Bee visitation, pollination services, and plant yield in commodity and hybrid seed canola

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Abstract

Insect-mediated pollination of crops is an important input to agricultural production, but pollination management suffers from key mechanistic gaps that hinder its greater utility. While pollination services to plants have a solid theoretical and mechanistic framework, agricultural pollination is often treated as a statistical "black box", without reference to the mechanisms underlying the process of pollination and fruit production. We present a causal model that links insect visitation to pollination to three separate components of yield, using two types of canola (*Brassica napus*) production systems. Commodity canola yield was mainly controlled by plant size, and there was no relationship between *Apis mellifera* visitation and pollen deposition, or deposition and seed yield. In comparison, seed canola yield was also controlled by plant size, but there was also a strong relationship between visitation and pollen deposition, as well as deposition and seed yield. We also found that *Megachile rotundata* visitation in seed canola strongly increased pollen deposition, but *A. mellifera* visitation did not. This model serves as a step towards a mechanistic model of pollination services, and points to the contextual importance of pollination services in seed canola production.

1 Introduction

Animal pollination of agricultural flowering plants is an important ecosystem service that contributes to about 10% of total crop production value worldwide (Gallai et al., 2009), and animal-pollinated plants produce a large number of important micronutrients in the human

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diet (Eilers et al., 2011). Therefore, understanding the process of animal pollination in crops is economically and ecologically important. Agricultural pollination, however, is largely treated as a single process, even though there are many links in the chain of events that result in the production of a fruit. Visitation of flowers by animals, typically bees and other insects, can result in pollen deposition on the stigma of the flower, followed by the growth of pollen tubes into the style and fertilization of ovules (Erbar, 2003). After fertilization, the plant may provide resources to fertilized fruits (or ovules within a fruit) to mature them into fruit (Goldberg et al., 1994). Each step has many other underlying processes (*e.g.* stigma receptivity, pollen tube growth, ovule abortion, fruit maturation, reviewed in Real, 1983; Giovannoni, 2001; Erbar, 2003; Takayama and Isogai, 2005, and others), but even at the level of this coarse approximation, most studies of agricultural pollination fail to account for important underlying processes. Pollinating animals rarely visit equally on all flowers in a blooming crop field(Currie, 1997; Brosi et al., 2008; Isaacs and Kirk, 2010), but some agronomic studies implicitly make this assumption (Jr. and Simpson, 1989; Bommarco et al., 2012; Bartomeus et al., 2014). Pollen deposition from visitors depends on a number of factors (*e.g* behaviour on flowers, size of pollinator), and whether this deposited pollen from visitors results in increased fruit production depends on the pollination context (*e.g.* self-pollination) and the life history and resource contexts of the plant (*e.g.* annual vs. perennial, determinate vs. indeterminate growth, light, soil nutrients and moisture). Moving beyond the "black-box" model of agricultural pollination requires accounting for these steps, and is necessary for understanding the contextual value of pollination services, as well as optimizing crop yield in novel circumstances.

Pollinator visitation is not spatially uniform within fields, as most pollinators are central-place foragers, meaning that visitation rates decline with distance away from their nest, and the bloom of flowering crops is not uniform. Smaller bees fly shorter distances than larger bees (Greenleaf et al., 2007; Zurbuchen et al., 2010), so their presence at the centre of large fields can be limited (Isaacs and Kirk, 2010). Hence, managing the location and density

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of managed pollinators in relation to their target crops is important for optimal yield of pollinator-dependent crops (Fries and Stark, 1983; Cresswell and Osborne, 2004). Foraging insects will often specialize on certain species or morphs of flowers in order to forage more efficiently (Heinrich, 1976; Goulson et al., 1997). However, pollination of hybrid seed crops requires movement of pollen between spatially separated lines of plants, so floral specialization can reduce the pollination services in these systems (Waytes, 2017; Gaffney et al., 2019). Competition between different species of foraging insects can occur if they deplete floral resources, but foragers can spatially or temporally separate their foraging to reduce competition (Schaffer et al., 1979; Thomson et al., 1987, but see Steffan-Dewenter and Tscharntke, 2000), thereby increasing their fitness. Both resource depletion or interference competition can motivate visitors to reduce competition by increasing their foraging distance, switching between floral morphs more often, or visiting less frequently (Heinrich, 1979; Greenleaf and Kremen, 2006). Thus, variation in visitation is driven by both distance from their nest (see Chapter 2), as well as competition with foragers from other aggregations, and increased competition can benefit plant fitness.

Insect visitation of flowers can enhance fruit production in flowering plants by increasing either the quantity or quality of pollen deposited on the stigma (Stephenson, 1981; Burd, 1994; Aizen and Harder, 2007), providing a larger range of female mate choice for each flower. Many flowering plant species are capable of self-pollination, but typically produce more fruit or seeds from outcrossed pollen (Knight et al., 2005) transported from conspecific plants by wind or an animal vector, but not all animal visitors are equal from a flowering plant's perspective. For example, large-bodied insects can deposit more pollen per visit on the stigma of the flower because they have a greater chance of contacting the stigmatic surface (Sahli and Conner, 2007). Pollinator behaviour is also important, as flower-visiting insects may steal nectar, clean off pollen between visits, or travel mainly between flowers on the same plant (Thomson, 1986; Herrera, 1987). Finally, the benefit of extra pollen deposition is diminishing (Plowright and Hartling, 1981), with very high numbers of pollen grains causing

less and less of an increase in fruit production (Ashman et al., 2004; Harder et al., 2016).

Seed production can be limited by plant resources as well as pollen (Galen et al., 1985; Haig and Westoby, 1988; Campbell and Halama, 1993), meaning that the benefits of insect pollination depend on the resources available to the plant (Stephenson, 1981; Tamburini et al., 2017). Pollen limitation can also occur at multiple levels within a plant, reducing the number of seeds per fruit, the number of mature fruit, or both (Burd, 1994). Low pollen deposition may reduce the number of mature fruit via flower abortion (Knight et al., 2006), where poorly-pollinated flowers are cut off from the plant. Plants with an indeterminate growth strategy may compensate for a high flower abortion rate by simply making more flowers, resulting in similar seed production to pollinated plants (Lovett-Doust and Eaton, 1982; Lawrence, 1993; Sabbahi et al., 2006; Bos et al., 2007). Whether individual plants can compensate for low pollination depends on the time remaining in the season, as well as the resources available to create extra shoots and flowers. Pollen limitation may also reduce the number of seeds per fruit, so additional pollen may result in a greater number of seeds per fruit (Knight et al., 2006), which in turn may result in a reduction in the size per seed (Free and Nuttall, 1968; Mazer, 1987) due to competition between ovules. Seed size can vary strongly among plants, and can be affected by resources available to the plant (Mazer, 1987; Venable, 1992). For example, Maddox and Antonovics (1983) observed a negative size-number tradeoff in *Plantago* seeds, but only after accounting for the positive effect of plant size, indicating that larger plants were better able to provision their seeds. Since the size and number of offspring are direct determinants of a given plant's fitness, and the yield of the plant in an agricultural setting, allocation strategies that plants use under situations of pollen or resource deficits are important both theoretically, and in the context of food production (Bos et al., 2007; Tamburini et al., 2019).

Insect pollination is especially important in the production of hybrid canola crops (*Brassica napus* L.). Hybrid "commodity canola" (used for oil and meal production) is the offspring of two parental "seed canola" breeding lines, a male-sterile "female" line and

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a hermaphroditic "male" line (Westcott and Nelson, 2001; Steffan-Dewenter, 2003; Clay, 2009). Seed canola production requires a large number of pollinators to ensure pollination of the female line (seed from the male line is not harvested), and extra pollination may also increase the yield of commodity canola (Morandin and Winston, 2005; Rader, 2010; Bommarco et al., 2012; Bartomeus et al., 2015; Perrot et al., 2018). However, many studies of commodity canola pollination suffer from either a lack of realistic context, have a number of potential confounding variables, or infer plant-level outcomes from flower-level treatments. Greenhouse experiments typically involve unrealistically high pollination, nutrient availability, and water, all of which can influence yield (Bartomeus et al., 2015; Marini et al., 2015). Field studies often relate yield to indirect measures of pollination services, such as insect abundance, species richness, or distance from sources of potential pollinators (Morandin and Winston, 2005; Ricketts et al., 2008), rather than direct measures, such as visitation rates or pollen deposition per stigma. These pollination proxies are then related to measures of yield, such as grams of seed per m^2, which may be useful to growers, but provide limited information about how plants dynamically respond to pollen exclusion or addition (but see Sabbahi et al., 2005). Net- or cage-treatments exclude insect vistiation from certain plants or flowers, but can alter wind pollination, humidity, light, or pest pressure (Olsson, 1960; Neal and Anderson, 2004; Jauker and Wolters, 2008), meaning that the sole effect of lower insect visitation is confounded by other factors. These methods offer an incomplete picture of how pollination relates to yield in canola crops (Ouvrard and Jacquemart, 2019), and obscure estimates of pollinator value in a globally valuable crop species (Melathopoulos et al., 2015). Thus, whether pollination impacts commodity canola production (or if not, why not) is poorly understood.

Fruit production in plants involves a sequence of processes (visitation $\rightarrow$ pollen deposition $\rightarrow$ fruit production $\leftarrow$ plant resources), that determine the magnitude of the link between pollination and the components of crop yield. However, most studies of how pollination relates to crop yield either examine each process independently, or omit intermediate steps

in the sequence of events (but see Sáez et al., 2018), meaning that the relative importance of visitation and plant resources are unresolved. Structural equation models (SEM) provide a framework for empirical analysis of this sequence, as they allow underlying causal assumptions to be formally stated and tested (Shipley, 2009; Grace et al., 2012), provide insight into alternative mechanisms that may be at play, and are flexible in many of their assumptions (Clough, 2012). SEMs represent an intermediate class of statistical models, occupying a space somewhere between regression-style models and dynamic or agent-based models, making them ideal for generating and testing sets of mechanistic hypotheses (Grace, 2006; Kline, 2013). Using both commodity and seed canola provides an opportunity to compare two plant varieties that differ strongly in their pollination requirements, using a similar type of structural model, while accounting for agricultural differences between varieties (spatial arrangement, planting density, irrigation).

In this study, we modeled how distance influences pollinator visitation, which in turn influences pollen deposition and seed yield, using commodity and hybrid seed canola crops in Alberta, Canada. Our five main hypotheses are outlined as follows:

1. Foraging honey bees and leafcutter bees are sensitive to distance due to cost of flight (Schmid-Hempel et al., 1985), and deplete floral resources with visitation. Therefore, insect visitation should decline with distance from their hive or shelter to achieve equivalent rewards (Dukas and Edelstein-Keshet, 1998; Cresswell et al., 2000).

2. Visiting bees can deposit pollen on stigmas, so areas with high rates visitation should have more pollen deposition on stigmas than areas with low rates of visitation (Mesquida et al., 1988; Hoyle et al., 2007), depending on foraging behaviour of the bee (Free and Ferguson, 1983).

3. Seed production for a given plant is limited by the resources it is able to sequester. Therefore, large plants should have more resources at their disposal, and should produce more fruit per plant and produce a higher number of larger seeds per fruit (Galen

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et al., 1985; Lawrence, 1993; Marini et al., 2015).

4. Seed production in resource-rich plants is also limited by pollination. Plants in areas with high pollen deposition should have a higher proportion of successful flowers (Sabbahi et al., 2005), and a higher number of seeds per pod (Morandin and Winston, 2005).

This study assesses the strength of the connections between visitation, pollination, and yield, in a globally important crop species, and identifies the relative importance of bee pollination for seed production, using in-field data from two distinct cropping systems. Other studies of crop pollination focus on individual components, such as visitation and pollination (Cresswell, 1999; Thomson and Goodell, 2001), or visitation and yield (Steffan-Dewenter, 2003; Manning and Wallis, 2005; Hudewenz et al., 2013), but have not incorporated the links in a single framework (but see Sáez et al., 2018, and few have used realistic field data (Morandin and Winston, 2005; Isaacs and Kirk, 2010). This work adds to the body of literature examining the resource context of pollination services (Haig and Westoby, 1988) within cropping systems (Marini et al., 2015; Tamburini et al., 2016; Fijen et al., 2018; Tamburini et al., 2019), and identifies directions of future research in seed production systems.

2 Methods

2.1 Data collection

From June through August of 2014 and 2015, we surveyed 29 commodity canola fields (14 in 2014, 15 in 2015) near Beaverlodge, Alberta and 31 fields (17 in 2014, 14 in 2015) near Lethbridge, Alberta. Commodity canola fields were selected based on the proximity of honey bee apiaries and site access. 28 of the 60 fields were stocked with honey bees (mean: 0.6 hives/hectare, SD: 0.58) while 32 fields were unstocked. 14 of 31 of the fields near Lethbridge were watered using central-pivot irrigation systems.

During 2015 and 2016, we also surveyed 35 hybrid seed canola fields (15 in 2015, 20 in 2016) near Lethbridge, Alberta, from June through August of each year. Seed fields were all stocked with honey bee hives at a rate of 3.6 hives/ha, with apiaries stationed in the corners of fields, and were also stocked with leafcutter bees in shelters throughout the field. Shelters used either "standard" or "double" leafcutter bee stocking (≈50,000 vs. 100,000 cocoons/ha), and shelters were placed at either "standard" or "double" densities (1.3 vs. 2.6 shelters/ha) in each field. Double stocking rates were only used in fields with double shelter density. All seed fields had central-pivot irrigation, and were mostly circular or semi-circular in shape.

In commodity fields, we established plots at 5, 20, 100, and 500m along a transect into the field, starting at the field margin closest to the set of honey bee hives (271 total plots). In unstocked fields, we began the transect at a field edge close to potential sources of natural pollinating insects, such as forests or grasslands, but observed very few wild pollinators (Table S1). In seed canola fields, bays of "male" and "female" plants were planted in 1- and 6-m wide bays, respectively, and leafcutter bee shelters were located in the female bays (Figure 1, 2). We established plots at 5, 20, 100 (250 in 2016), and 400m into the field along a transect from the nearest set of honey bee hives. We made paired observations in adjacent male and female plots at each distance from the edge of the field (Figure 2). At the edge and centre of each field (5m and 400m), we established another plot in the centre of the female bay to examine the effect of distance away from the male bay. We also used plot-level leafcutter and honey bee visitation data from Waytes (2017, and unpublished; same years and locations) to more accurately estimate the effect of distance from shelter on visitation rates (647 total plots). We used a Nikon™Laser 800S Rangefinder to measure the distance from each plot to the nearest shelter. All surveys occurred on fair-weather days (median air temperature: 24.5°C., range: 17–33) with no rain and as minimal wind as possible (less than 30km/hr). Mean air temperature was similar between years in Grande Prairie (≈ 22°C), but Lethbridge was warmer in 2015 (23 vs. 28°C). Plots were marked with coloured stakes

Figure 1: Hybrid seed field near Rainer, AB, showing the outlines of male and female bays in the foreground, with orange leafcutter bee shelters stationed throughout the field. The linear structure on the horizon is the central-pivot irrigation sprinkler.

driven into the soil to locate them later in the season.

