 1969; Levin, 1981; Handel, 1983; reviewed by Barrett, 2003). High densities of flowering plants can increase pollinator abundance and flower visitation frequency, leading to reduced autogamous (within-flower) selfing (Schmitt, 1983; Karron et al., 1995; Routley et al., 1999). Further, pollinators that visit few flowers per plant and/or move large distances between individual plants will tend to promote outcrossing and reduce geitonogamous (within-plant, among-flower) selfing (Lloyd and Schoen, 1992; Cresswell et al., 2002; Ivey et al., 2003; Karron et al., 2009). However, cropping environments can add another degree of complexity to the relationship between pollinators and cross-pollination: although the high flowering plant densities in croplands may increase pollinator visitation frequency, the genetic diversity within certain crops can be low, particularly in monocrop fields populated by clones (e.g. blueberry, strawberry). In such fields, the potential for geitonogamous pollen transfer would be high, regardless of pollinator foraging patterns.

Studies linking pollen movement with bee foraging behaviours have mainly focused on natural plant communities (Waser, 1982; Herrera, 1987; Karron et al., 2009; Cranmer et al., 2012) and large-bodied bee species (e.g., *Bombus* spp., Pyke, 1978; Heinrich, 1979; Zimmerman, 1982;

Thomson and Thomson, 1989; Pyke and Cartar, 1992; Karron et al., 1995; Goulson, 2000; Javorek et al., 2002), including honey bees (Free, 1962; Free, 1968; Waddington, 1980; Ginsberg, 1986; Morris, 1993; Walters and Schultheis, 2009). These studies have found that large-bodied bees often exhibit a high degree of directionality, and generally arrive and depart a flower in the same direction. This tendency to fly straight ahead to the nearest neighbouring flower likely maximizes foraging efficiency, and/or reduces the probability of revisiting flowers (Pyke, 1978). However, it is unclear whether foraging patterns observed in these large bee species are also typical of smaller bee species, which can often be the dominant pollinators on farms (Winfree et al., 2007, Mandelik et al., 2012; Forrest et al., 2015; Blitzer et al., 2016). The number of studies focused on the foraging patterns of small-bodied species is limited (Waddington, 1979; Herrera, 1987; Raw, 2000), mostly likely due to the difficulty of tracking small bees. One study that successfully followed several small-bodied *Lasioglossum* bees found that although they typically exhibited a high degree of directionality, they also made occasional ‘looping’ flights, where the distance between visited flowers increased with each successive loop (Waddington, 1979). This behaviour has not been observed in honey bees, the most widely employed crop pollinator.

The interactive effect of field design and pollinator movement on pollen transfer and fruit production within crops has been largely unexplored (but see Vezvaei and Jackson, 1997; Raw, 2000; Walters and Schultheis, 2009). Here, we investigated the effects of field design and pollinator foraging patterns on fruit mass in strawberry in experimental fields dominated by managed honey bees and small, wild pollinators (*Lasioglossum* spp.). Wild bee pollination has been found to increase strawberry size over honey bee pollination (Horth and Campbell, 2018;

MacInnis and Forrest, 2019), as has cross-pollination between certain strawberry varieties (Colbert and de Oliveira, 1992; Tuohimetsä et al., 2014). The potential for strawberry yield to be increased through cross-pollination in the field depends on the propensity of foraging bees to successfully transfer allogamous pollen between plants, and on the genetic diversity within a crop. However, many commercial strawberry (*Fargaria x ananassa* Duch.) cultivars are vegetatively propagated through cloning in nurseries to preserve varietal traits. The cloned plants are subsequently sold and typically planted as field crops with one variety per row, for several rows or hectares consecutively. Pollinator foraging patterns may have a greater influence on outcrossing rates and subsequent crop yield in strawberry fields that contain multiple varieties (i.e. that are more genetically diverse) than in single-variety fields. To test whether wild bees transfer better-quality (outcrossed) pollen by moving more often between rows than honey bees, we controlled the visits of both bee types to strawberry flowers in fields with one variety and those with two varieties in adjacent rows, and measured subsequent fruit mass. We hypothesized that wild bee visitation would yield larger strawberries than visitation by honey bees, but only in multiple-variety fields, because of more frequent between-variety movements by wild bees.

2 Methods

2.1 Study system and experimental design

The study was conducted at The McGill Horticultural Research Centre in Ste-Anne-de-Bellevue, Québec, Canada (45°24’36.9”N 73°56’7.3”W), from May to October 2017. The research centre is situated in an urban–suburban landscape, with patches of agricultural and forested areas. Two popular commercial day-neutral strawberry varieties adapted to regional conditions were used for the study: *Seascape* (SS) and *Albion* (ALB). These two varieties were chosen as they had similar growth forms (plant height, leaf size), floral morphologies (corolla diameters and petal numbers), flowering densities, and bloom times (Bringhurst and Voth, 1991; Shaw and Larson, 2006). Day-neutral strawberry varieties were used to increase the length of the sampling period, as they bloom consistently for several months. Bare-root seedlings were planted in May and bloom began in mid-July and continued until early October. The field plots were surrounded on all sides by several other crops, which provided alternative floral resources for pollinators periodically over the extended strawberry bloom. These crops included bell pepper (*Capsicum annuum*), cucumber (*Cucumis sativus*), zucchini (*Cucurbita pepo L.*), and asparagus (*Asparagus officinalis* L.).

