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Bee visitation, pollination service, and crop yield in commodity and hybrid seed canola

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ABSTRACT

Insect-mediated pollination of crops is an important service to agriculture, as increased insect visitation can increase fruit production by increasing pollen deposition. Unfortunately, pollination is often treated as a "black box", and pollination management suffers from key knowledge gaps that hinder its greater utility, particularly the specific mechanisms underlying the processes of visitation, pollination, and fruit production. We present a causal model that links insect visitation to pollination to three separate components of yield, using field data from two types of canola (*Brassica napus*) production systems. Our results demonstrate that yield in commodity canola fields is primarily determined by plant size, and we found no relationship between honey bee (*Apis mellifera*) visitation and pollen deposition, or pollen deposition and seed yield. In contrast, yield in hybrid seed canola fields was similarly controlled by plant size, but there was also a strong relationship between alfalfa leafcutting bee (*Megachile rotundata*) visitation and pollen deposition, as well as pollen deposition and seed yield, meaning that leafcutting bee visitation in increased pollen deposition in seed canola fields, while honey bee visitation did not. This model serves as a step towards a dynamic model of pollination services, and highlights the relative importance of bee pollination in 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 diet (Eilers et al., 2011). Pollination of these crops, however, is largely treated as a single step, but in reality there are many links in the chain of events that result in fruit production. Visitation of flowers by animals (typically bees or other insects) can increase the deposition of pollen onto the stigma of the flower, but must be preceded by gathering plant resources via vegetative growth, followed by fertilization of ovules and maturation of fruit (Erbar, 2003; Goldberg et al., 1994). Each step has many other underlying constituent components (e.g. stigma receptivity, pollen tube growth, ovule abortion), but even at this coarse level of approximation, most agricultural pollination studies fail to account for important underlying processes. Moving beyond this "black-box" model (inputs and outputs known, but intervening processes are not) of crop pollination requires incorporating these steps, and is needed for contextualizing the value of pollination services and managing crop yield in novel circumstances.

Pollinator visitation is not uniform within fields: visitation rates typically decline with distance away from the pollinators' nest sites (Ricketts et al., 2008). Smaller bees fly shorter distances than larger bees (Greenleaf et al., 2007; Zurbuchen et al., 2010), so their abundance at the centre of large fields can be low (Isaacs and Kirk, 2010). Hence, managing the location and density of pollinators is important for optimal yield of pollinator-dependent crops (Fries and Stark, 1983; Cresswell and Osborne, 2004). Similarly, foragers will often specialize on certain species or morphs of flowers in order to forage more efficiently (Heinrich, 1976; Goulson et al., 1997). Pollination of hybrid seed crops presents a challenge for specialized foragers, as it requires movement of pollen between separate lines of plants, meaning that specialization can reduce pollen transfer (Gaffney et al., 2019; Waytes

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et al., 2022). Competition for floral resources can occur between different species of foragers, but they can spatially separate their foraging to reduce competition (Schaffer et al., 1979; Thomson et al., 1987 but see Steffan-Dewenter and Tscharntke, 2000). Thus, variation in visitation can be driven by distance, competition with other foragers, or floral specialization; however, commercial pollinators are often treated as a single agricultural "input", and this spatial variation is seldom considered.

Seed production can be limited by plant resources, meaning that the benefits of insect pollination are context-dependent (Stephenson, 1981; Marini et al., 2015; Tamburini et al., 2017, 2019). Pollination 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); many species can readily self-pollinate, but may produce more fruit or seeds from outcrossed pollen (Knight et al., 2005). However, the benefits from this extra pollen deposition are diminishing: high amounts of pollen cause decreasing improvement in fruit production (Plowright and Hartling, 1981; Ashman et al., 2004; Harder et al., 2016). Low pollen deposition can also cause flower abortion, where poorly-pollinated flowers are abcised from the plant (Stephenson, 1981), but plants with an indeterminate growth strategy can offset this by producing more flowers (Lovett-Doust and Eaton, 1982; Lawrence, 1993; Sabbahi et al., 2006; Bos et al., 2007). Finally, pollen limitation can occur at multiple levels within a plant: additional pollen may result in a greater number of seeds per fruit (Knight et al., 2006), which in turn may reduce seed size due to competition between ovules or fruit (Free and Nuttall, 1968; Mazer, 1987). Therefore, understanding how plants reproduce under pollen or resource deficits is important for managing agricultural production (Bos et al., 2007; Tamburini et al., 2019).