Within each $1m^2$ plot, we recorded the number of insect contacting the stigmas and anthers of flowers during 10 minutes (5 min for seed fields during 2015), as well as their taxonomic identity. We counted visitable flowers in each plot, where "visitable" was defined as an opened flower whose petals had not yet started to dehisce, and whose style had not elongated more than 3-4 millimeters beyond the anthers. To assess pollen deposition at the plot level, we collected stigmas from five random open, receptive flowers at each plot, mounted them in fuchsin gel (Beattie, 1971) on depression slides, and counted the pollen on each stigma using a Leica™DME 13595 light microscope under 100x magnification (1294
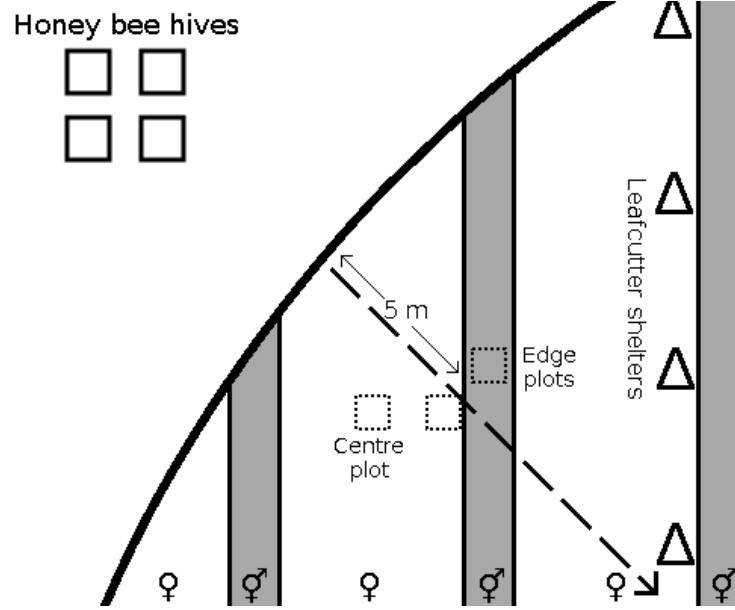
Figure 2: Plot arrangement for surveys in hybrid seed fields, showing hypothetical arrangement of leafcutter shelters (Δ), and male-fertile ($\male$) and female bays ($\female$) at 5m from the edge of the field. Plots were placed 5, 20, 100, and 400m along a transect (dashed line) from the field edge nearest to the set of honey bee hives. Plots were placed side-by-side in the male bay and edge of the female bay ("edge" plots), and at the 5m and 400m distances, a plot was placed in the centre of the female bay ("centre" plots).

commodity and 1050 seed canola stigmas). Each field was visited once during the main canola bloom (late June - late July), and again before harvest (mid - late August) to collect plant samples. We collected three plants and recorded the density of plants per m^2 at the same plot where we conducted the visitation observations (789 commodity canola plants, 582 seed canola plants). After drying the plants at 50°C, we weighed the entire plant, counted mature pods, and counted the number of remaining flower pedicels to estimate total flower production. We randomly sampled five pods from each plant, and counted and weighed the seeds from each pod, (3872 commodity canola pods, 2885 seed canola pods). Finally, we threshed all the pods for each plant by hand, winnowed them using an air separator, and weighed the total mass of cleaned seeds.

2.2 Analysis

To examine how yield is influenced by visitation, we used a piecewise structural equation model framework (pSEM, Shipley, 2009). Structural equation models are comprised of a set of underlying linear models arranged in a causal network, and provides a framework for testing hypotheses about a complex system (Grace et al., 2012; Lefcheck, 2015). Starting with a simple model (visitation → pollen deposition → fruit production ← plant resources), we built more complex models that related measured variables within a causal framework (Figures 3 and 4). These models allowed us to infer the relative strength of the main terms (e.g. pollen deposition, plant size) while controlling for other confounding factors (e.g. distance into field). Fruit set can suppress future vegetative growth and flower production (Stephenson, 1981), but SEMs do not allow for causal loops (Grace et al., 2012), so we included a path from fruit set to flower production. The direction of the path could plausibly be reversed (whereby large number of flowers reduce the proportion of fruit set), but we considered only the first scenario, as Sabbahi et al. (2006) showed that the converse process is more likely (low fruit set causes increased flower production).

The underlying models of each pSEM were specified as generalized linear mixed-effects models (GLMMs, see Equation sets S1 and S2 for model specifications). We used hierarchical models in order to include processes that occur at different levels; for example, seed size-number trade-offs were modelled at the pod level, whereas pollen deposition was modeled at the flower level. Normal random effects were used to model variance between fields, within-field (pollen, flower survival, seed count & size), and within-plot (seed count & size); if the lowest-level variance term was inestimable, we fit the model without it. Continuous responses were modeled using log-normal (plant density, plant size), square-root normal (flower density), and exponential-normal distributions (weight per seed), while counts were modeled as a negative-binomial (honey bee visits, pollen grains per stigma, flowers per plant, seeds per pod) or zero-inflated negative-binomial distribution (leafcutter bee visits) with a log-link function. Visitation models used a log(time) term with a slope of 1 ("offset" variable)

to account for differences in observation times. Fruit set (fraction of flowers that matured into pods) was modeled using a beta-binomial distribution with a logit-link function. Interactions between predictors were evident in honey bee visitation rate (Year:Locality interaction) and plant density (Irrigation:Year) in commodity canola, and for leafcutter bee visitation (Tent Stocking:Distance from edge) in seed canola, and were included in each model (represented as Y-shaped path in Figures 3 and 4). Finally, we created bivariate partial-effect plots of relevant terms within each model to aid in visualising each relationship.

Structural equation models do not have paths between all variables, which may bias the model results if this independence assumption is not true. We evaluated evaluating independence claims ("basis set") by using Fisher's C statistic from Shipley's d-separation criteria (Shipley, 2000, 2009). The initial commodity canola pSEM was misspecfied, as several missing paths were identified for the initial commodity model (Fisher's C=202.1, df=100, p<<0.001), but the updated pSEM that included missing paths was judged adequate (C=81.6, df=86, p=0.62). Similarly, the initial seed field pSEM also had several missing paths (C=37.54, df=56, p=0.027), which we corrected (C=58.10, df=64, p=0.68). D-separation criteria sets were generated using the `dagitty` library in R 3.5.1.

All component GLMMs of the pSEM were written in Stan 2.17.1 (Gelman et al., 2015), and run using `rstan` 2.18.1. We used informative normal priors ($\mu = 0, \sigma = 5$) for fixed effects, and gamma priors ($\alpha = 1, \beta = 1$) for the variance components. We ran three separate chains with an adaptive phase of 2000 iterations, and a sampling phase of 2000 iterations, then checked for convergence of the chains ($\hat{R} \approx 1$) and low autocorrelation within chains (high N_{eff}). We assessed the adequacy of the underlying probability distribution functions of each model using posterior predictive checks (Gelman et al., 2013), and found that the probability distributions were specified correctly (p~0.5) for all components except seed count. This means that while the average seed counts (per plant) were unbiased, the variance within a plant was not. However, the negative binomial distribution had the closest posterior predictive checks of any other distribution.

3 Results

The SEMs revealed that plant size and pollen deposition were the main drivers of yield in seed canola, while only plant size mattered in commodity canola. Distance from the field edge had a negative effect on honey bee visitation in commodity and seed canola (Z=-3.7, -2.5, respectively), and unexpectedly, had a negative effect on leafcutter bee visitation (Z=-4.4), showing that overall visitation decreases with distance into the field. The path from leafcutter bee visitation to pollen deposition was strong in seed canola (Z=3.2), but there was no path from honey bee visitation to pollen deposition in either crop type. Pollen deposition increased fruit set (Z=3.1) and seeds per pod (Z=2.3) in seed canola, but was not present in commodity canola, showing that yield in seed canola, but not commodity canola, is strongly dependent on pollination. Both crop types had strong negative paths from flower survival to flowers per plant (commodity Z=-12.5, seed Z=-12.1), indicating that high flower survival suppressed future flower production. Commodity canola had a similar weight per seed, regardless of the plant size, but in seed canola, plant size had a strong influence on seeds per pod (Z=5.6) and weight per seed (4.6). Finally, in both crop types, the paths leading from plant size were the dominant signal influencing fruit set (commodity Z=5.8; seed Z=19.9), but the path from pollen deposition to fruit set was only present in seed canola, showing that plant resources matter strongly for both crop types, but that increased pollen deposition only benefits seed canola.

The results of the underlying components of each pSEM are shown below:

3.1 Prediction 1: Decline in visitation with distance

Bee visitation strongly declined with distance away from the hives and shelters, in both commodity and seed canola fields. In commodity canola, honey bee visitation sharply declined with distance into the field (Z=-3.7, p=0.0002, Figure 5), decreasing from 8.5 visits/hr at the edge of the field to 3.1 visits/hr at 100 m into the field (at a stocking level of 20 hives).

Figure 3: Path diagram for the commodity canola model, with positive and negative terms shown in black and red, respectively. Line thicknesses are proportional to effect size (mean/SD) of coefficients. Coefficients with 95% posterior quantiles overlapping zero are shown with a transparent line. Interactions are shown as an inverse Y-shaped path, with the two branches representing main effects, and the final branch representing the interaction term (*e.g.* effect of site and year on honey bee visitation rate). Year:site interaction is also shown in Figure 5. "Year" indicates the year effect of 2015, and "Site" indicates the site effect of Grande Prairie.
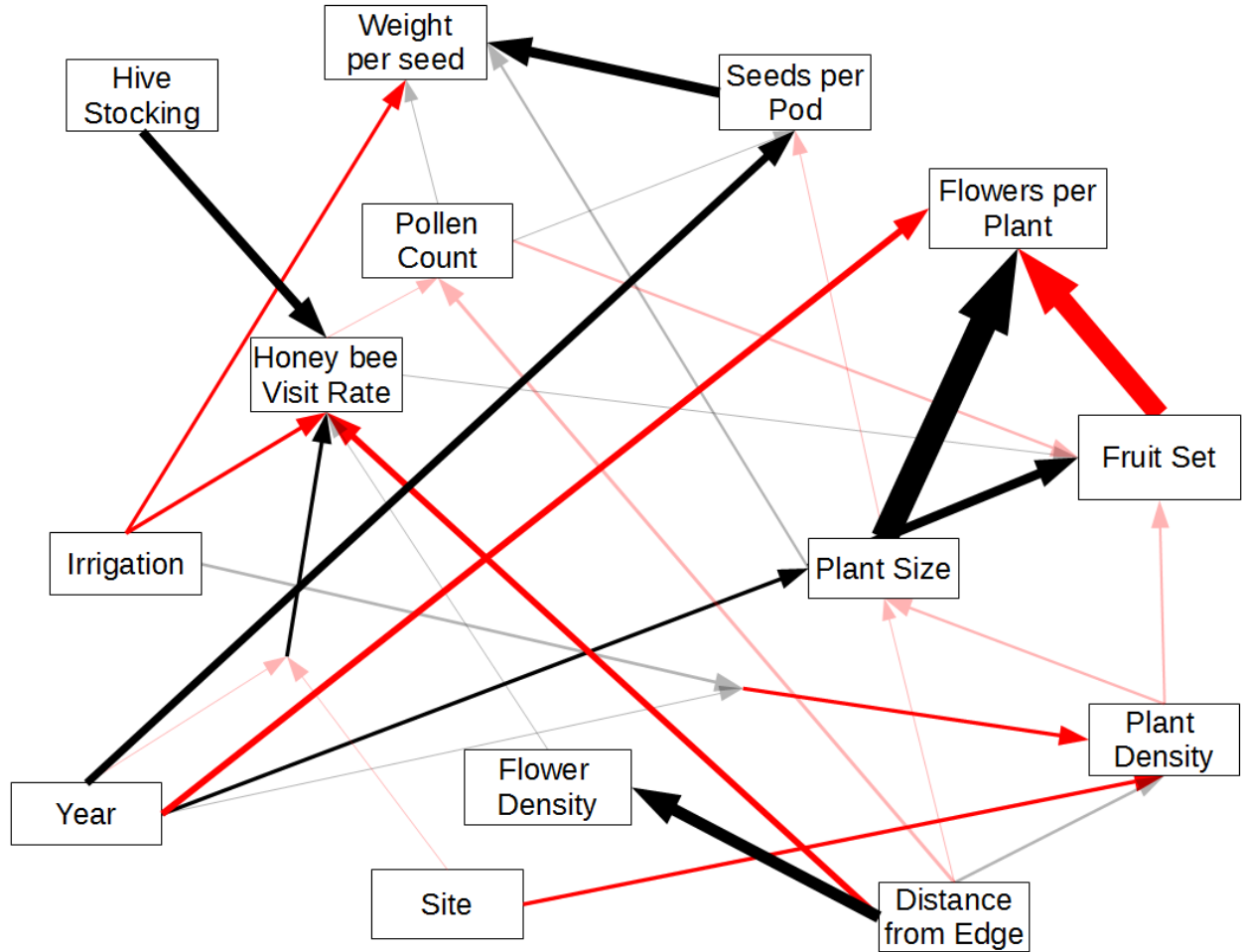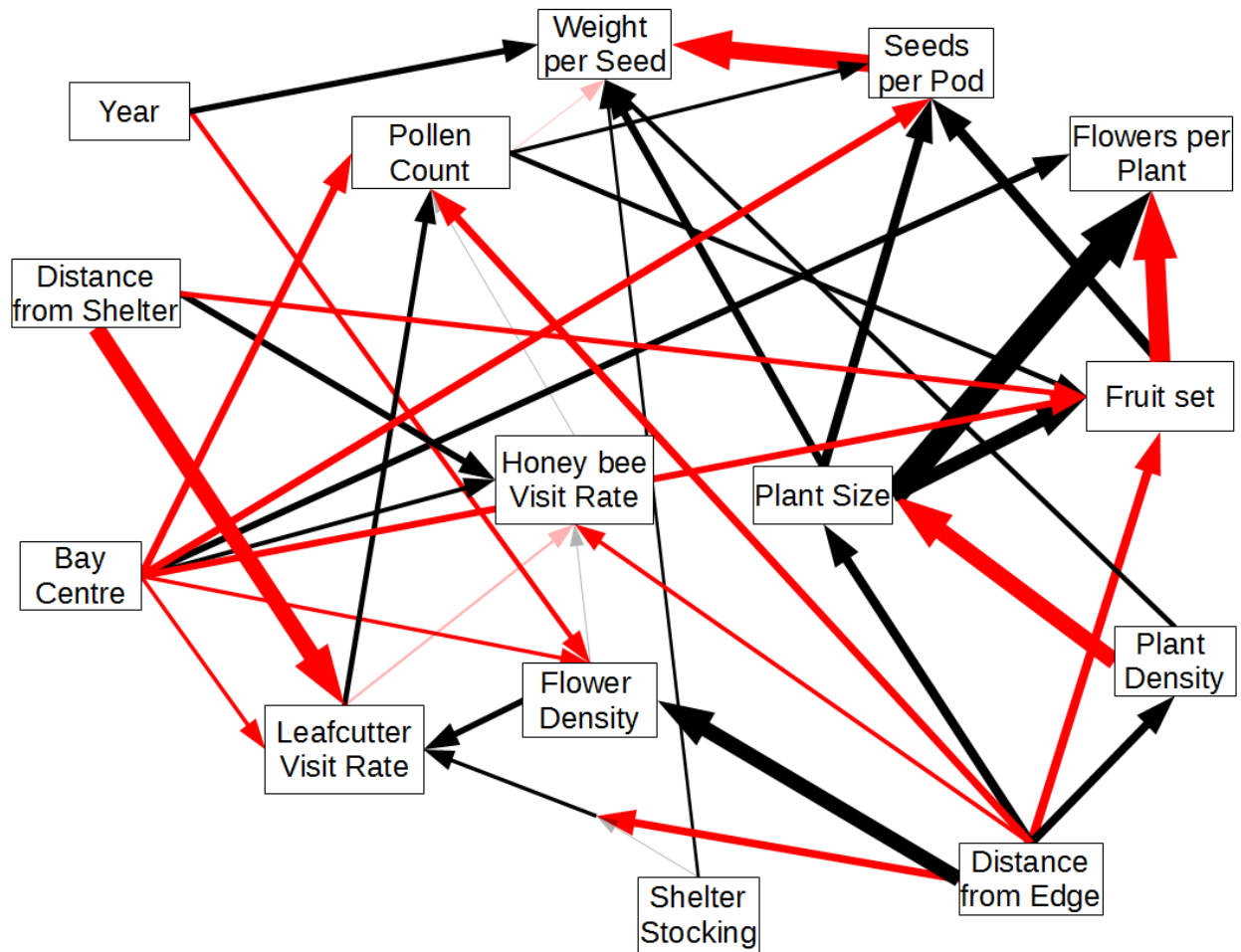
Figure 4: Path diagram for the seed canola model with positive and negative terms shown in black and red, respectively. Line thicknesses are proportional to effect size (mean/SD) of coefficients. Coefficients with 95% posterior quantiles overlapping zero are shown with a transparent line. Interactions are shown as an inverse Y-shaped path, with the two branches representing main effects, and the final branch representing the interaction term (*e.g.* effect of distance from edge and shelter stocking rate on leafcutter bee visitation rate). Stocking:Distance interaction is also shown in Figure 6. "Year" indicates the year effect of 2015.