A split-plot, 2 x 3 factorial design was used to test the influence of bee type (wild and honey bee) on strawberry quality in multiple-variety and single-variety strawberry fields. We used a complete randomized block design with four blocks containing plots of each of the three field types: single-variety SS, single-variety ALB and a multiple-variety plot of ALB and SS (MULT). The two bee treatments, wild bee (WB) and honey bee (HB), were assigned to individual plants within each plot each sampling day, as described below. Each of the twelve plots contained 4 rows of strawberry plants, 20 m in length (Fig. 1). The cultivation and spacing of plants corresponded to standard day-neutral cultivation practices. Strawberries were grown on raised beds covered with black plastic mulch (polyethylene), under which drip irrigation lines were installed. Plants were irrigated daily at a rate of 5 L/m2. Soil moisture levels were monitored with a tensiometer and the irrigation schedule was adjusted as needed. The spacing was 0.2 m between plants within rows and 1.2 m between rows (OMAFRA, 2016).

Climate and overall growing conditions were average for strawberry in the study region (ISQ, 2017). Precipitation was above average in 2017 but sampling was only done on warm, sunny days (air temperature > 20 ° C) with little wind (<10 km/h). Sampling was done between 9h and 17h and all sampled plants were in the two middle rows of each plot, at least 1 m from the edge in any direction to avoid edge effects. As day-neutral strawberries have several blooming periods, some plants received a second treatment at subsequent blooms. Previous work on pollen deposition in strawberry showed that 4 bee visits provides full pollen deposition for a strawberry flower (Chagnon et al., 1989, MacInnis and Forrest, 2019). So, to ensure adequate pollen quantity, the HB treatment consisted of 5 consecutive visits by honey bees to a flower, and the WB treatment consisted of 5 consecutive visits by wild bees. The two bee treatments, honey bee (HB) and wild bee (WB), were replicated as many times as possible in each plot (SS, ALB, MULT) each day.

To obtain the bee treatments, one secondary unopened flower on a single plant in each plot was haphazardly chosen, covered with 'no-see-um' nylon mesh (BioQuip, CA, USA) to exclude pollinators, and given a blank label. Secondary flowers were used because they are more abundant than primary flowers and more likely to set fruit than those flowering later in the inflorescence hierarchy. When ready, an observer would unbag a labelled flower and watch the flower until a HB or WB visited. The flower was then assigned a treatment based on the identity of the first visitor. For example, if a WB was the first to enter one of the sampled flowers, all HBs that subsequently approached the flower would be waved away. It was also noted whether each bee approached the focal flower from within the same row (within-row) or not. We could only reliably categorize bees that originated within the same row, as most (especially small) WB visitors coming from elsewhere appeared in the flowers too quickly to determine their exact origin. Consequently, all bees that did not appear to originate within the same row were classified as “unknown” origin. When a WB visited a sample flower, a large (46 cm diameter) net was carefully placed over the whole plant with the top of the net held well above the plant so as not to disturb the visitor. Once the bee finished foraging she would typically fly upward into the top of the net where she was caught and later identified to species. Bees were identified to species using the keys developed by Ascher and Pickering (2017); bees in the genus *Lasioglossum* were identified to species using Gibbs (2011; 2013). Once a treatment was completed (5 visits of one bee type per flower), the sampled flower was covered with a mesh bag for two days or until stigmas browned. We attempted to perform an equal number of bee treatments in each varietal plot (ALB, SS, MULT) each day, but this was not possible due to variability in flower visit frequencies, resulting in unequal sample sizes between plots and bee types. Beginning two weeks after each pollination treatment, strawberry development of the treated flowers was monitored each day. Individual strawberries were harvested when they ripened (i.e., when they were bright red and easily detachable from the pedicel). All strawberries were harvested in the morning, 17–24 days post-pollination, and were weighed on an analytical balance within two hours of harvesting to minimize water loss.

We also implemented positive and negative control treatments (i.e., hand-cross-pollinated and autonomously self-pollinated flowers) within each plot. For the cross-pollinated treatments, in each of the single-variety and multiple-variety plots (two plots per block), five ALB flower buds on five different plants were bagged with pollinator-exclusion mesh until open and subsequently pollinated with SS pollen. The pollen was collected from a combination of 10 SS flowers from 10 different plants by shaking the flower and pollen into a small petri dish. The pollen mixture was then immediately brushed onto the flower stigmas with a small paintbrush. In the same manner, five SS flowers in the single- and multiple-variety plots were cross-pollinated by hand with ALB pollen. All control flowers were re-bagged with mesh until the end of receptivity (petals abscised and stigmas browned) to exclude pollinator visits. This resulted in 20 cross-pollinated flowers per variety and row configuration. These hand-cross-pollinated flowers were used as a baseline against which to compare the cross-pollination effectiveness of each bee type (HB and WB).

For the self-pollination treatment, 25 flowers each of SS, ALB, and MULT were bagged with mesh from the bud stage to petal abscission to exclude pollinators. In the bud stage, five flowers from five plants of each variety (SS, ALB) and field design (single- and multiple-variety) were bagged with pollinator-exclusion mesh in each plot. The bag was removed once stigmas were no longer receptive (petal abscission, stigmas browned) and flowers were then monitored until fruit development. This treatment was used to determine fruit mass for each variety in the absence of pollinators (autonomous self-pollination).