Insect pollination is especially important in the production of canola (*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" and a hermaphroditic "male" line (Westcott and Nelson, 2001; Steffan-Dewenter, 2003; Clay, 2009). Seed canola production requires a large number of pollinators to ensure pollen transfer from the male to the female line (seeds from the male line are not harvested), but not all species of visiting insects are equally effective at pollen deposition, and few studies examine pollination in these seed production systems (Mesquida and Renard, 1981; Mesquida et al., 1991; Waytes et al., 2022). Bee 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), but this is unclear, as many key studies suffer from either a lack of realistic context, have a number of potential confounding variables, or infer plant-level outcomes from flower-level treatments without accounting for within-plant allocation of resources (reviewed by Ouvrard and Jacquemart, 2019). Greenhouse experiments typically involve unrealistically high levels of pollination, nutrient availability, and water, all of which can interact to affect yield (Bartomeus et al., 2015; Marini et al., 2015). Field studies often relate yield to indirect measures of pollination services, such as species richness or distance from sources of potential pollinators, or do not examine production at the plant level (Morandin and Winston, 2005; Ricketts et al., 2008). These proxies 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 visitation from certain plants or flowers, but can cause unrealistic yields by altering wind pollination, humidity, light, or pest densities (Olsson, 1960; Neal and Anderson, 2004; Jauker and Wolters, 2008). All of these methods give 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).

Seed production in canola involves a sequence of processes (visitation → pollen deposition → fruit production ← plant resources), that determine the relationship between pollination and the resulting components of crop yield (seed size/number). Studies of canola pollination have typically focused on individual processes, 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, and few have used realistic field data (Morandin and Winston, 2005; Isaacs and Kirk, 2010). In this study, we examine how distance influences managed bee visitation, which in turn influences pollen deposition and seed yield, using commodity and seed canola crops in Alberta, Canada. Using both commodity and seed canola provides an opportunity to compare two plant varieties that differ strongly in their pollination requirements, while accounting for agricultural differences between varieties. We expected that bee visitation would decrease with distance from each species' hive or shelter, that lower visitation would result in lower pollen deposition, and that species may differ in their pollination ability. We also expected that higher pollination would increase seed production in canola crops, but would have the greatest effect in seed canola, and that plant size (a proxy for resource availability) would similarly increase seed production. 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.

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 (Figure S1). Fields were selected based on the proximity of honey bee apiaries and site access. Colonies of Western honey bees (*Apis mellifera* L., hereafter HB) were located at the corner or side of 28 of the 60 fields (stocking rates: 0.03–3.1 hives/ha, 32 fields were unstocked). Stocking rates were calculated using the area of the focal field, but since other canola fields were in different stages of bloom around the focal field, the *effective* stocking rates were likely lower. Irrigation systems were present at 14 of the 31 fields near Lethbridge, and growers were also asked for canola variety information, but there was not enough replication to test for differences.

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, all of which were irrigated and stocked with HB hives at a rate of 2.5 hives/ha (160 hives per quarter section, with apiaries stationed in the corners or sides of field). In seed fields, bays of hermaphroditic (hereafter "male") and female plants are typically planted in 1- and 6-m wide linear strips ("bays"), respectively. Seed fields were stocked with shelters (1.3–2.6 shelters/ha, Figure S2) containing alfalfa leafcutting bee cocoons (*Megachile rotundata* F., hereafter LCB) at a density of 50–100,000 cocoons/ha. Both HBs and LCBs are managed pollinators that are not native to Alberta, and are uncommon outside of managed pollination systems and honey production yards, so we assumed that the hives and shelters were the sole sources of visiting bees in the observed fields.