Visitation rates were higher in both years in Lethbridge (2014: 9.3 visits/hr, 2015: 7.1), but were higher in 2015 than 2014 at Grande Prairie (Z=2.3, p=0.02), rising from 5 visits/hr at the field edge in 2014 to 17 visits/hr in 2015. Honey bee visitation increased with the number of hives used for stocking (Z=5.3, p<0.0001); plot-level visitation at the edge of the field increased from 14.5 visits/hr with an apiary of 20 hives to 22.7 visits/hr with an apiary of 40 hives, while unstocked field edges had 1.8 visits/hr. In seed canola fields, honey bee visitation also declined with distance into the field (Z=-2.5, p=0.01), but not as strongly as in commodity fields (126 visits/hr at edge of field vs. 78 visits/hr at 100 m). Honey bee visitation was lower near leafcutter shelters (Z=3.9, p=0.001), dropping from 60 visits/hr at 10 m to 34 visit/hr at 2 m, likely due to competition with leafcutter bees (Figure 6, 7).

Leafcutter bees were much more sensitive to distance from their shelter than honey bees. Leafcutter bee visitation sharply declined with distance from their shelters (Z=-11.4, p=0.0001, 350 visit/hr at 2 m to 83 visit/hr at 10 m), and unexpectedly, was higher at the edge of the field than the centre (Z=-4.4, p=0.0001, 114 visits/hr vs 28 visits/hr). However, there was no difference in visitation rates when the stocking rate of cocoons per shelter was lower (Z=2.2, p=0.028), indicating that leafcutters at high stocking densities may migrate to shelters close to the edge of the field (Figure 6). Both leafcutter bees and honey bees visited at similar rates in the male and female bays (leafcutter bee: p=0.72, honey bee: p=0.32), but within the female bay, leafcutter bee visitation was lower in the centre of the bay (p=0.04, 51 vs. 29 visits/hr), while honey bee visitation was higher at the centre of the bay (p=0.008, 71 vs. 117 visits/hr, Figure 8).

3.2 Prediction 2: Pollen deposition increased by bee visitation

Pollen deposition was enhanced by bee visitation in seed canola, but not in commodity canola. In commodity canola, pollen deposition on stigmas was high (mean: 293 grains per stigma, SD: 385, range: 0–3981), but honey bee visitation did not affect deposition (p=0.77, Figure 9). Pollen grains per stigma weakly declined with distance from the edge of the field
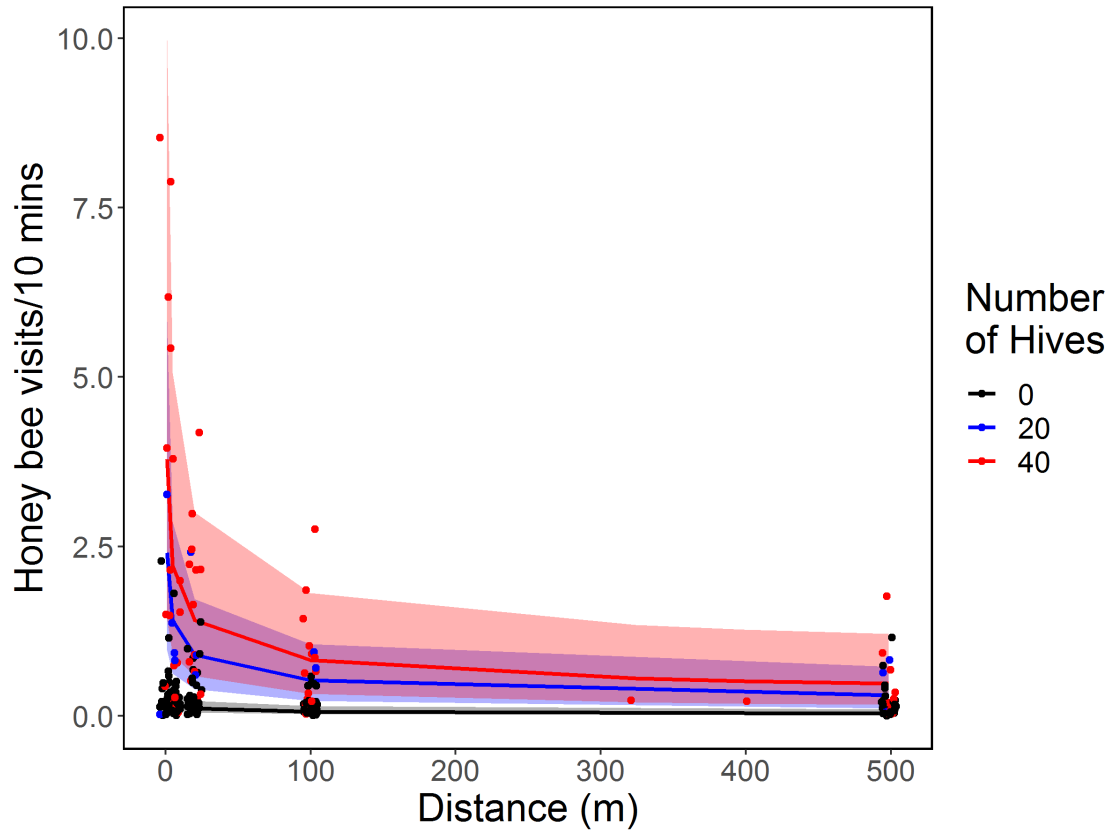
Figure 5: Partial effect of distance away from field edge and stocking on honey bee visitation in commodity canola fields. Solid lines represents median, and shaded areas represent 95% CIs. Red line represents overall slope (controlling for region and year).
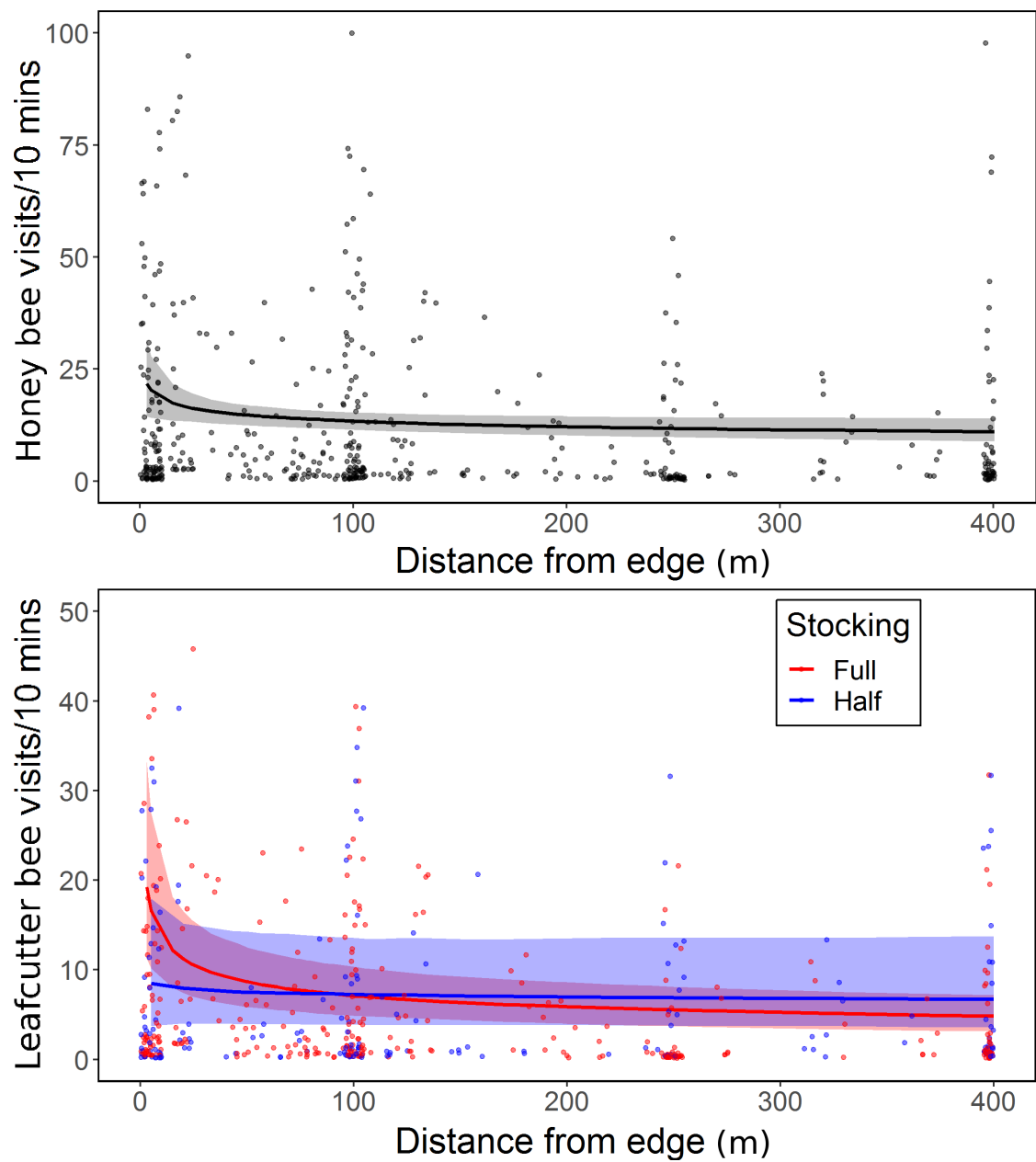
Figure 6: Partial effect of distance from field edge on honey bee and leafcutter bee visitation in seed canola fields. Solid lines represent medians, and shaded areas represent 95% CIs.
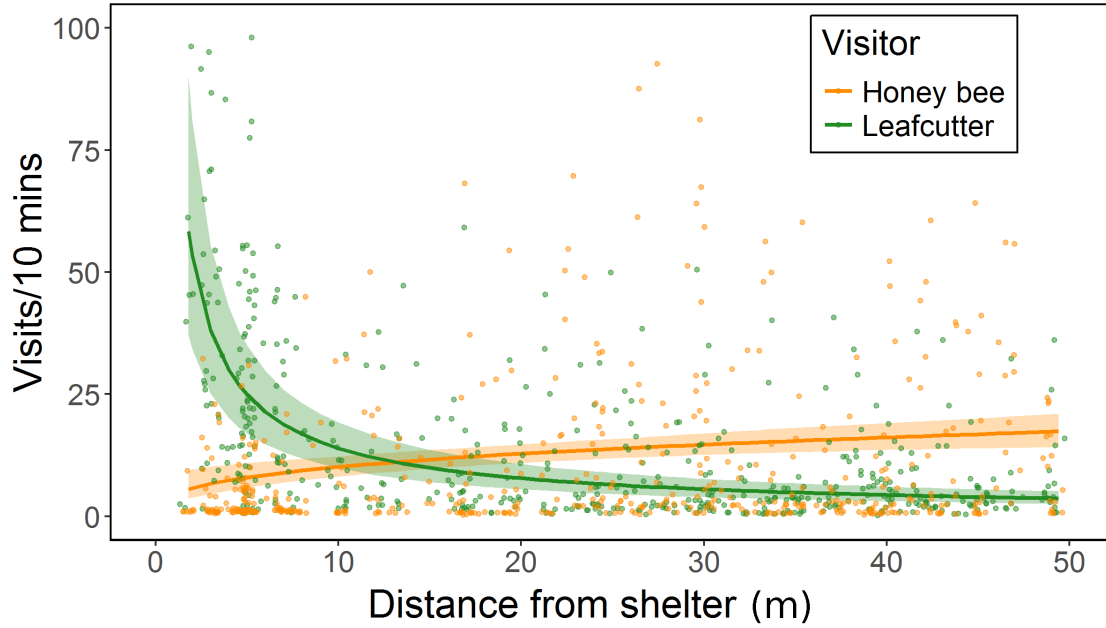
Figure 7: Partial effect of distance from leafcutter shelter on honey bee and leafcutter bee visitation in seed canola fields. Solid lines represent medians, and shaded areas represent 95% CIs.