2.2 Statistical analyses

All statistical analyses were conducted with R v.3.3.3 (R Core Team, 2017). To investigate the effects of pollination treatment (WB, HB, cross-pollinated, self-pollinated), field design (single-variety, multiple variety) and variety (*Seascape, Albion*) on berry mass we used a linear mixed-effects model (LMM; lme4 package, Bates et al., 2015) fitted with restricted maximum likelihood (REML) due to the unbalanced design (Bolker et al., 2008). Model assumptions (homogeneity of variance, linearity, and normality of residuals) were tested using Levene's test for homogeneity of variance (package: car; Fox and Weisberg, 2011) and visual inspection of residual plots. Berry mass was the response variable, and field design, variety, pollination treatment, and all interactions among these variables were fixed effects. Plant ID nested within plot and block was included as a random factor in the model, as some plants had two treated flowers over the sampling period. Sampling date was also included as a fixed continuous variable to account for the influence of plant age, and other environmental variables that may have changed directionally through the season, on strawberry plant growth and fruit development. The effects of pollination treatment and field design on strawberry mass were analysed separately for each variety with the 'phia' package (De Rosario-Martinez, 2015), designed to analyse interaction contrasts for mixed-effects models. Specifically, we tested the effects of bee pollination treatments (HB, WB) in both field designs (single-variety, multiple-variety) on strawberry mass, then we compared the bee pollination treatments to the cross-pollinated treatments in each field design.

3 Results

3. 1 Bee community

Weather conditions permitted 42 days (336 hours) of sampling over the 66 day blooming period. The number of flowers that received the 5 bee visits required varied each day (6.6 ± 3.9 flowers/day), potentially due to the attractiveness of other crops flowering nearby. Herbivory damage further reduced the sample size to a total of 156 flowers (780 bee visits) suitable for subsequent yield analyses. Honey bees (*Apis mellifera* L.) comprised 380 visits and wild bees from 8 genera and 22 species comprised 400 visits (see Table 1 for full species list). The wild bee community was dominated by bees in the genera *Lasioglossum* (n = 363 visits), *Augochlora* (n = 27), and *Halictus* (n = 6). Only one male bee was caught over the study period, so we considered only females in our analysis.

3.2 Fruit mass, field design, and foraging behaviour

The effect of field design (single or multiple variety) on strawberry mass depended on pollination treatment and strawberry variety (significant pollination treatment × field design × variety interaction; $\chi2= 10.40$, $p = 0.015$). In the multiple-variety fields, WB-visited ALB flowers produced strawberries that were significantly larger (mean ± SD, 24.05 ± 3.61 g) than HB-visited flowers (16.38 ± 7.45 g, $\chi2 = 14.52$, $p < 0.001$; Fig. 2; Table 2). WB-visited ALB flowers in multiple-variety fields also yielded significantly larger fruit than WB-visited ALB flowers in single-variety fields (19.47 ± 4.06 g, $\chi2= 9.35$, $p = 0.009$; Table 2). HB-visited ALB flowers in multiple-variety fields (16.38 ± 7.45 g) did not differ in mass from HB-visited ALB strawberries in single-variety fields (15.41 ± 5.80 g, $\chi2= 1.06$, $p = 0.31$; Table 2). There were no significant differences in strawberry mass between HB-pollinated (15.41 ± 5.80 g) and WB-pollinated ALB flowers (19.47 ± 4.06 g) in the single-variety plots ($\chi21= 2.45$, $p = 0.12$). SS flowers produced strawberries of the same mass regardless of bee identity in the multiple-variety plots ($\chi2= 2.32$, $p = 0.13$; Fig. 2; Table 2) and in the single variety plots ($\chi2= 3.74$, $p = 0.11$).

There were significant differences in the pre-visit origin (within-row vs. unknown) between bee types ($\chi21= 258.89$, $p < 0.001$). Out of 380 HB visits, 318 originated within the same row (84%), whereas only 108 out of 400 of wild bee visits visibly originated within the same row (27%).

However, as it was difficult to track the location of the wild bees before they landed in the sample flower, this may be a conservative estimate of the fraction of wild bees that came from the same row.

3.3 Cross-pollinated and autonomously self-pollinated controls

Contrasting the cross-pollinated control flowers with the bee-pollinated flowers revealed that honey bee-pollinated ALB strawberries weighed less (15.41 ± 5.79 g) than cross-pollinated strawberries in single-variety plots (23.40 ± 3.86 g, $\chi2 = 15.84$, $p < 0.001$), as did wild bee-pollinated strawberries ($\chi2 = 5.63$, $p = 0.035$; Fig. 3a; Table 3). However, only the honey bee-pollinated strawberries weighed less than the cross-pollinated strawberries in multiple-variety ALB plots ($\chi2 = 4.45$, $p = 0.034$; Fig. 3b; Table 3); wild bee-pollinated strawberries in these plots actually weighed marginally more than hand-crossed strawberries ($\chi2 = 2.74$, $p = 0.098$; Table 3). Autonomously self-pollinated flowers produced ALB strawberries that were smaller than both HB- and WB-pollinated strawberries in the single-variety (Fig. 3a; Table 4) and multiple-variety plots (Fig. 3b; Table 4). There was no significant difference in SS strawberry mass among pollination types (WB, HB, selfed) in the single-variety plots (Fig. 3c; Table 4) or in the multiple-variety plots (Fig. 3d; Table 4).

4 Discussion

The configuration of plants and varieties within the field has the potential to influence the type of pollen (self vs. outcrossed) transferred between crop plants (Levin 1979; Kumar et al. 2013). Our results show that bee identity significantly influenced strawberry mass in experimental fields inter-planted with two strawberry varieties. Hand-cross-pollinated flowers and wild bee-pollinated flowers were of similar mass in multiple-variety plots, suggesting that wild bees transferred more outcrossed pollen to *Albion* plants in the multiple-variety plots than did honey bees. However, the greater strawberry mass of wild bee-visited flowers was specific to the *Albion* variety: strawberries of the more self-compatible *Seascape* variety (Bringhurst and Voth, 1991) attained a similar mass, regardless of pollinator identity (Fig 2). This highlights the effect of variety on fruit characteristics, irrespective of the influence of field design and pollinator foraging behaviour.