In both field types, we established sets of plots at varying distances from the nesting sources of pollinators. In commodity fields, 1 m^2 plots (271 total plots) were located at 5, 20, 100, and 500 m away from the field edge closest to the set of HB hives or potential sources of wild pollinators in unstocked fields (forests, shrublands, or grasslands); however, we observed very few wild bees in either field type (Table S2), so these were excluded from the analysis. In seed fields, we established plots at 5, 20, 100 (250 m in 2016), and 400 m into the field along a transect from the nearest set of HB hives, using pairs of plots at the edge of adjacent male and female bays (Figure S3). To examine within-bay variation in visitation, we established a plot at the centre of the female bay at the 5 m and 400 m plot in each field. Distances to nearest shelters were measured using a Nikon™ Laser 800S Rangefinder. Finally, we incorporated plot-level visitation data from Waytes et al. (2022); same years and locations) to more accurately gauge the effect of distance from shelter on visitation rates (647 total plots). All surveys occurred on fair-weather days (median temperature: 24.5˚C., range: 17–33˚C.) with no rain and minimal wind (> 30 km/hr); wind speed and temperature were measured at each site with a Kestral™ 2500 weather

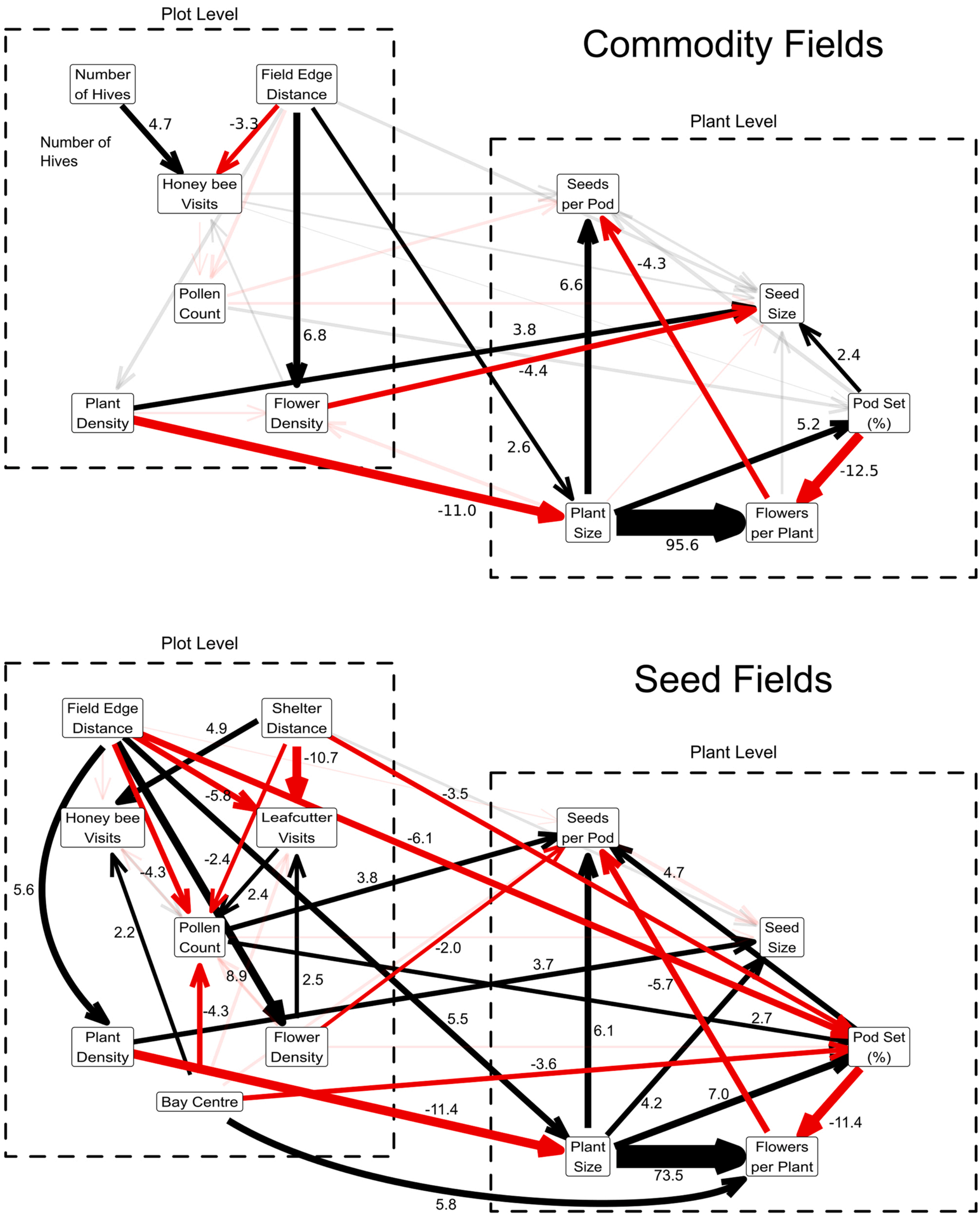

Fig. 1. Results of path analyses in commodity and seed fields. *Field Edge Distance* refers to the distance to the edge of the field (and location of HB apiary) and *Shelter Distance* refers to the distance to the nearest LCB shelter. The width of each arrow is proportional to the effect size of each component path (number also displayed), with black and red lines representing positive and negative effects, respectively. Transparent arrows show path coefficients whose 95% CIs overlapped zero.

meter.

Visitation and pollination data were collected at each field during the main bloom (late June - late July), and plants were collected just prior to harvest (late August). We recorded the number of insect visits that contacted the stigmas and anthers of flowers during 10 min of observation (5 min for seed fields during 2015), recorded the identity of the visitor, and counted the number of open flowers in each plot (petals had not yet started to wilt, style had not elongated more than 3–4 millimeters beyond the anthers). To measure pollen deposition, we collected stigmas from five random flowers at each female plot, mounted them in fuchsin gel (Beattie, 1971) on slides, and counted the pollen on each stigma using a Leica™ DME 13595 light microscope under 100x magnification (1294 commodity and 1050 seed canola stigmas). We visited each field once during the bloom, as we opted to collect data from a larger number of fields rather than having multiple samples per field. At the end of the growing season, we collected three plants and recorded plant density from the same female plot (789 commodity canola plants, 582 seed canola plants total). We dryed and weighed each plant, counted mature pods to estimate pod set, and counted flower pedicels to estimate total flower production. We estimated seed size and seeds per pod by averaging the seed count and weight from five pods on each plant. Finally, we threshed all the pods for each plant by hand and weighed the total mass of cleaned seeds (hereafter "plant yield").