(p=0.07), but this only amounted to an average decrease of 290 grains per stigma at the edge compared to 240 at the field centre (6% decrease), meaning that distance did not strongly affect pollen deposition either. Flies were common visitors in commodity fields (Table S1), but had no detectable effect on pollen deposition (p=0.577), and other flower visitors were rare, so only honey bees and leafcutter bees were considered as potential pollinators. In seed canola, overall pollen deposition was much lower (mean: 22 grains per stigma, SD: 43, range: 0–578), was strongly increased by leafcutter bee visitation (Z=3.2, p=0.002, Figure 10, 12 grains/stigma at 6 visits/hr vs. 16 pollen grains at 60 visits/hr), and also decreased with distance from the edge of field (Z=-4.4, p=0.0001, Figure 11, 23 vs. 11 grains/stigma). Pollen deposition was lower in the centre of the female bay (Z=-4.5, p=0.0001, 23 vs. 13 grains/stigma) independent of visitation rate, suggesting that pollen is lost from bees crossing from male bays, who likely visit flowers at the edge of the bay first (Pinnisch and McVetty, 1990). There was no direct effect of honey bees on pollen deposition (Z=0.98, p=0.33), implying that most of the pollen deposition occurs via leafcutter visitation.
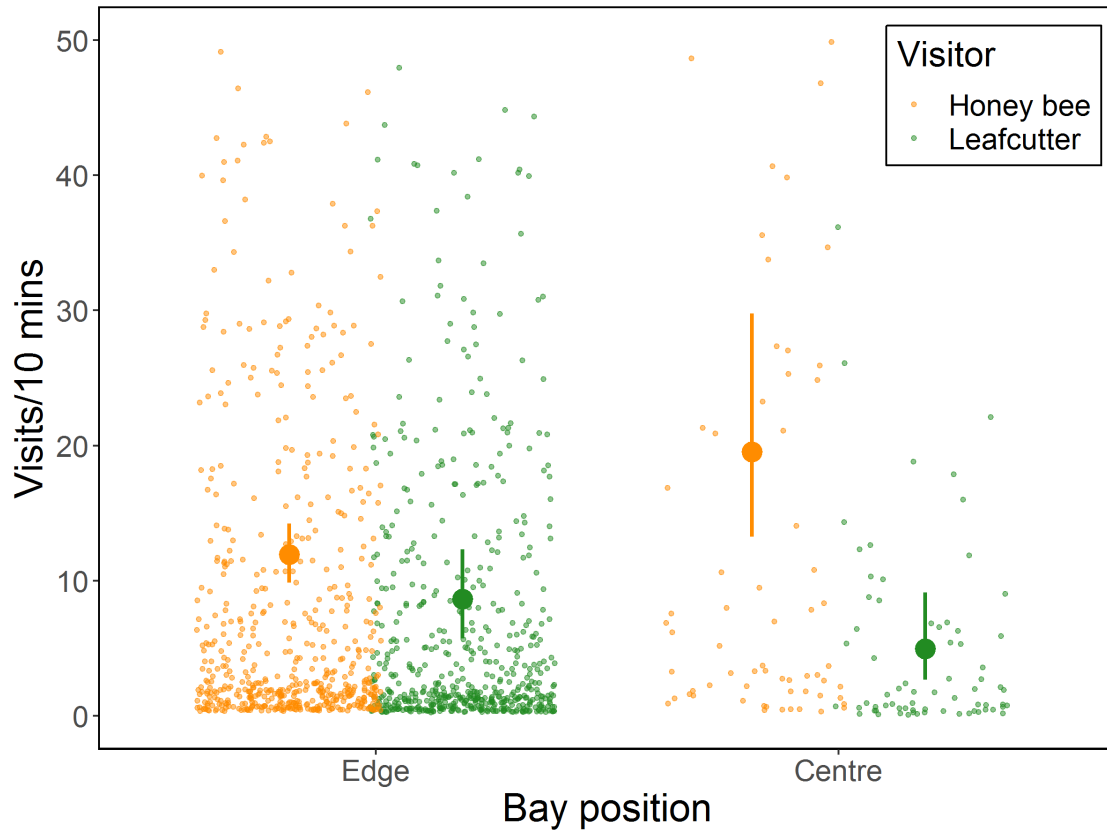
Figure 8: Partial effect of bay position (edge or centre of female bay) on honey bee and leafcutter bee visitation. Coloured points represents median value, and vertical bars represent 95% CIs.
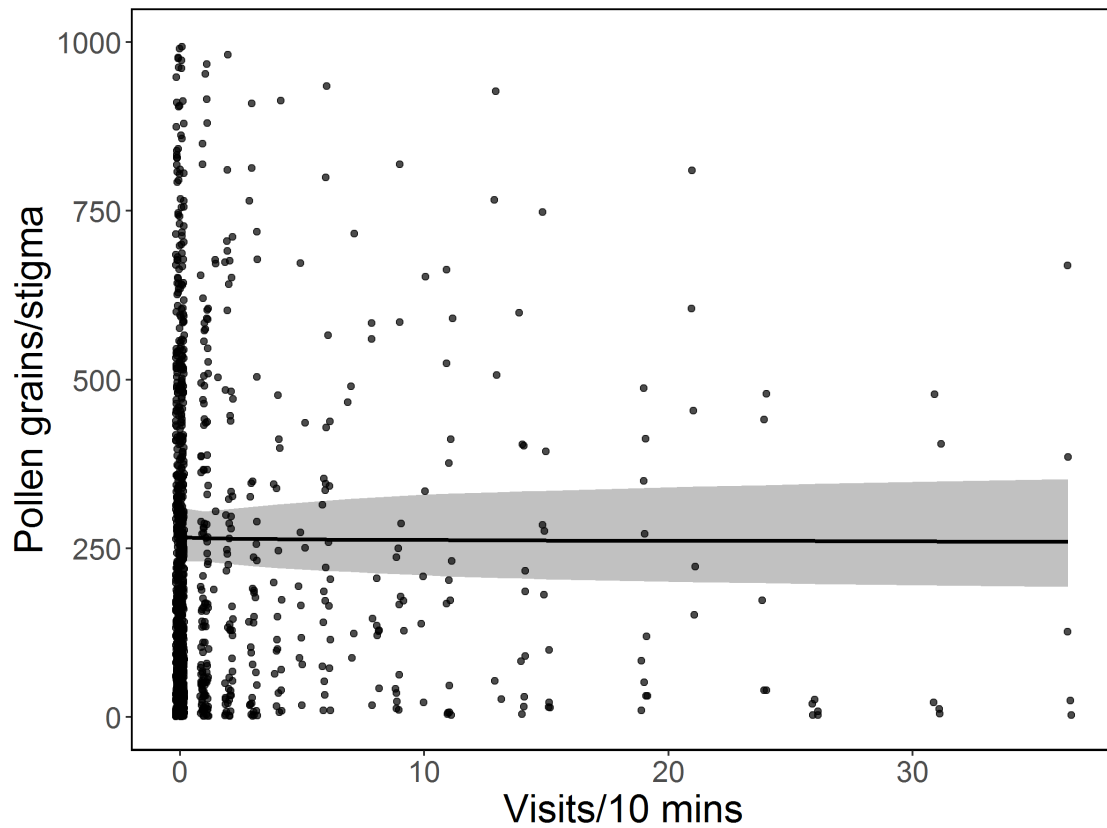
Figure 9: Partial effect of honey bee visitation on pollen deposition in commodity canola. Solid line represents median, and shaded areas represent 95% CIs.
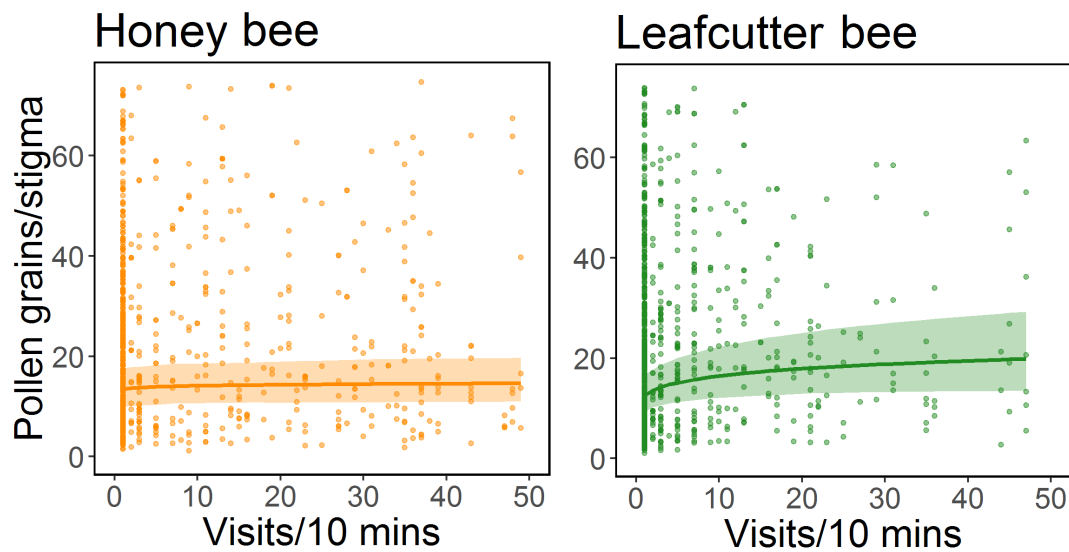
Figure 10: Partial effects of honey bee and leafcutter bee visitation on pollen deposition in seed canola. Solid lines represent medians, and shaded areas represent 95% CIs.
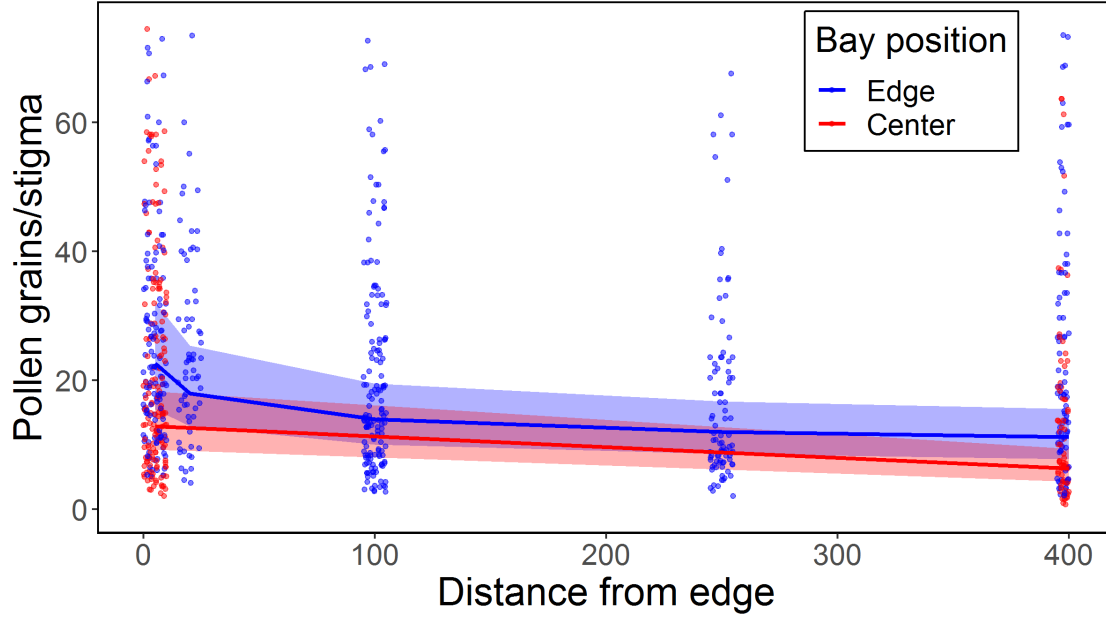
Figure 11: Partial effect of distance from field edge and bay position on pollen deposition in seed canola. Coloured points represents median, and shaded areas represent 95% CIs.

3.3 Prediction 3: Larger plants produce more seeds

Plant size was largely influenced by plant density, but this differed between commodity and seed canola crops. Plant density was higher overall in commodity fields (mean: 48.5 plants/m^2, SD: 22.9, range: 6–151) than seed fields (mean: 39.4 plants/m^2, SD: 17.0, range: 11–89), and commodity canola plants were smaller on average (mean: 18.2 g, SD: 14.4, range: 0.8–110.2) than seed canola plants (mean: 30.7 g, SD: 21.2, range: 1.2–144.3). However, commodity canola plant size was not influenced by plant density (Z=-1.62, p=0.10, Figure 12), indicating that any density-dependence was overwhelmed by other factors, but plant size in seed canola was negatively influenced by planting density (Z=-13.2, p<0.0001), and plants were larger at the centre of the field independent of density (Z=5.4, p<0.0001).Plant density was slightly lower at the edge of commodity canola fields (Z=1.68, p=0.09), but was much lower in seed canola (Z=5.2, p<0.0001), indicating lower seedling survival or seeding density at the edges of the field. Neither irrigation (p=0.76), site (p=0.86), nor distance from field edge (p=0.70) directly influenced commodity canola plant size, but plants were
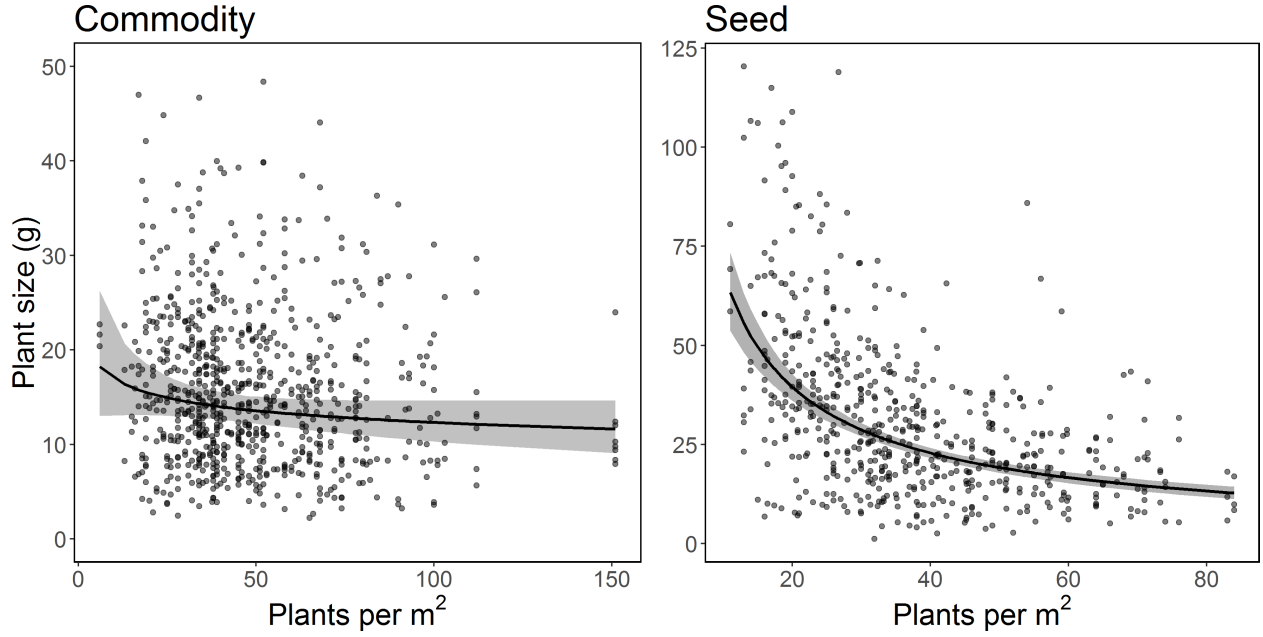
Figure 12: Partial effects of plant density on plant size, for commodity and seed canola plants. Solid lines represents median, and shaded areas represent 95% CIs.

larger in 2015 (Z=2.5, p=0.01).