The positive influence of wild bees on strawberry mass seen in the *Albion* variety was largely driven by bees in the genus *Lasioglossum*, the dominant wild pollinators in this community. Our results suggest that, unlike honey bees, *Lasioglossum* bees tend to move between rows rather than within rows, as 73% did not visibly originate within the row, whereas 85% of honey bees did. Therefore, the wild bees in this community are more likely than managed honey bees to achieve cross-pollination, provided suitable outcross pollen is available in adjacent rows. It is unlikely that differences between bee types in the quantity of pollen deposited were responsible for differences in yield, as previous work showed no differences in the quantity of pollen deposited among bee species (MacInnis and Forrest, 2019), and five bee visits should have been more than sufficient to saturate stigmas.

Honey bees characteristically forage in a straight line to the nearest-neighbouring plant or flower (Waddington, 1980; Ginsberg, 1986; Morris, 1993; Walters and Schultheis, 2009). In an agricultural environment, this strategy means that honey bees typically move within, rather than between crop rows, unless forced to deviate from this pattern by interactions with other insects (DeGrandi-Hoffman and Watkins, 2000; Greenleaf and Kremen, 2006; Brittain et al., 2013). Interspecific competition between pollinator species may have influenced wild bee foraging behaviour in this study. We observed that smaller bees were more prone to adjust foraging behaviour (i.e., leave a flower) when encountering honey bees, which may have resulted in an increase in the distance between plants visited by small wild bees. Furthermore, a forager that increases the distance travelled between flower visits lowers the probability of visiting a previously-visited flower (Zimmerman, 1979). Because managed pollinators were abundant within the relatively small experimental field site (~ 4000 m2), the probability of visiting a previously-visited strawberry flower may have been high. In this context, the abundant honey bee population may have forced wild bees to travel long distances between visited plants. Further research is needed to gain more insight on the influence of interspecies interactions on pollinator movement in strawberry.

The relationship between pollinator movement and pollen transport is complex, and the connection between the two can be difficult to establish. Pollen transport is affected not only by pollinator movement patterns, but also by inter- and intraspecific differences in pollination efficiency and pollen carryover. Bees can vary in pollination efficiency for a variety of reasons, including their inherent pollen-carrying capacity, the degree to which they groom pollen from their bodies, and their within-flower foraging behaviours. Pollen carryover occurs when flowers receive pollen from several flowers, not just the last flower visited (Price and Waser 1979; Thomson and Plowright 1980); this can cause gene flow to exceed the average distance travelled by foragers (Schaal 1980; Levin 1981; Karron et al. 1995). Pollen carryover can also be affected by the degree of grooming between and during flower visits (Rademaker et al. 1997; Holmquist et al. 2012). The positive effect of *Lasioglossum* pollination on strawberry yield could have resulted from a combination of high pollen carryover and a low degree of directionality in our experimental fields. Experiments using dyes (e.g. Thomson et al. 1986; Adler and Irwin, 2006) or genes (e.g. Ellstrand et al. 1989, Kohn and Casper 1992) to track pollen movement would be needed to investigate this possibility further.

Emerging studies are finding wild bees to be more effective pollinators than the European honey bee for many crops, including strawberry (Hoehn et al. 2008, Holzschuh et al. 2012, Garibaldi et al. 2013, Rogers et al 2014, Mallinger and Gratton 2014, Horth and Campbell 2018; MacInnis and Forrest 2019; Castle et al. 2019), and interspecific differences in foraging behaviour are an important factor driving this effect (DeGrandi-Hoffman and Watkins, 2000; Greenleaf and Kremen, 2006; Brittain et al., 2013). If the low degree of directionality observed in *Lasioglossum* bees here is consistent at the farm scale, this behaviour could be utilized to increase strawberry yield (particularly for varieties with limited self-compatibility) when coupled with an increase in varietal diversity on the farm.

5 Conclusions

Research on the influence of foraging behaviour on cross-pollination is limited. Further studies are needed to determine whether the foraging behaviour of the bees observed here is repeated in other contexts, on larger scales and for other strawberry varieties. If particular species of wild bees are found to consistently travel between rather than within rows, designing the farmed landscape with pollinator foraging patterns in mind may benefit crop yields. Incorporating multiple varieties in close proximity may increase cross-pollination by wild bee species, and potentially by managed honey bees if multiple varieties are planted within-row—a possibility that was not explored here. Currently, many strawberry farmers in our area plant multiple varieties per field based on proven performance and consumer preferences (G. MacInnis, pers. communication with growers). However, each variety is typically planted in ten or more adjacent rows. Seedlings are either planted by hand directly into the ground as a mechanical transplanter moves along the rows, or they are fed manually into transplant slots. Therefore, alternating varieties by row would simply be a matter of positioning the seedlings with the plant handlers accordingly, and could likely be implemented without additional costs or labour.

6 Declarations of interest

None.

7 Acknowledgements

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Table 1

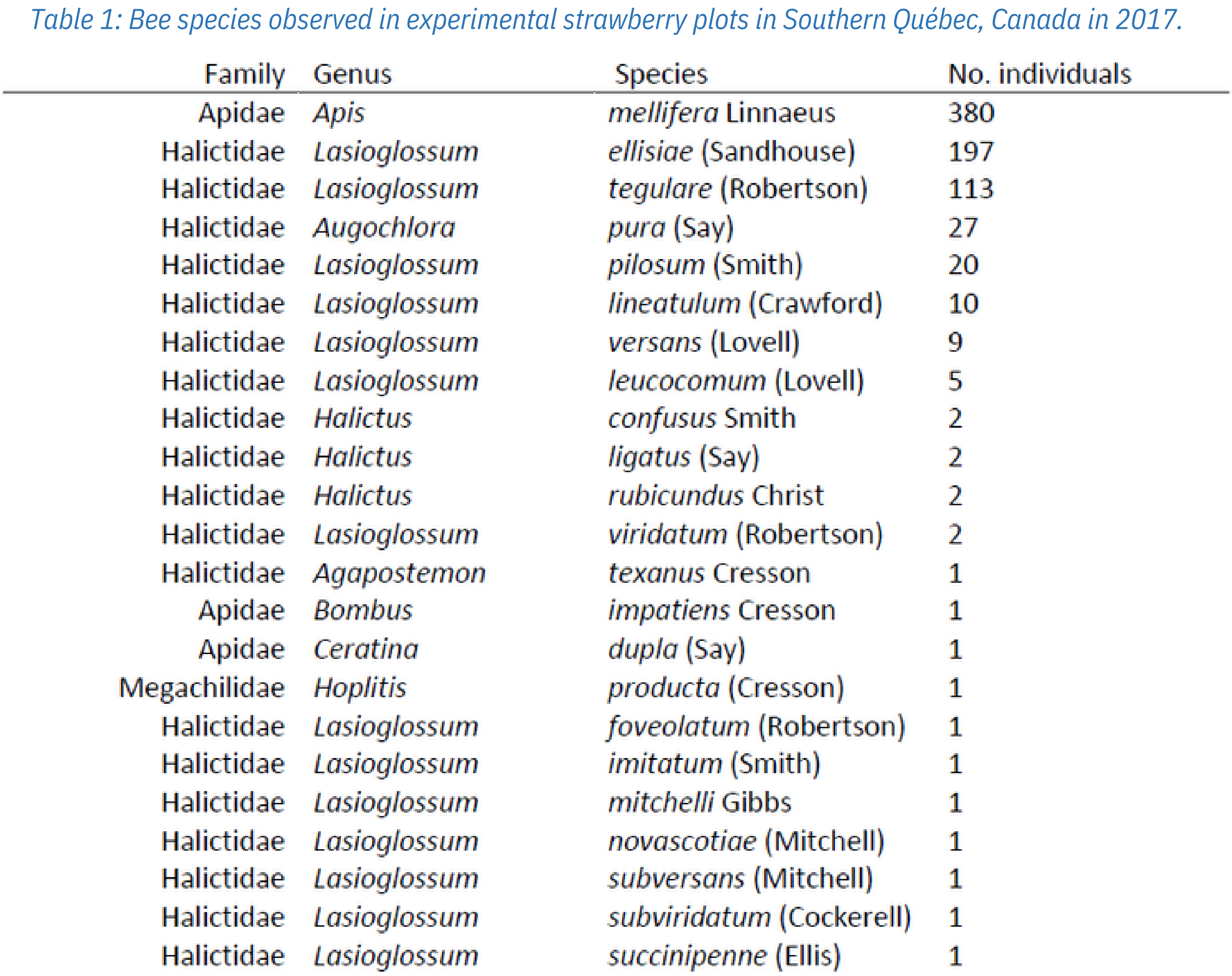

Table 1: Bee species observed in experimental strawberry plots in Southern Québec, Canada in 2017.

Family	Genus	Species	No. individuals
Apidae	*Apis*	*mellifera* Linnaeus	380
Halictidae	*Lasioglossum*	*ellisiae* (Sandhouse)	197
Halictidae	*Lasioglossum*	*tegulare* (Robertson)	113
Halictidae	*Augochlora*	*pura* (Say)	27
Halictidae	*Lasioglossum*	*pilosum* (Smith)	20
Halictidae	*Lasioglossum*	*lineatulum* (Crawford)	10
Halictidae	*Lasioglossum*	*versans* (Lovell)	9
Halictidae	*Lasioglossum*	*leucocomum* (Lovell)	5
Halictidae	*Halictus*	*confusus* Smith	2
Halictidae	*Halictus*	*ligatus* (Say)	2
Halictidae	*Halictus*	*rubicundus* Christ	2
Halictidae	*Lasioglossum*	*viridatum* (Robertson)	2
Halictidae	*Agapostemon*	*texanus* Cresson	1
Apidae	*Bombus*	*impatiens* Cresson	1
Apidae	*Ceratina*	*dupla* (Say)	1
Megachilidae	*Hoplitis*	*producta* (Cresson)	1
Halictidae	*Lasioglossum*	*foveolatum* (Robertson)	1
Halictidae	*Lasioglossum*	*imitatum* (Smith)	1
Halictidae	*Lasioglossum*	*mitchelli* Gibbs	1
Halictidae	*Lasioglossum*	*novascotiae* (Mitchell)	1
Halictidae	*Lasioglossum*	*subversans* (Mitchell)	1
Halictidae	*Lasioglossum*	*subviridatum* (Cockerell)	1
Halictidae	*Lasioglossum*	*succinipenne* (Ellis)	1

Table 2

Table 2: Results of LMMs of strawberry mass (mass per strawberry) by field design and bee type. The interaction between bee identity and field design is subdivided into two orthogonal contrasts for each strawberry variety. Results of the comparisons of bee type in each field design for each variety are also listed. n is the number of strawberries for each group. Significant differences are indicated in bold.