Plant size had a strong effect on the number of pods produced, and there was evidence of fruit set suppressing future flower production. Commodity canola plants produced fewer flowers per plant (mean: 198, SD: 157, range: 13–1419) than seed canola plants (mean: 468, SD: 328, range: 26–2712), and also produced fewer pods per plant (mean: 143, SD: 114, range: 5–892) than seed canola plants (mean: 303, SD: 208, range: 10–1410). In both commodity and seed canola, plant size had a strong positive effect on the total number of flowers per plant (commodity: Z=92.4, p<0.0001, seed: Z=82.7, p<0.0001, Figure 13), as well as fruit set (commodity: Z=5.5, p=0.0002, seed: Z=19.9, p<0.0001, Figure 14). Fruit set had a strong negative influence on total flowers per plant (p<0.0001) in both commodity (Z=-12.5) and seed canola (Z=-12.1), indicating that high levels of fruit set suppressed future flower production. Finally, commodity plants were also lower-yielding (mean: 6.8 g of seeds per plant, SD: 6.0, range: 0.01–47.9) than seed canola plants (mean: 9.6, SD: 7.9, range: 0.02–60.8). However, the harvest index of commodity canola (mean: 0.26, SD: 0.08, range: 0.005–0.65) was higher than seed canola (mean: 0.23, SD: 0.09, range: 0.003–0.55), meaning
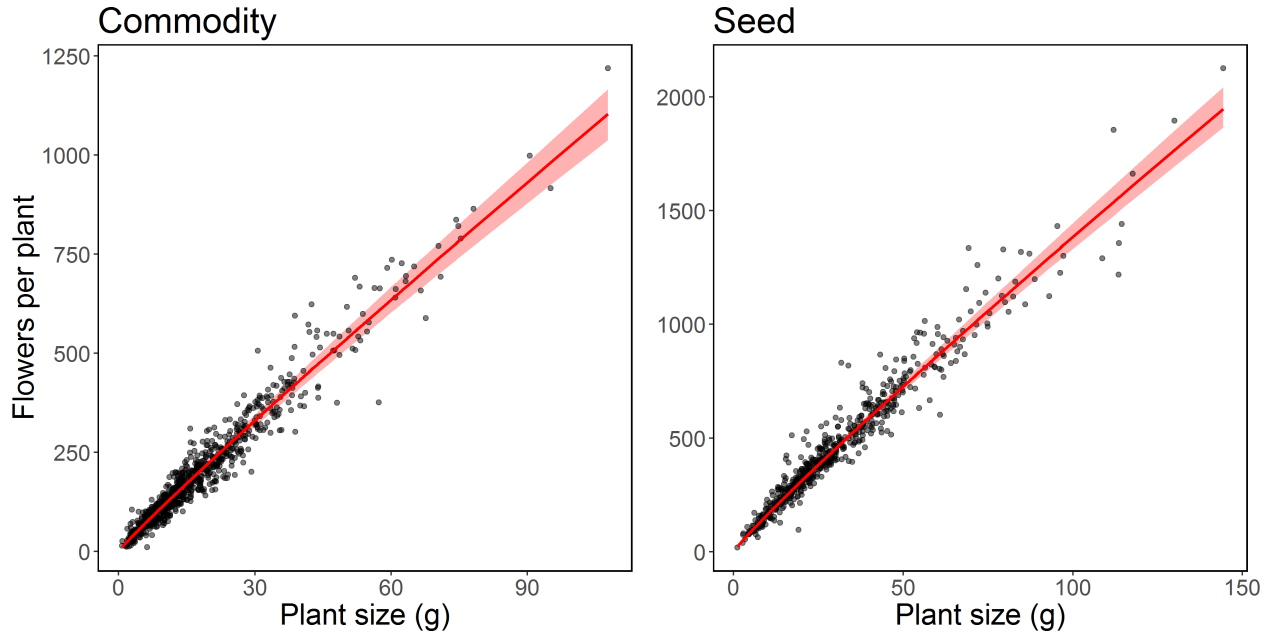
Figure 13: Partial effect of plant size on number of flowers per plant, for commodity and seed canola plants. Solid lines represent median, and shaded areas represent 95% CIs.

that commodity plants produced more seeds per gram of biomass than seed canola plants, likely due to the lack of pollen limitation (see below).

Plant size had a positive effect on seed size and seeds per pod in seed canola, but not in commodity canola, and the relationship between seed size and number was negative in seed canola but positive in commodity canola. Commodity canola plants produced more seeds per pod (mean: 23.0 seeds per pod, SD: 7.4) than seed canola (mean: 16.3 seeds per pod, SD: 9.1), but seed mass was lower in commodity canola (mean: 2.74 mg/seed, SD: 1.04) than seed canola mean (mean: 3.59 mg/seed, SD: 1.33). In commodity canola, plant size did not impact seeds per pod (Z=1.00, p=0.32) or seed size (Z=-0.40, p=0.69, Figure 15), but eed size was positively related to seeds per pod (Z=6.1, p<0.0001, Figure 15). In seed canola, however, seed size increased with plant size (Z=4.7, p<0.0001, Figure 15), decreased with seeds per pod (Z=-13.1, p<0.0001), and interestingly, increased with plant density (Z=2.9, p=0.004), suggesting resource limitation at both the pod and the plant level. There were also between-year differences in seeds per pod (commodity canola only: Z=4.7, p<0.0001, 21.7 seeds per pod in 2014, 24.6 in 2015) and seed size (commodity canola: Z=2.2, p=0.031,
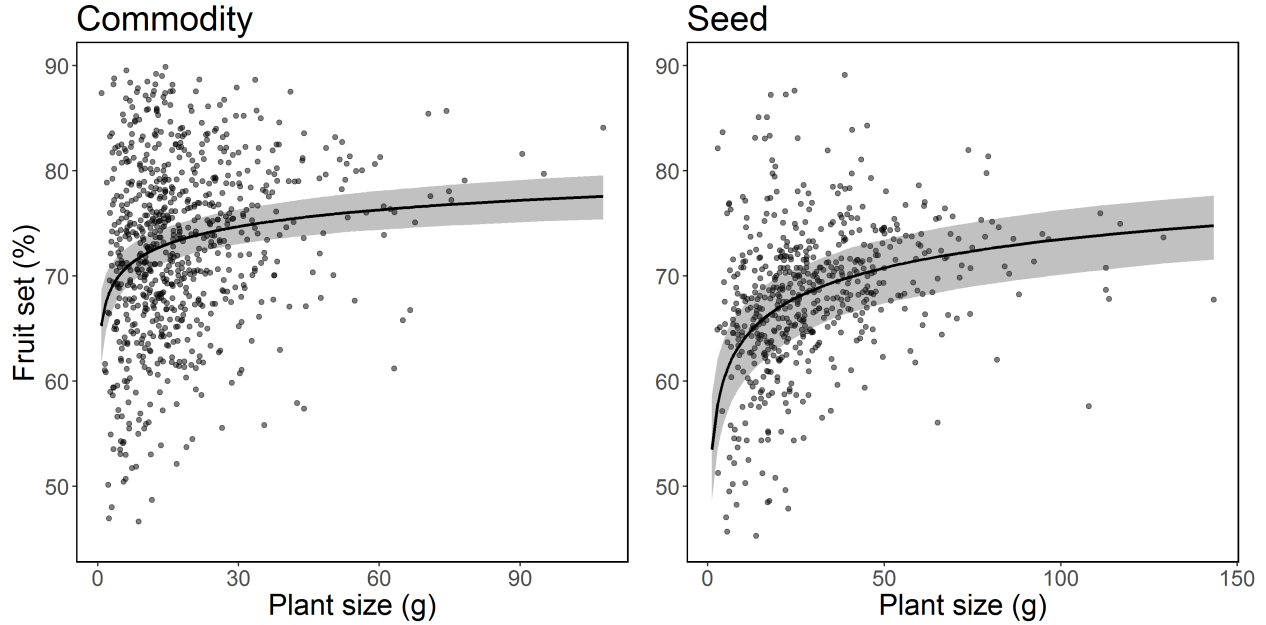
Figure 14: Partial effect of plant size on fruit set (% of flowers that became pods), for both commodity and seed canola. Solid lines represent median, and shaded areas represent 95% CIs.

2.04 mg/seed in 2014, 2.31 mg/seed in 2015; seed canola: Z=3.6, p=0.0003, 3.11mg/seed in 2015, 3.59mg/seed in 2016), pointing to differences in overall growing conditions between years.

3.4 Prediction 4: Pollinated plants produce more seeds

Pollen deposition increased fruit production and seed production in seed canola, but not in commodity canola. Pollen deposition had no effect on fruit set (p=0.12), seeds per pod (p=0.94) or seed size (p=0.56) in commodity canola, and there was also no direct effect of honey bee visitation on fruit set (p=0.38), seeds per pod (p=0.55), or seed size (p=0.34). Seed canola, in contrast, was highly dependent on pollen deposition. Pollen deposition increased fruit set (Z=3.1, p=0.002), and seeds per pod (Z=2.3, p=0.02), but had no direct effect on seed size (p=0.35). Fruit set also decreased with three types of distance: distance into the field (Z=-5.3, p<0.0001), distance from leafcutter shelters (Z=-3.2, p=0.002), and distance from the edge of the female bay (Z=-4.0, p=0.0001). Seeds per pod decreased in

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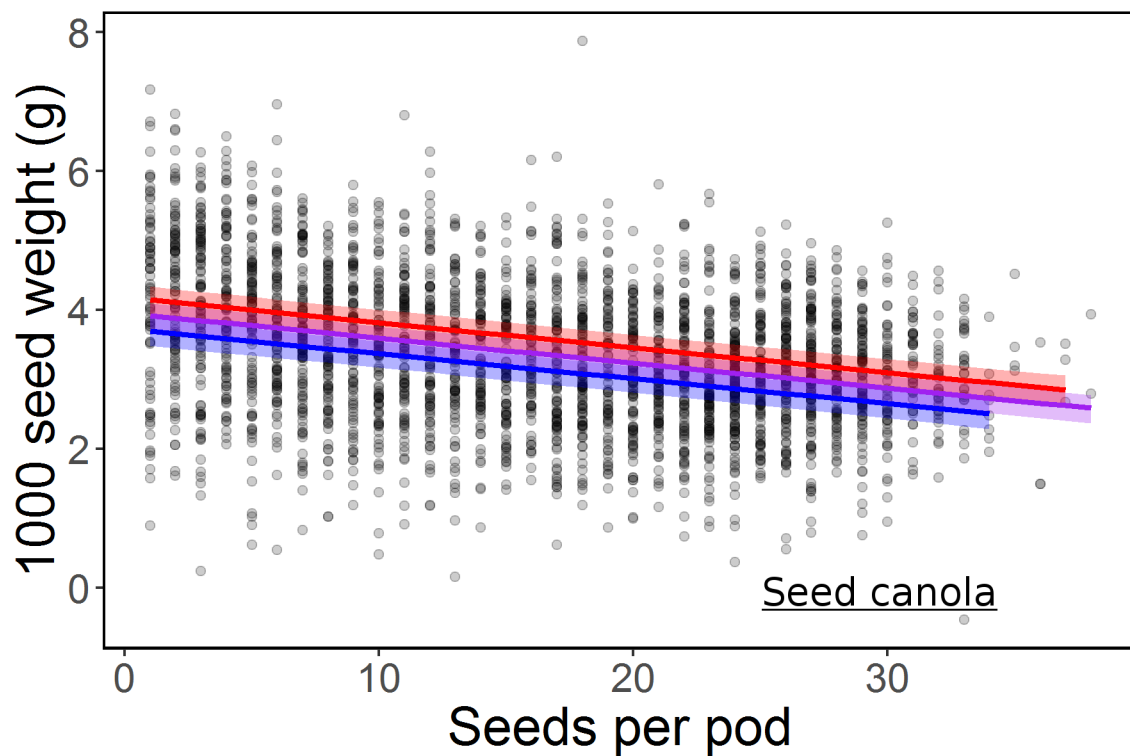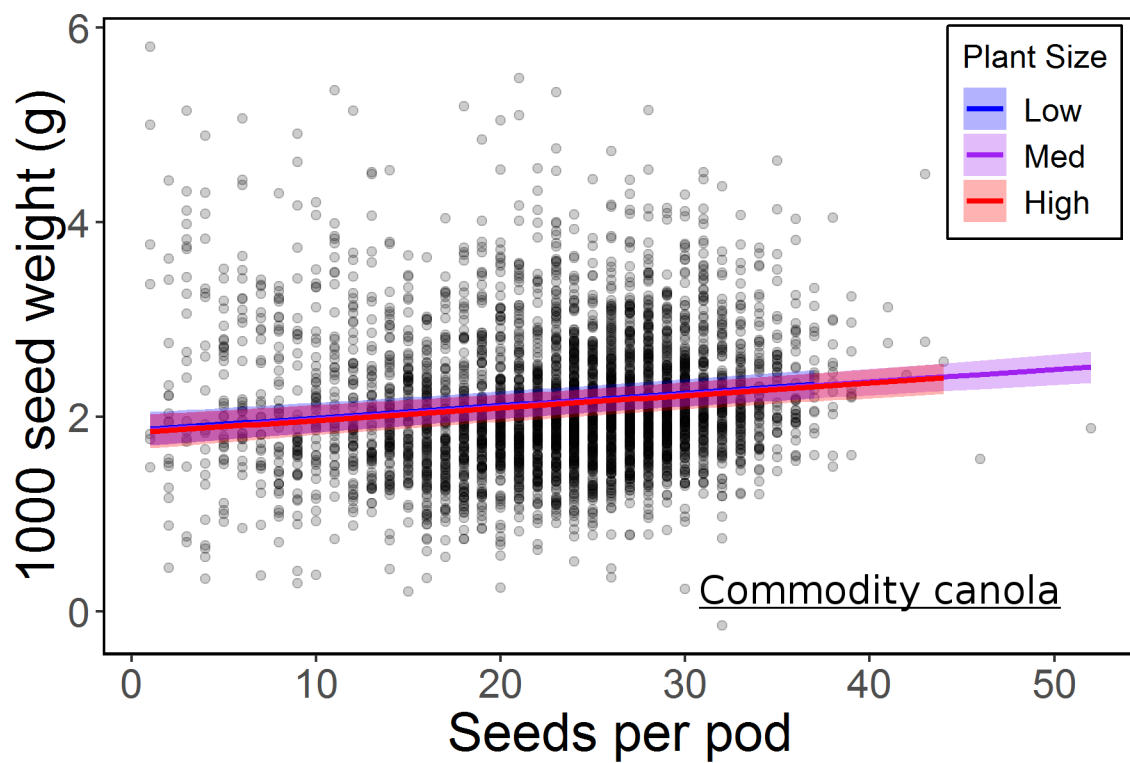
Figure 15: Partial effects of seed count and plant size on seed size, for both commodity and seed canola. Solid lines represent median, and shaded areas represent 95% CIs.

the centre of the female bay (Z=-4.6, p<0.0001), and was higher in plants with high fruit set (Z=6.0, p<0.0001).

4 Discussion

This study examined the relative strength of the path between visitation, pollination, and yield, in two types of canola crops, and showed a strong path between visitation and yield in seed canola, but not in commodity canola. First, honey bee and leafcutter bee visitation decreased with distance from their hive or shelter, but unexpectedly, leafcutter bees visited more frequently at the edge of the field. Secondly, honey bees had little (direct) influence on pollen deposition in either crop type, leafcutter bees had a positive effect on pollen deposition in seed canola. Finally, the model revealed that commodity canola production is largely limited by plant size, while seed canola production is limited by both pollen and plant size.

4.0.1 Bee visitation

Honey bee visitation in both field types declined with distance into the field, but overall visitation was much higher than commodity fields, due to the higher honey bee stocking rate used in seed fields (3.6 vs. mean 0.6 hives/ha). Since honey bees travel from their hive outside the edge of the field, this decline was not surprising, but we did not expect the similar decrease observed in leafcutter bee visitation with distance into the field, as their shelters are located *within* the field. This decrease with distance into the field may have been caused by leafcutter bees migrating from shelters at the centre of the field to the edge (Goerzen et al., 1995). Like honey bees, female leafcutter bees are central-place foragers, and tend to not forage far from their nests (Peterson and Roitberg, 2005; Pitts-Singer and Cane, 2011; Brunet et al., 2019). However, leafcutter bees are not as constrained to their nest site as honey bees, and can drift between shelters in a given field (Goerzen et al., 1995;

Pitts-Singer, 2013). Leafcutter bees must also forage for leaf materials to create cocoons, but they prefer to build cocoons out of thinner, non-canola leaf types, mainly plants in the families Fabaceae and Rosaceae (Sinu and Bronstein, 2018). Seed canola fields have very few weeds within the area of the crop, meaning that leafcutter bees at the centre of the field may have few choices of leaf material, or alternative pollen and nectar sources. Therefore, leafcutter bees likely move from the shelters at which they were released in the centre of the field to the shelters at the edge of the field, so as to gain access to better leaf material (Horne, 1995a), which is more available off-field, or to better forage for off-field pollen or nectar (Horne, 1995b). This would explain why greater visitation occurred at the edge of the field, and may also explain why this pattern was not seen in fields with half-stocked shelters. To test this, a mark-recapture study of female leafcutter bees could be done to see if bees migrate to shelters at the edge of the field, or if visitation is higher due to other reasons (*e.g.* feral populations migrating to edge of field, long-distance foraging from centre of field as in Peterson and Roitberg, 2005). It would be interesting to see if there is a critical threshold of leafcutter bee density per-shelter that causes them to move to shelters at the edge of the field (similar to Pitts-Singer, 2013).

Honey bee visitation in hybrid seed fields was lower at areas near to leafcutter shelters. This may have been driven by avoidance of nectar and pollen competition near shelters, as areas close to leafcutter shelters may become depleted in nectar and pollen, deterring honey bee visitation (similar to Currie, 1997). Honey bees also suffer from direct interference by leafcutter bees near to their shelters. Several times during the study, *M. rotundata* females and males directly harassed honey bees during the plot-level observations, tackling honey bees both on the flowers and in the air (also seen by Batra, 1978 and Waytes, 2017). Honey bees were never the aggressor in these interactions, so interference between leafcutter bees and honey bees may be unidirectional, at least in areas near leafcutter bee shelters. For this reason, we treated high leafcutter visitation as causing lower honey bee visitation in our SEM (Figure 4, arrow from leafcutter visit rate to honey bee visit rate).

Honey bee visitation and foraging behaviour varied strongly between the male and female bays of seed fields, as well as within the female bays. Visitation rates of honey bee foragers were almost twice as high in the centre of the female bay, and conversely, leafcutter bee visitation was almost twice as low. This could be due to leafcutter bees avoiding competition for nectar with honey bees, but more likely reflects a stronger need for pollen among leafcutter bees than honey bees (Cane et al., 2011). Only 1.4% of the honey bees in the female bay were pollen foragers (Table S2), meaning that foragers who have (recently) come into contact with pollen rare. Both Waytes (2017) and Gaffney et al. (2019) showed that honey bees exhibit floral fidelity during foraging trips, with minimal crossing between male and female bays (~5% of observations, Waytes, 2017), limiting pollen transfer between the male and female flowers. Side-working was a very common behaviour among honey bees in commodity fields (65% of the total visits from honey bees during 2015 were side-working), as well as the male bays of seed fields (36%), but not in the female bays (3%, Table S2). This behaviour is relatively common on male-fertile flowers of *Brassica* (Free and Williams, 1973; Free and Ferguson, 1983; Delbrassine and Rasmont, 1988; Mohr and Jay, 1988) as well as other flowering crop flowers (Thomson and Goodell, 2001), and may be due to honey bees avoiding contact with the stigmas to increase ease of access to nectar, or to reduce the amount of grooming needed during a nectar foraging bout. The foragers who were side-working tended to not switch to top-working (personal observation), so this is likely a consistent individual behaviour (at least in experienced foragers). Therefore, honey bees pollen foragers in seed canola fields appear to avoid flowers in the female bay, and commonly engage in side-working behaviour in both commodity and seed canola fields, limiting their opportunities for pollen transfer (see below).

4.1 Pollen deposition

Honey bee visitation did not increase pollen deposition in commodity canola fields compared to unstocked fields, meaning that wind and/or self-pollination are the likely agents of pollen

transfer. The stigmas and flowers of *Brassica* are not aligned for optimal dispersal and deposition from the wind, so cross-pollination likely occurs mainly via insects (Mesquida and Renard, 1982; Cresswell et al., 2004). However, wind-induced self-pollination (plant shaking) can increase yield in *Brassica* (Williams et al., 1986; Mesquida et al., 1988), and fields without bee pollination have outcrossing rates of about 20% within the field (Rakow and Woods, 1987; Becker et al., 1992). The style of *Brassica* grows past the anthers during maturation, allowing deposition of large amounts of self-pollen, suggesting that self-pollination is the dominant mode of pollination. Honey bees can assist in deposition of self-pollen, as Ali et al. (2011) found that *Apis dorsata* and *Apis florea* can both deposit 100-200 grains of pollen per visit on a canola flower (*B. napus* var. *Bulbul*). However, Waytes (2017) used male-sterile flowers and found that *A. mellifera* deposit far less outcrossed pollen (~ 2 grains per visit), suggesting that much of the pollen deposited by honey bees on canola stigmas is self-pollen. Because the overall pollen deposition rates found in this study were so high (mean: 293, SD: 385), honey bee visitation seems to have made little difference in the amount of self-pollination. The typical lifetime of a canola flower is approximately 3 days, and the stigmatic surface is receptive for 24–36 hours within this period (Eisikowitch, 1981; Hoyle et al., 2007), so it may be that 10-minutes of observing flower visitors was too short of a time interval to relate to pollen deposition. This is unlikely, however, as large amounts of pollen were present on commodity canola stigmas even at the centre of unstocked fields (average plot-level visitation rate was 0.23 visits/hr). These results suggest that stigmas are largely saturated with self-pollen, swamping any extra pollen deposition by honey bees.

Honey bee behaviour in seed fields made pollen transfer between male and female plants unlikely, and this was also reflected in the measurements of stigma deposition. Deposition was not affected by honey bee visitation, but was strongly increased by leafcutter bee visitation. Leafcutter bees tend to switch between male and female flowers more frequently than honey bees do (Waytes, 2017), transport more viable pollen between flowers (Parker et al., 2015), and tend not to side-work canola flowers (Soroka et al., 2001, personal observation), which

may explain their increased pollination efficacy. We also found that pollen deposition also decreased with distance from the edge of the field, was lower in the centre of the female bays, and that this was not solely explained by leafcutter bee abundance (Figure 4). During foraging bouts, leafcutter bees may travel further between flowers than honey bees do; Brunet et al. (2019) found that leafcutter bees foraging in alfalfa (*Medicago sativa* L.) travelled an average of 21 cm between flowers, while honey bees only travelled 16 cm. However, pollen carryover (Thomson, 1986) to the middle of the bay female is likely reduced, as leafcutters likely visit the edge of the female bay before venturing into the centre. The decrease of pollen deposition with distance into the field (independent of visitation rates) also suggests that the same visitation rate of pollinators in the centre of the field results in less pollen deposition. This may be due to lower levels of competition at the centre of the field, leading to a higher nectar (or pollen) standing crop. Foraging *Bombus* take smaller trips between flowers and will forage in smaller areas under nectar-rich conditions (area-restricted search, Pyke, 1978; Heinrich, 1979), so leafcutter foraging may follow a similar pattern, causing lower pollen deposition at the centre of the field where competition is lower.

Honey bees may have an indirect positive effect on pollen deposition, as they may cause leafcutter bees to travel farther by lowering overall nectar and pollen standing crop, or release airborne pollen from male-fertile flowers. Pierre et al. (2010) showed that honey bees can increase the amount of airborne pollen by foraging on male-fertile flowers and releasing pollen from the anthers, causing increased yields in nearby male-sterile flowers; therefore, honey bees may indirectly contribute to a higher rate of wind pollination. Honey bees may also cause leafcutter bees to forage at further distances away from their shelters. Bumble bees move further between flowers when foraging in *Trifolium* fields that have been depleted by honey bees Heinrich (1979), so a similar process could occur in canola seed fields. Leafcutter bees do not appear to use area-restricted search (Brunet et al., 2019), but we expect that the foraging range of leafcutter bees around their shelters would sitill decrease, because if honey bees lower pollen and nectar levels at the edge of the field, then leafcutter bees should

travel shorter distances to gather the same reward (according to the predictions of Chapter 2). We also expect that foraging leafcutter bees would make shorter trips between flowers (similar to Heinrich, 1979), and possibly may switch between bays less frequently (Waytes, 2017; Gaffney et al., 2019), due to a greater floral fidelity on higher-rewarding flowers in the male bay (Mesquida and Renard, 1978). If this is true, this would result in a lower rate of (overall) pollen deposition by leafcutter bees during the same period. However, testing this would require observations of seed canola fields that were only stocked with leafcutter bees, which is extremely rare in southern Alberta.

4.2   Pod production

Fruit set (i.e. pod production) in commodity canola was positively affected by plant size, but not by pollen deposition or honey bee visitation. Both pod production and seeds per pod can increase with extra pollination (Jauker and Wolters, 2008; Sabbahi et al., 2005, 2006; Durán et al., 2010), so this lack of effect may be due to a high overall level of pollen deposition (Figure 9), even in fields without honey bees. There was no effect of honey bee visitation on fruit set, seeds per pod, or seed size, indicating that visitation did not seem to cause either *a)* a greater quantity of pollen (see above) or *b)* higher quality (outcrossed) pollen. Self-pollination (geitanogamy) in canola can result in similar fruit production as outcrossing (Rosa et al., 2011), implying that pollen quality is not likely a limiting factor in canola fruit set, at least in some varieties. Flower number was negatively related to fruit set, which implies a response to pollination (high flower fertilization suppresses further flower production) and/or a reproductive trade-off (greater pod development rate means more competition among pods for resources). We considered the first scenario to be the stronger effect, as Sabbahi et al. (2006) and Mesquida and Renard (1981) both found that canola plants compensated for experimental removal of flowers by increasing branch and flower production, until the plant reached about 170 pods. Their final number of pods is similar to the plants from our study (median: 112, range: 5–892), but we found that larger

plants also had greater fruit set, in addition to higher flower production, presumably caused by the larger pool of resources that large plants are able to invest into reproduction.

Pollination increased pod production in seed canola, but not in commodity canola, meaning that extra pollination is valuable for seed canola crops, but not commodity canola. This is similar to the findings of Mesquida and Renard (1981) and Steffan-Dewenter (2003), who found that fruit set in male-sterile plants responded positively to visitation, while male-fertile plants ("male" plants in seed fields, all plants in commodity fields) had no response (but see Adegas and Nogueira Couto, 1992). Pod production in seed canola increased with both pollen deposition and plant size, suggesting that both pollen availability and plant resources constrain pod production. However, the effect size of pollen deposition (Z=3.1) was much smaller than that of plant size (Z=19.9), indicating that the factors controlling plant size (fertilizer, plant density, and soil quality) likely constrain pod production more strongly than pollination alone, in both commodity and seed canola plants. There were also effects of distance on fruit set, independent of pollen deposition: pod set decreased with distance from the edge of the field and distance to leafcutter shelters independent of pollen deposition, and was lower in the centre of the female bays. Mesquida and Renard (1978) also found that fruit set in male-sterile canola declined quickly with distance from the male-fertile plants (due to wind pollination), but the effect we found is likely related to the earlier effect of lower pollen carryover at the centre of the female bays, and possibly the centre of the field. However, our analysis points to the strong relative importance of plant resources, as well as pollination services (Marini et al., 2015), mediated through the effect of leafcutter bee visitation, to the production of hybrid seed canola.

4.3   Seed number and size

In commodity canola plants, the number of seeds per pod was only affected by between-year variation, and was unaffected by plant size and pollination. In contrast, the number of seeds per pod in seed canola was increased by pollen deposition, flower survival, and plant size,

and was reduced in the centre of the female bay. Position in the female bay influenced pollen deposition, both by wind and insects, indicating that the decrease in seed number at the centre of the bay is ultimately caused by reduced pollen deposition from lower visitation (Mesquida and Renard, 1981, 1982). Seeds per pod also increased with pollen deposition and plant size, but the effect size of pollen deposition ($Z=2.3$) was smaller than that of plant size ($Z=5.6$), suggesting that plant resources limit seed production more strongly than pollen deposition in seed canola. Mesquida and Renard (1982) found that in seed canola, pod production, rather than seeds per pod, was the main variable that was reduced by low pollen deposition. Interestingly, plant density had a positive effect on seed size in seed canola, pointing to a possible reduction in seed count because of shading or crowding, causing an increase in seed size (but see Angadi et al., 2003).

Plant size was one of the dominant factors controlling seed size in seed canola, while in commodity canola, plant size did not influence seed size. Plant size can positively influence seed size in some plant species (Maddox and Antonovics, 1983), and this appears to be true in canola (Riffkin et al., 2012) as well as other Brassicaceae (Mazer, 1987). Similarly, seeds per pod and seed weight varied positively in commodity canola, this pattern was reversed in seed canola (Figure 15). These differences likely occurred because of variation in available seed resources among the parts of the plant (van Noordwijk and de Jong, 1986), which can cause a positive size-number relationship even in resource-limited plants. In commodity canola, pollen is readily available, and there seems to be little difference between outcrossed- and self-pollen (Steffan-Dewenter, 2003; Rosa et al., 2011). Canola plants produce flowers from the bottom up, and produce fewer, smaller seeds at the ends of the branches because the younger pods have access to fewer resources at the end of the season (Sabbahi et al., 2006), resulting in an increased rate of seed abortion (Clarke, 1979). Pods with low resources at the end of the season are forced to abort more ovules (Wang et al., 2011), causing a positive relationship between seed number and size. Thus, in commodity canola, variation in resources with plant size is masked by resource variation over time. In seed canola,

pollen is much rarer (median: 7 grains/stigma vs. 155 in commodity), but plant sizes are similar (or larger) than commodity canola, such that plant resources are still available to developing pods at the end of the season. This causes a size-number trade-off within pods that is mediated by plant size. Most studies on commodity canola report a seed size-number trade-off at the level of plant (Angadi et al., 2003; Kołtowski, 2005), we found a positive relationship at the pod level (but see Sabbahi et al., 2005). Perhaps within-plant resource variation is a more likely driver of seed number than pollen deposition, as pollination did not appear to be limiting (Figure 3, weak paths from pollen to yield metrics).