Variety	Bee/field type	Contrast	Mean ± SD (g)	n	χ^2	p
Albion	Honey bee	Single-variety vs.	15.41 ± 5.80	11	1.06	0.31
		Multiple-variety	16.38 ± 7.45	14		
	Wild bee	Single-variety vs.	18.80 ± 4.25	15	**9.35**	**0.009**
		Multiple -variety	24.05 ± 3.61	12		
	Single-variety field	Honey bee vs.	15.41 ± 5.80	11	2.45	0.12
		Wild bee	19.47 ± 4.06	15		
	Multiple-variety field	Honey bee vs.	16.38 ± 7.45	14	**14.52**	**<0.001**
		Wild bee	24.05 ± 3.61	12		
Seascape	Honey bee	Single-variety vs.	17.30 ± 5.29	30	2.74	0.30
		Multiple-variety	16.27 ± 6.22	21		
	Wild bee	Single-variety vs.	18.62 ± 4.05	18	3.14	0.24
		Multiple-variety	18.14 ± 4.70	35		
	Single-variety field	Honey bee vs.	17.30 ± 5.29	30	3.74	0.11
		Wild bee	18.62 ± 4.05	18		
	Multiple-variety field	Honey bee vs.	16.27 ± 6.22	21	2.32	0.13
		Wild bee	18.14 ± 4.70	35		

Table 3

Table 3: Results of the comparisons of strawberry mass (weight per strawberry) of strawberries pollinated by each bee type to the hand-cross-pollinated controls (Cross-pollinated). Single-variety Albion in plots that contained only strawberry plants of the Albion variety. Multiple-variety Albion plots had both Albion and Seascape plants in alternating rows. Single-variety Seascape in plots that contained only strawberry plants of the Seascape variety. Multiple-variety Seascape plots had both Seascape and Albion plants in alternating rows. n is the number of strawberries for each group, $\chi2$ is the test statistic, and p is the significance. Significant differences are indicated in bold.

	Strawberry mass Mean ± SD (g)	n	χ^2	p
Single-variety Albion				
Cross-pollinated	23.40 ± 3.86	14		
Honey bee	15.41 ± 5.79	11	15.84	**<0.001**
Wild bee	18.80 ± 4.25	15	5.63	**0.035**
Multiple-variety Albion				
Cross-pollinated	21.48 ± 4.63	15		
Honey bee	16.38 ± 7.44	14	4.45	**0.034**
Wild bee	24.05 ± 3.60	12	2.74	0.098
Single-variety Seascape				
Cross-pollinated	15.57 ± 2.82	13		
Honey bee	17.30 ± 5.29	30	1.79	0.36
Wild bee	18.61 ± 4.05	18	3.74	0.11
Multiple-variety Seascape				
Cross-pollinated	17.24 ± 3.48	16		
Honey bee	16.27 ± 6.22	21	0.11	0.73
Wild bee	18.15 ± 4.70	35	2.32	0.13

Table 4

Table 4: Results of the comparisons of strawberry mass (weight per strawberry) of strawberries pollinated by each bee type to the bagged, autonomously self-pollinated controls. Single-variety Albion in plots that contained only strawberry plants of the Albion variety. Multiple-variety Albion plots had both Albion and Seascape plants in alternating rows. Single-variety Seascape in plots that contained only strawberry plants of the Seascape variety. Multiple-variety Seascape plots had both Seascape and Albion plants in alternating rows. n is the number of strawberries for each group, χ2 is the test statistic, and p is the significance. Significant differences are indicated in bold.

Single-variety Albion	**Strawberry mass Mean ± SD (g)**	**n**	**χ^2**	**p**
Selfed	11.19 ± 4.79	22		
Honey bee	15.41 ± 5.79	11	6.41	**0.031**
Wild bee	19.47 ± 4.06	15	23.36	**<0.001**
Multiple-variety Albion				
Selfed	12.45 ± 4.28	23		
Honey bee	16.38 ± 7.44	14	7.33	**0.013**
Wild bee	24.05 ± 3.60	12	45.75	**<0.001**
Single-variety Seascape				
Selfed	16.82 ± 4.53	19		
Honey bee	17.30 ± 5.29	30	0.36	0.92
Wild bee	18.61 ± 4.05	18	3.34	0.14
Multiple-variety Seascape				
Selfed	17.51 ± 4.55	21		
Honey bee	16.27 ± 6.22	21	0.46	0.94
Wild bee	18.15 ± 4.70	35	1.01	0.31