4.4   Summary

This study assesses the relative importance of pollination and plant resources for the production of canola crops, using field-realistic data from central and southern Alberta. First, it shows that insect visitation changes across small spatial scales (meters for leafcutter bees, tens of meters for honey bees), and are at odds with the large scales of Albertan crop fields (Fritz et al., 2015). Visitation of both honey bees and leafcutter bees in canola fields is concentrated at the edge of fields, and is lower at the centre of the female bays in seed canola. Second, honey bees have little direct influence on pollen deposition in either crop system, likely due to a high background level of pollen deposition on stigmas in commodity canola, whereby extra pollen deposition is of little benefit to plant reproduction. Seed canola plants, in contrast, have much lower levels of pollen deposition overall, and leafcutter bees deliver a large direct benefit to fruit and seed production. The centre of the female bays illustrates this effect: honey bees have a higher visitation rate, but pollen deposition, fruit set, and seed set are all lower. Finally, both plant size and pollination limit seed production in seed canola, but only plant size limits commodity canola production, showing the relative importance of both pollination and plant resources using in-field data.

Several future lines of work could be followed based on this study. First, other factors besides total seed yield are important for commodity canola production, such as green seed and

oil content (Tautorus and Low, 1994; Abbadi and Leckband, 2011; Ghazani and Marangoni, 2013). Our work identified the effect of bee pollination on seed production in terms of total weight, but may have overlooked these aspects of yield valuation (Bommarco et al., 2012). Secondly, we found that honey bees appear to add little pollination value for seed canola crops, but since we did not use fields that had no honey bees, there may be unobserved indirect benefits that honey bees add. For example, they may contribute to better pollination by leafcutter bees by reducing the nectar and pollen standing crop, causing leafcutter bees to forager further away from their shelter (Pyke, 1978; Heinrich, 1979), or by increasing the amount of airborne pollen (Eisikowitch, 1981; Mesquida and Renard, 1982). Third, while the random-intercept model that we used accounts for field-to-field variation in growing conditions, this also means that we may have marginalized across other factors that were not accounted for by plant size, such as nutrients, soil moisture, crop pests, and variety. Pollination benefits to all flowering crops are contextual, even in highly-pollination dependent crops (Tamburini et al., 2017, 2019); that is, the effect of additional pollination depends on the levels of other plant resources available during growth (Marini et al., 2015; Bartomeus et al., 2015; Gagic et al., 2017). Finally, SEMs cannot model causal loops (Grace, 2006), which is closer to the method by which plants respond to lack of pollination (*i.e.* pollination failure → plant growth → flower production). Our model serves as an approximation of this process, but could be built upon by using dynamic linear programming techniques (Iwasa, 2000; Nord et al., 2011) to examine how plants dynamically respond to pollen failure. These would lend greater understanding to the process of hybrid seed production, and could be used to more accurately predict crop yields in novel scenarios.

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Appendix A: Additional figures and tables

Extra figures and tables go here

Appendix B: Supplementary information on visitation

Floral visitors in canola fields

	Commodity fields		Seed fields	
Taxon	Visits	%	Visits	%
Honey bee	470	53.5	4850	77.1
Fly	222	25.3	74	0.878
Hover fly	94	10.7	151	1.79
Other bee	47	5.35	30	0.356
Bumble bee	25	2.85	0	0
Butterfly	16	1.82	0	0
Leafcutter bee	4	0.456	1675	19.9

Table S1: Number of flower visitors recorded over a total of 44.8 hours of observation in commodity fields (2014 and 2015), and 46.9 hours of observation in the seed fields (2015 and 2016). "Fly" refers to larger calyptrate muscoid flies (families Muscidae, Anthomyiidae, Caliphoridae), while "Hover fly" refers to Syrphid flies. "Other bee" included Halictid and Andrenid bees, while "Bumble bee" was *Bombus* spp. "Butterfly" refers to all visiting Lepidopterans, mostly Pierids.

Top-working and side-working by honey bees in canola fields

During 2015, we recorded whether honey bees were top-working or side-working flowers (see also Free and Williams, 1973; Free and Ferguson, 1983; Mohr and Jay, 1988). Top-working bees landed on the top of the flower and inserted their proboscis down between the petals to access the nectaries of the flower, while side-working bees landed on the side of the flower and stole nectar by inserted their proboscis between the petals, avoiding contact with the stigma or anthers. Additionally, we recorded whether honey bees were pollen or nectar foragers (pollen foragers had a visible pollen load on their corbicula, while nectar foragers had none).

Pollen- and nectar-foraging honey bees had different patterns of side-working, both on commodity canola, and the male and female lines of seed canola. Side-working was common in nectar foragers, but was more common in commodity canola (64%) than in the male (36%) or female bays (2.8%) of seed canola, indicating that a large proportion of honey bees foraging on canola flowers may never come in contact with the stigmas. Pollen foragers were almost uniformly top-foragers in both commodity and seed fields (Table S2), and pollen foragers were much less common in the female bays (1.4%) than in the male bays (15%), or in commodity fields (18%). Therefore, foraging honey bees in seed canola fields tend to treat male-fertile flowers similar to commodity canola flowers, but seem to top-work flowers more in commodity canola than seed fields. Leafcutter bee foraging behaviours were not recorded, but seemed to almost exclusively top-work flowers in seed canola fields.

	Commodity fields		Seed fields (female bay)		Seed fields (male bay)	
	Top	Side	Top	Side	Top	Side
Pollen forager	44	2	12	0	115	0
Nectar forager	75	138	832	24	428	242

Table S2: Foraging behaviours of honey bees on commodity and seed canola flowers, recorded during 2015. "Top" (top-working) indicates that the bee inserted their proboscis down between the petals from the top of the flower, while "side" (side-working) indicates that the bee fed from the side of the flower and did not contact the anthers or stigma. Pollen foragers had pollen visible on their corbicula, while nectar foragers had none.

Appendix C: Supplementary information on models

Commodity canola models

Formulas for commodity canola model using `lmer`-style R formulas. Terms on right side of $\sim$ indicate fixed effects, while terms in brackets indicate random effects (heirarchical intercepts), with Field/Plot indicating *Plot* is nested below *Field*. $*$ indicates an interaction between fixed effects. *distribution* indicates the type of probability distribution function used to model each variable.

Plant Density $\sim$ Year $*$ Irrigation + Distance + Site + (1|Field), distribution = log-normal

Plant Size $\sim$ Plant Density + Distance + Site + Irrigation + Year + (1|Field/Plot),
distribution = log-normal

Flower Density $\sim$ Plant Size + Distance + (1|Field), distribution = square root-normal

Honey bee visits $\sim$ offset(log(Time)) + Year $*$ Site + Irrigation + Distance+
Hive Stocking + Flower Density + (1|Field), family = negative binomial

Pollen per Stigma $\sim$ Honey bee visits + Distance + (1|Field/Plot), distribution = negative binomial

Fruit Set $\sim$ Honey bee visits + Pollen + Plant Size + Plant Density + Irrigation+
Year + (1|Field), distribution = beta-binomial

Flowers per Plant $\sim$ Plant Size + Fruit Set + Year + (1|Field), distribution = negative binomial

Seeds per Pod $\sim$ Honey bee visits + Pollen + Plant Size + Year + (1|Field/Plant),
distribution = negative binomial

Weight per Seed $\sim$ Honey bee visits + Pollen + Seeds per Pod + Plant Size + Irrigation+
Year + (1|Field/Plant), distribution = exponential-normal

Seed canola models

Formulas for seed canola model using `lmer`-style R formulas. Terms on right side of $\sim$ indicate fixed effects, while terms in brackets indicate random effects (heirarchical intercepts), with Field/Plot indicating *Plot* is nested below *Field*. $*$ indicates an interaction between fixed effects. *distribution* indicates the type of probability distribution function used to model each variable.

$$\text{Plant Density} \sim \text{Edge Distance} + (1|\text{Field}), \text{distribution} = \text{log-normal}$$

$$\text{Plant Size} \sim \text{Edge Distance} + \text{Plant Density} + (1|\text{Field}), \text{distribution} = \text{log-normal}$$

$$\text{Flower Density} \sim \text{Plant Size} + \text{Bay Centre} + \text{Year} + \text{Edge Distance} + (1|\text{Field}),$$
$$\text{distribution} = \text{square root-normal}$$

$$\text{Leafcutter bee visits} \sim \text{offset}(log(\text{Time})) + \text{Tent Distance} + \text{Bay Centre} + \text{Male Bay}+$$
$$\text{Tent Stocking} * \text{Edge Distance} + \text{Year} + \text{Bay Centre} : \text{Edge Distance}+$$
$$(1|\text{Field}), \text{family} = \text{negative binomial}$$

$$\text{Honey bee visits} \sim \text{offset}(log(\text{Time})) + \text{Edge Distance} + \text{Tent Distance} + \text{Leafcutter bee visits}+$$
$$\text{Bay Centre} + \text{Flower Density} + \text{Male Bay} + (1|\text{Field}),$$
$$\text{family} = \text{zero-inflated negative binomial}$$

$$\text{Pollen per Stigma} \sim \text{Honey bee visits} + \text{Leafcutter bee visits} + \text{Bay Centre} + \text{Edge Distance}+$$
$$\text{Flower Density} + (1|\text{Field/Plot}), \text{family} = \text{negative binomial}$$

$$\text{Fruit Set} \sim \text{Pollen} + \text{Plant Size} + \text{Bay Centre} + \text{Edge Distance} + \text{Tent Distance}+$$
$$\text{Flower Density} + (1|\text{Field/Plot}), \text{family} = \text{beta-binomial}$$

$$\text{Flowers per Plant} \sim \text{Plant Size} + \text{Bay Centre} + \text{Fruit Set} + (1|\text{Field}),$$
$$\text{family} = \text{negative binomial}$$

$$\text{Seeds per Pod} \sim \text{Pollen} + \text{Plant Size} + \text{Bay Centre} + \text{Edge Distance} + \text{Flower Density}+$$
$$\text{Fruit Set} + (1|\text{Field/Plant}), \text{family} = \text{negative binomial}$$

$$\text{Weight per Seed} \sim \text{Pollen} + \text{Seeds per Pod} + \text{Plant Size} + \text{Year} + \text{Tent Distance}+$$
$$\text{Plant Density} + \text{Tent Stocking} + (1|\text{Field/Plot}), \text{family} = \text{exponential-normal}$$

Commodity canola model coefficients

Dependent	Independent	Median	Lwr	Upr	mean	sd	z	overlap	pvalue
Plant density	Intercept	0.060	-0.081	0.197	0.058	0.071	0.822	TRUE	0.4108
Plant density	Year	0.059	-0.144	0.260	0.056	0.103	0.542	TRUE	0.5878
Plant density	Irrigation	0.255	-0.028	0.522	0.255	0.140	1.826	TRUE	0.0679
Plant density	Year:Irrigation	-0.491	-0.918	-0.077	-0.496	0.214	-2.322	FALSE	0.0202
Plant density	Distance	0.016	-0.003	0.034	0.016	0.009	1.681	TRUE	0.0927
Plant density	Site	-0.237	-0.429	-0.042	-0.237	0.099	-2.395	FALSE	0.0166
Plant density	Residual σ	0.309	0.281	0.341	0.309	0.016	19.872	-	-
Plant density	Field-level σ	0.327	0.260	0.413	0.331	0.039	8.543	-	-
Plant size	Intercept	-0.112	-0.308	0.099	-0.111	0.104	-1.075	TRUE	0.2823
Plant size	Plant density	-0.139	-0.315	0.020	-0.141	0.087	-1.617	TRUE	0.1059
Plant size	Distance	-0.006	-0.033	0.023	-0.006	0.015	-0.382	TRUE	0.7026
Plant size	Site	-0.021	-0.270	0.215	-0.021	0.123	-0.170	TRUE	0.8648
Plant size	Irrigation	0.102	-0.164	0.356	0.100	0.131	0.761	TRUE	0.4468
Plant size	Year	0.266	0.066	0.472	0.268	0.106	2.533	FALSE	0.0113
Plant size	Field-level σ	0.295	0.208	0.399	0.297	0.047	6.297	-	-
Plant size	Plot-level σ	0.347	0.276	0.419	0.347	0.036	9.595	-	-
Plant size	Residual σ	0.603	0.570	0.641	0.603	0.018	33.607	-	-
Flower density	Intercept	-0.077	-0.963	0.831	-0.079	0.457	-0.173	TRUE	0.8624
Flower density	Plant size	0.385	-0.843	1.678	0.399	0.645	0.618	TRUE	0.5364
Flower density	Distance	0.705	0.497	0.917	0.706	0.107	6.571	FALSE	<0.0001
Flower density	Residual σ	3.515	3.198	3.883	3.522	0.175	20.078	-	-
Flower density	Field-level σ	3.665	2.991	4.567	3.692	0.399	9.246	-	-
Hbee visitation	Intercept	-1.849	-2.893	-0.968	-1.878	0.493	-3.812	FALSE	0.0001
Hbee visitation	Year	-0.243	-1.274	0.758	-0.239	0.517	-0.462	TRUE	0.6438
Hbee visitation	Site	-0.618	-1.593	0.495	-0.605	0.533	-1.135	TRUE	0.2565
Hbee visitation	Year:Site	1.478	0.215	2.672	1.470	0.629	2.339	FALSE	0.0194
Hbee visitation	Irrigation	-1.619	-3.065	-0.402	-1.654	0.679	-2.434	FALSE	0.0149
Hbee visitation	Distance	-0.333	-0.517	-0.159	-0.335	0.091	-3.685	FALSE	0.0002
Hbee visitation	Hives	0.677	0.432	0.933	0.679	0.128	5.323	FALSE	<0.0001
Hbee visitation	Flower density	0.055	-0.031	0.139	0.055	0.043	1.269	TRUE	0.2044

Hbee visitation	Field-level σ	0.982	0.418	1.605	0.990	0.303	3.269	-	-
Hbee visitation	Field-level λ (skew)	2.208	1.050	4.703	2.374	0.969	2.450	-	-
Hbee visitation	Dispersion (NB ϕ)	0.342	0.231	0.508	0.350	0.073	4.818	-	-
Pollen count	Intercept	5.581	5.448	5.720	5.582	0.070	80.271	FALSE	<0.0001
Pollen count	Hbee visitation	-0.007	-0.079	0.068	-0.006	0.038	-0.147	TRUE	0.8828
Pollen count	Distance	-0.030	-0.063	0.002	-0.030	0.017	-1.824	TRUE	0.0681
Pollen count	Field-level σ	0.451	0.349	0.577	0.455	0.058	7.876	-	-
Pollen count	Plot-level σ	0.227	0.089	0.570	0.257	0.129	1.990	-	-
Pollen count	Dispersion (NB ϕ)	0.674	0.628	0.721	0.674	0.024	28.271	-	-
Flowers per plant	Intercept	5.070	5.025	5.116	5.070	0.023	220.033	FALSE	<0.0001
Flowers per plant	Plant size	0.945	0.924	0.964	0.945	0.010	92.436	FALSE	<0.0001
Flowers per plant	Fruit set	-0.162	-0.188	-0.137	-0.162	0.013	-12.512	FALSE	<0.0001
Flowers per plant	Year	-0.116	-0.175	-0.059	-0.117	0.030	-3.874	FALSE	0.0001
Flowers per plant	Field-level σ	0.561	0.366	0.794	0.567	0.109	5.180	-	-
Flowers per plant (dispersion)	Intercept	3.661	3.456	3.874	3.662	0.106	34.543	FALSE	<0.0001
Flowers per plant (dispersion)	Plant size	0.663	0.484	0.826	0.662	0.088	7.518	FALSE	<0.0001
Flowers per plant (dispersion)	Field-level σ	0.129	0.104	0.163	0.130	0.015	8.865	-	-
Fruit set	Intercept	1.038	0.928	1.149	1.038	0.056	18.518	FALSE	<0.0001
Fruit set	Hbee visitation	0.017	-0.022	0.056	0.017	0.020	0.875	TRUE	0.3815
Fruit set	Pollen	-0.155	-0.348	0.044	-0.154	0.098	-1.575	TRUE	0.1152
Fruit set	Plant Size	0.124	0.079	0.168	0.124	0.023	5.488	FALSE	<0.0001
Fruit set	Plant Density	-0.079	-0.182	0.023	-0.079	0.051	-1.534	TRUE	0.1250
Fruit set	Irrigation	0.031	-0.142	0.207	0.031	0.088	0.352	TRUE	0.7249
Fruit set	Year	-0.075	-0.228	0.079	-0.075	0.077	-0.976	TRUE	0.3292
Fruit set	Field-level σ	0.245	0.187	0.315	0.247	0.032	7.604	-	-
Fruit set (dispersion)	Intercept	3.450	3.240	3.672	3.449	0.109	31.586	FALSE	<0.0001
Fruit set (dispersion)	Plant size	0.303	0.099	0.502	0.303	0.103	2.956	FALSE	0.0031
Fruit set (dispersion)	Field-level σ	0.593	0.428	0.804	0.598	0.096	6.230	-	-
Seeds per pod	Intercept	3.073	3.038	3.108	3.073	0.018	174.969	FALSE	<0.0001
Seeds per pod	Hbee visitation	-0.006	-0.025	0.014	-0.006	0.010	-0.595	TRUE	0.5521
Seeds per pod	Pollen	-0.004	-0.074	0.069	-0.003	0.036	-0.075	TRUE	0.9404
Seeds per pod	Plant size	0.011	-0.010	0.031	0.010	0.010	1.004	TRUE	0.3153

Seeds per pod	Year	0.130	0.074	0.184	0.129	0.027	4.714	FALSE	<0.0001
Seeds per pod	Field-level σ	0.075	0.052	0.102	0.076	0.013	5.904	-	-
Seeds per pod	Plant-level σ	0.150	0.134	0.167	0.150	0.008	17.918	-	-
Seeds per pod	Dispersion (NB ϕ)	22.246	20.784	23.812	22.248	0.778	28.587	-	-
Weight per seed	Intercept	1.865	1.681	2.064	1.865	0.099	18.791	FALSE	<0.0001
Weight per seed	Hbee visitation	-0.036	-0.105	0.036	-0.034	0.036	-0.961	TRUE	0.3364
Weight per seed	Pollen	-0.080	-0.370	0.190	-0.082	0.144	-0.569	TRUE	0.5695
Weight per seed	Seeds per pod	0.013	0.009	0.017	0.013	0.002	6.061	FALSE	<0.0001
Weight per seed	Plant size	-0.015	-0.090	0.056	-0.015	0.037	-0.400	TRUE	0.6889
Weight per seed	Irrigation	-0.345	-0.645	-0.034	-0.341	0.155	-2.205	FALSE	0.0274
Weight per seed	Year	0.270	0.022	0.513	0.271	0.125	2.162	FALSE	0.0306
Weight per seed	Field-level σ	0.321	0.239	0.423	0.323	0.047	6.837	-	-
Weight per seed	Plant-level σ	0.551	0.508	0.600	0.552	0.023	23.600	-	-
Weight per seed	Residual σ	0.468	0.428	0.507	0.468	0.020	23.146	-	-
Weight per seed	Residual λ (skew)	1.709	1.572	1.867	1.712	0.076	22.411	-	-

Table S3: Coefficients from commodity model. Terms with a colon between them indicate interactions.

Seed canola model coefficients

Dependent	Independent	Median	Lwr	Upr	mean	sd	z	overlap	pvalue
Plant density	Intercept	0.033	-0.095	0.160	0.033	0.064	0.518	TRUE	0.6046
Plant density	Hbee distance	0.055	0.033	0.074	0.054	0.010	5.234	FALSE	<0.0001
Plant density	Residual σ	0.274	0.247	0.306	0.275	0.015	18.358	-	-
Plant density	Field-level σ	0.360	0.283	0.475	0.366	0.050	7.291	-	-
Plant size	Intercept	0.032	-0.015	0.081	0.032	0.025	1.281	TRUE	0.2003
Plant size	Plant density	-0.780	-0.902	-0.667	-0.781	0.059	-13.198	FALSE	<0.0001
Plant size	Hbee distance	0.076	0.050	0.104	0.076	0.014	5.373	FALSE	<0.0001
Plant size	Residual σ	0.614	0.580	0.649	0.614	0.017	35.245	-	-
Flower density	Intercept	0.430	-0.661	1.609	0.441	0.577	0.766	TRUE	0.4440
Flower density	Plant size	0.901	-1.891	3.621	0.863	1.421	0.608	TRUE	0.5434
Flower density	Bay position	0.904	0.118	1.728	0.899	0.411	2.188	FALSE	0.0287
Flower density	Year	-2.696	-4.402	-0.888	-2.686	0.914	-2.939	FALSE	0.0033
Flower density	Hbee distance	1.228	0.941	1.495	1.224	0.141	8.666	FALSE	<0.0001
Flower density	Residual σ	5.067	4.785	5.376	5.071	0.154	32.992	-	-
Flower density	Field-level σ	3.334	2.647	4.286	3.375	0.415	8.131	-	-
Lbee visitation	Intercept	2.242	1.787	2.686	2.242	0.234	9.598	FALSE	<0.0001
Lbee visitation	Hbee distance	-0.282	-0.413	-0.156	-0.282	0.065	-4.362	FALSE	<0.0001
Lbee visitation	Lbee distance	-0.839	-0.980	-0.696	-0.838	0.074	-11.353	FALSE	<0.0001
Lbee visitation	Bay position	-0.547	-1.065	-0.024	-0.549	0.265	-2.072	FALSE	0.0383
Lbee visitation	Male bay	-0.052	-0.332	0.237	-0.051	0.142	-0.357	TRUE	0.7211
Lbee visitation	Stocking	0.044	-0.584	0.678	0.044	0.329	0.134	TRUE	0.8936
Lbee visitation	Year	-0.575	-1.213	0.045	-0.574	0.317	-1.810	TRUE	0.0703
Lbee visitation	Bay position:Hbee distance	-0.192	-0.410	0.030	-0.191	0.113	-1.696	TRUE	0.0900
Lbee visitation	Stocking:Hbee distance	0.225	0.029	0.435	0.225	0.102	2.191	FALSE	0.0284
Lbee visitation	Flower density	0.051	0.023	0.080	0.051	0.014	3.572	FALSE	0.0004
Lbee visitation	Field-level σ	0.973	0.721	1.305	0.987	0.152	6.508	-	-
Lbee visitation	Dispersion (NB ϕ)	0.406	0.352	0.467	0.407	0.029	13.953	-	-
Hbee visitation	Intercept	2.992	2.724	3.279	2.995	0.139	21.612	FALSE	<0.0001
Hbee visitation	Hbee distance	-0.130	-0.234	-0.031	-0.130	0.053	-2.469	FALSE	0.0136

Hbee visitation	Lbee distance	0.350	0.176	0.523	0.349	0.089	3.934	FALSE	0.0001
Hbee visitation	Lbee:Hbee distance	0.071	-0.047	0.195	0.072	0.064	1.131	TRUE	0.2581
Hbee visitation	Lbee visitation	-0.061	-0.165	0.042	-0.062	0.052	-1.184	TRUE	0.2365
Hbee visitation	Bay position	0.564	0.149	0.974	0.564	0.213	2.647	FALSE	0.0081
Hbee visitation	Flower density	0.001	-0.021	0.024	0.001	0.012	0.110	TRUE	0.9121
Hbee visitation	Male bay	0.139	-0.147	0.418	0.139	0.141	0.987	TRUE	0.3238
Hbee visitation	Dispersion (NB ϕ)	0.608	0.473	0.763	0.611	0.074	8.225	-	-
Hbee visitation	Dispersion (ZI θ)	0.331	0.266	0.388	0.330	0.031	10.820	-	-
Pollen deposition	Intercept	2.389	2.045	2.747	2.390	0.180	13.248	FALSE	<0.0001
Pollen deposition	Hbee visitation	0.034	-0.034	0.102	0.034	0.035	0.979	TRUE	0.3275
Pollen deposition	Lbee visitation	0.172	0.064	0.277	0.172	0.054	3.171	FALSE	0.0015
Pollen deposition	Bay position	-0.548	-0.782	-0.309	-0.547	0.121	-4.510	FALSE	<0.0001
Pollen deposition	Hbee distance	-0.157	-0.226	-0.086	-0.157	0.036	-4.403	FALSE	<0.0001
Pollen deposition	Flower density	-0.017	-0.055	0.024	-0.017	0.020	-0.830	TRUE	0.4067
Pollen deposition	Field-level σ	0.839	0.629	1.131	0.850	0.126	6.733	-	-
Pollen deposition	Plot-level σ	0.644	0.525	0.772	0.646	0.064	10.117	-	-
Pollen deposition	Dispersion (NB ϕ)	0.816	0.737	0.897	0.817	0.041	19.724	-	-
Flowers per plant	Intercept	5.912	5.880	5.943	5.912	0.016	371.493	FALSE	<0.0001
Flowers per plant	Plant size	0.930	0.910	0.952	0.930	0.011	82.693	FALSE	<0.0001
Flowers per plant	Bay center	0.086	0.055	0.122	0.085	0.018	4.636	FALSE	<0.0001
Flowers per plant	Fruit set	-0.149	-0.172	-0.126	-0.149	0.012	-12.148	FALSE	<0.0001
Flowers per plant	Field-level σ	0.068	0.043	0.100	0.069	0.015	4.750	-	-
Flowers per plant (dispersion)	Intercept	4.044	3.630	4.401	4.035	0.197	20.500	FALSE	<0.0001
Flowers per plant (dispersion)	Plant size	0.294	0.018	0.576	0.289	0.137	2.114	FALSE	0.0345
Flowers per plant (dispersion)	Field-level σ	0.759	0.524	1.140	0.774	0.154	5.013	-	-
Fruit set	Intercept	0.747	0.587	0.910	0.747	0.081	9.259	FALSE	<0.0001
Fruit set	Pollen	0.148	0.057	0.245	0.148	0.048	3.095	FALSE	0.0020
Fruit set	Plant size	0.198	0.179	0.217	0.198	0.010	19.887	FALSE	<0.0001
Fruit set	Bay position	-0.236	-0.349	-0.120	-0.235	0.059	-3.961	FALSE	0.0001
Fruit set	Hbee distance	-0.107	-0.145	-0.066	-0.107	0.020	-5.344	FALSE	<0.0001
Fruit set	Lbee distance	-0.201	-0.328	-0.080	-0.202	0.064	-3.159	FALSE	0.0016
Fruit set	Flower density	-0.009	-0.026	0.008	-0.009	0.009	-1.065	TRUE	0.2870

Fruit set	Field-level σ	0.367	0.276	0.485	0.371	0.054	6.913	-	-
Fruit set	Plot-level σ	0.348	0.309	0.393	0.349	0.021	16.274	-	-
Seeds per pod	Intercept	2.834	2.736	2.930	2.835	0.049	57.527	FALSE	<0.0001
Seeds per pod	Pollen	0.061	0.010	0.117	0.062	0.027	2.279	FALSE	0.0226
Seeds per pod	Plant size	0.189	0.123	0.253	0.188	0.033	5.648	FALSE	<0.0001
Seeds per pod	Bay center	-0.135	-0.190	-0.075	-0.134	0.029	-4.597	FALSE	<0.0001
Seeds per pod	Hbee distance	-0.008	-0.025	0.010	-0.008	0.009	-0.897	TRUE	0.3696
Seeds per pod	Flower density	-0.005	-0.013	0.002	-0.005	0.004	-1.370	TRUE	0.1708
Seeds per pod	Fruit set	0.136	0.091	0.180	0.136	0.023	6.030	FALSE	<0.0001
Seeds per pod	Field-level σ	0.117	0.083	0.162	0.118	0.020	5.831	-	-
Seeds per pod	Plant-level σ	0.089	0.019	0.141	0.088	0.029	2.997	-	-
Seeds per pod	Dispersion (NB ϕ)	3.459	3.214	3.723	3.462	0.129	26.757	-	-
Weight per seed	Intercept	3.556	3.321	3.813	3.564	0.127	28.130	FALSE	<0.0001
Weight per seed	Pollen	0.069	-0.021	0.168	0.072	0.050	1.452	TRUE	0.1464
Weight per seed	Seeds per pod	-0.036	-0.041	-0.031	-0.036	0.002	-15.019	FALSE	<0.0001
Weight per seed	Plant size	0.260	0.150	0.362	0.260	0.056	4.640	FALSE	<0.0001
Weight per seed	Year	0.463	0.230	0.723	0.471	0.121	3.906	FALSE	0.0001
Weight per seed	Lbee distance	0.090	-0.046	0.223	0.090	0.067	1.347	TRUE	0.1779
Weight per seed	Plant density	0.475	0.258	0.658	0.472	0.103	4.583	FALSE	<0.0001
Weight per seed	Lbee stocking	0.231	0.003	0.458	0.235	0.121	1.948	FALSE	0.0514
Weight per seed	Plant density: Plant size	-0.204	-0.421	0.010	-0.203	0.109	-1.866	TRUE	0.0620
Weight per seed	Field-level σ	0.303	0.214	0.425	0.309	0.054	5.684	-	-
Weight per seed	Plot-level σ	0.645	0.593	0.716	0.648	0.032	20.510	-	-
Weight per seed	Residual σ	1.032	0.977	1.069	1.031	0.023	45.490	-	-
Weight per seed	Dispersion (Exp λ)	4.927	2.852	9.739	5.364	1.869	2.869	-	-

Table S4: Coefficients from seed field model. Terms with a colon between them indicate interactions. Shorthand terms: "Lbee" = "Leafcutter bee", "Hbee" = "Honey bee".