Figure 1

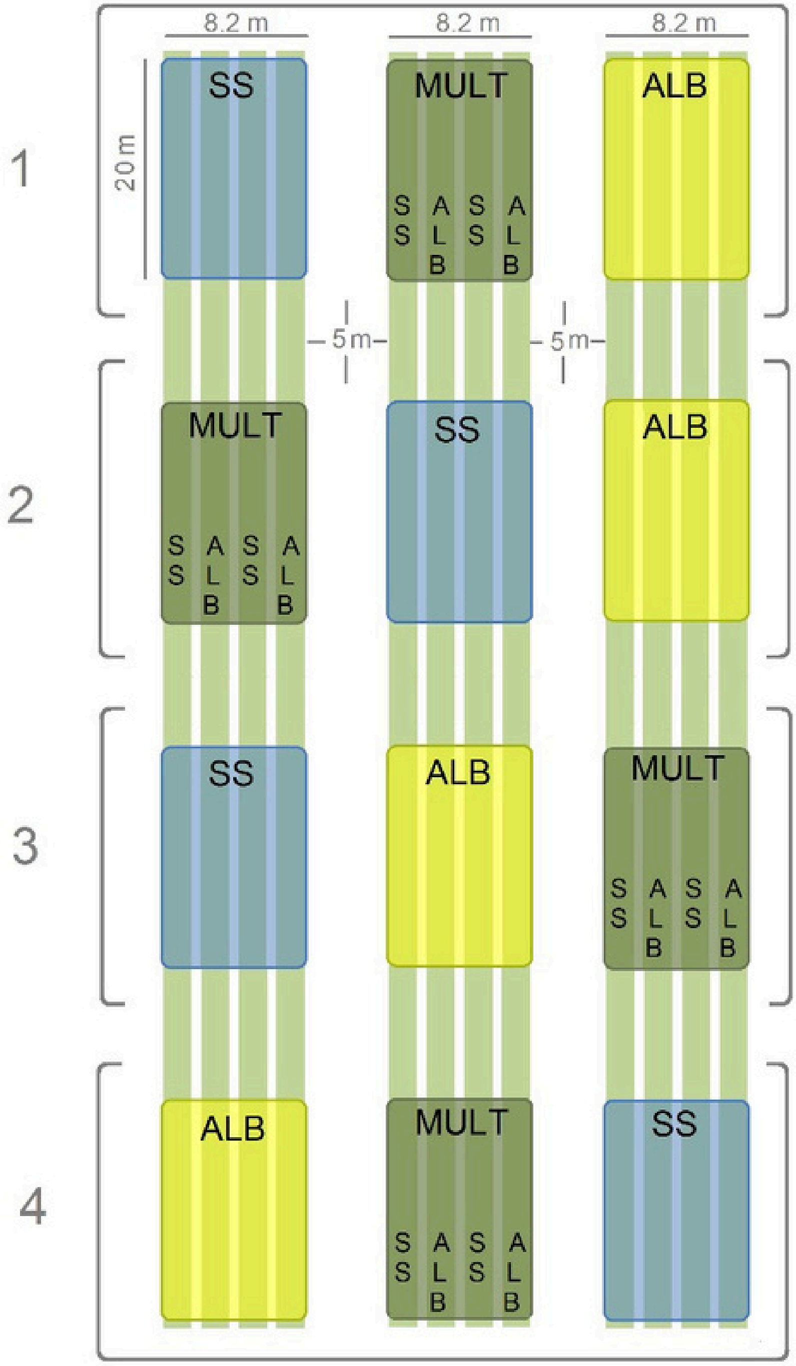

Figure 1: Experimental design. Field plots were arranged in a randomized complete block design with each plot containing four rows of strawberry plants 20 m long and 8.2 m wide. Numbers at left refer to the four experimental blocks. 'SS' indicates plots containing only strawberry plants of the Seascape variety in each of the 4 rows. 'ALB' indicates plots containing only strawberry plants of the Albion variety. 'MULT' plots contained two rows of Albion and two rows of Seascape interplanted within the plot.

Figure 2

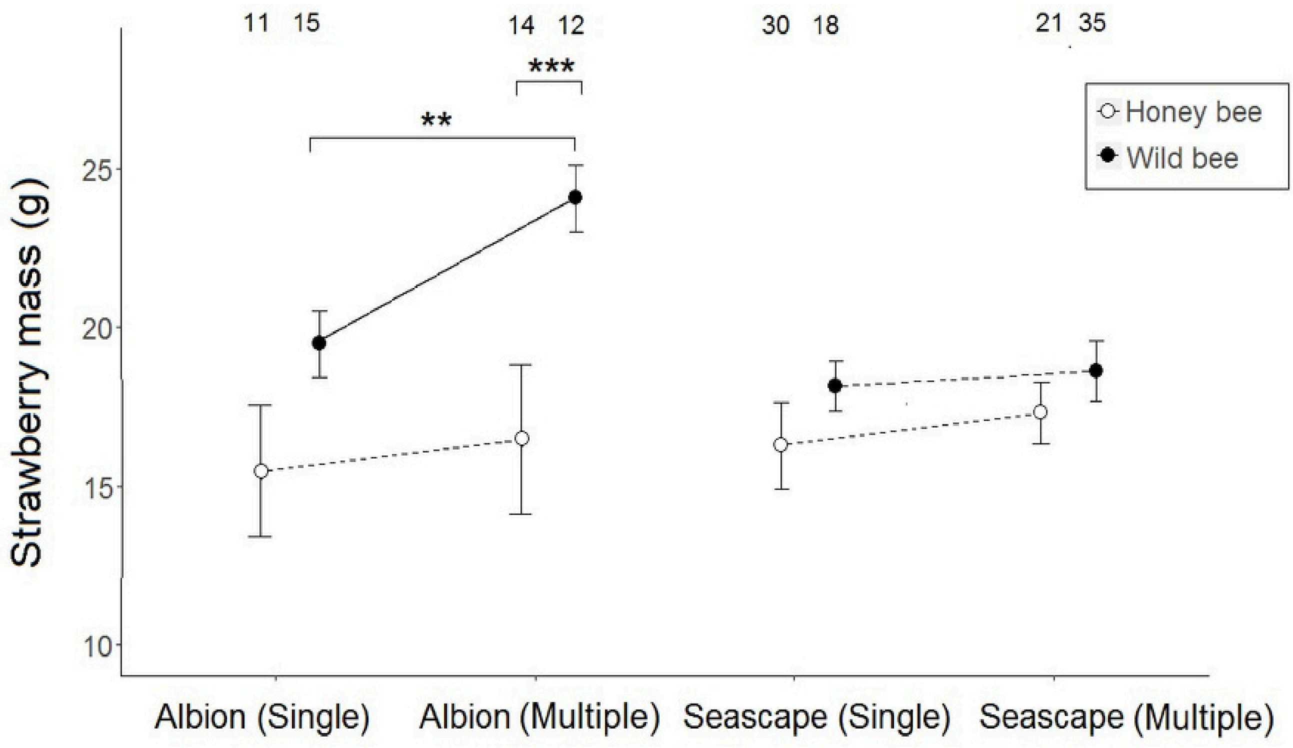

*Figure 2: Interactive effects of bee type and field design on the mass of two strawberry varieties. 'Albion (Single)' were strawberries in plots that contained only plants of the Albion variety. 'Albion (Multiple)' indicates Albion strawberries in plots that had Albion and Seascape plants in alternating rows. 'Seascape (Single)' were strawberries in plots that contained only strawberry plants of the Seascape variety. 'Seascape (Multiple)' were plots that contained Albion and Seascape plants in alternating rows. Open circles indicate strawberries that developed from honey bee-pollinated flowers and closed circles indicate strawberries that developed from wild bee-pollinated flowers. Error bars represent the standard error. Sample sizes are listed above. Solid line connecting symbols indicates $p < 0.05$; dashed lines indicate no significant difference between field designs. Asterisks indicate significant differences within field designs; *** = $p < 0.001$.*

Figure 3

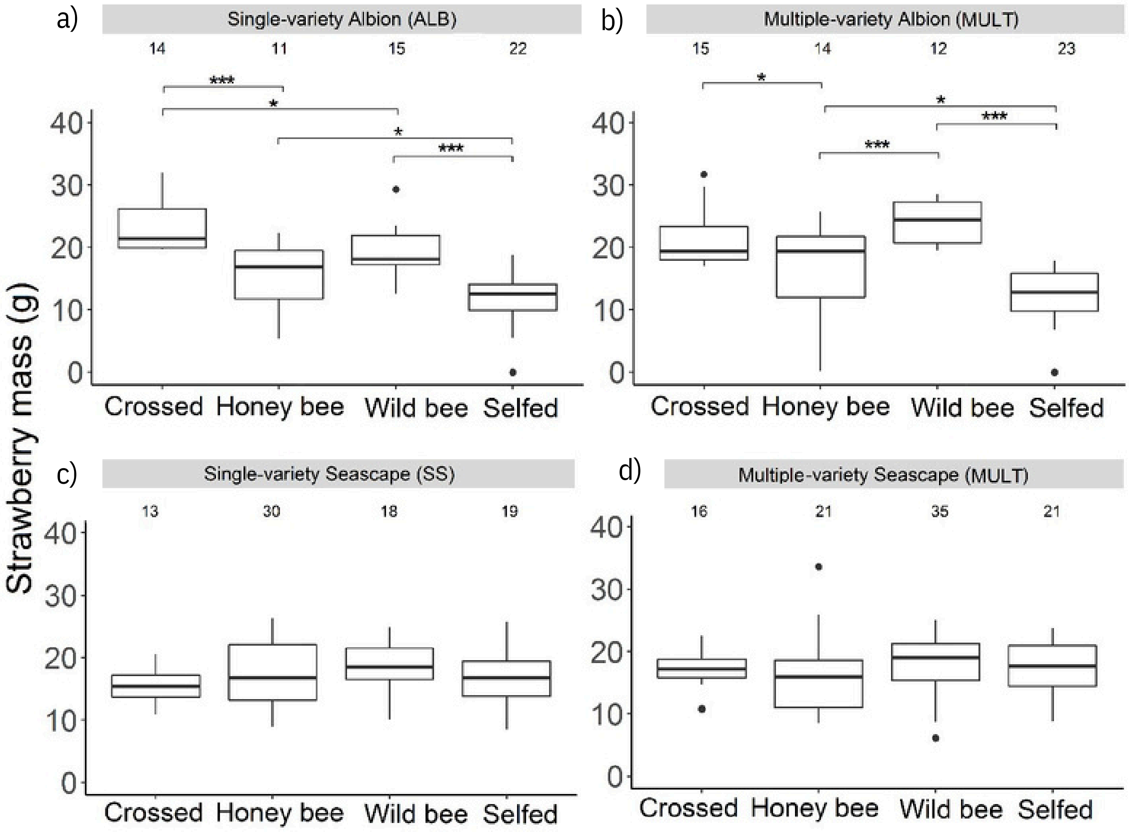

*Figure 3: Mean mass of strawberries produced by honey bee- and wild bee-pollinated flowers in each field type compared with the hand-cross-pollinated ("Crossed") and bagged ("Selfed") controls. 'Single-variety Albion (ALB)' were strawberries of the Albion variety in plots that contained only Albion plants. 'Multiple-variety Albion (MULT)' indicates Albion strawberries in plots that had both Albion and Seascape plants in alternating rows. 'Single-variety Seascape (SS)' were strawberries in plots that contained only strawberry plants of the Seascape variety. 'Multiple-variety Seascape (MULT)' were Seascape strawberries in plots that contained both Albion and Seascape plants in alternating rows. Sample sizes are listed above. Asterisks indicate significant differences, * = p < 0.05, *** = p < 0.001.*