2.2. Analysis

To examine how yield is influenced by visitation, we used piecewise structural equation models (pSEM, Shipley, 2009) implemented in R 4.2.2 (R Core Team, 2022). Structural equation models (SEMs) are a set of linear models arranged in a causal network, which provides a framework for testing hypotheses about complex systems (Grace et al., 2012; Lefcheck, 2015). SEMs provide a framework for empirical analysis of complex systems, as they allow causal relationships to be formally tested, can provide insight into alternative mechanisms, and are flexible in their assumptions (Shipley, 2009; Clough, 2012; Grace et al., 2012). Starting with a simple model (visitation → pollen deposition → fruit production ← plant resources), we built a detailed model relating visitation to pollination to seed and pod production within a causal framework (Fig. 1). We also ran a linear model outside of each SEM to predict plant yield (g of seed per plant) as a function of the seed size, seeds per pod, and pods per plant (see Table S6), which can be converted into *total yield* for a given area (t of seed per ha) by multiplying plant yield by plant density. After the sub-models were fit and validated, we simulated seed size and total yield at varying distances from pollinators using the coefficients from each model to integrate the effect of pollination on total yield. To justify excluding wind-borne pollen, we simulated a "minimum visitation" scenario in seed canola, using the minimum recorded HB/LCB visitation and maximum distances in order to gauge wind pollen deposition under reduced visitation, and found that predicted pollen deposition in this scenario was only 3.5 grains/stigma. This could not be done in commodity canola because it is impossible to realistically separate self pollination from wind pollination in male-fertile plants unless flowers are emasculated or genetic markers are used.

The underlying models of each pSEM were specified as generalized linear mixed-effects models (GLMMs, see Equations S1 and S2, Table S1 for a summary of the SEM variables). Random intercepts were used to model field- and plot-level variance, but plot-level variance terms had poor traces and low effective sample sizes, indicating low plot-level variance or insufficient sampling; therefore, we omitted plot-level random effects for all models (except for pollen count and pod set in seed fields, see Table S5). Field-level random intercepts accounted for between-field variation and seasonal changes in bee visitation rates (see Figure S4). Commodity HB visitation models using stocking rate rather than number of hives fit the data equally well (ΔAIC = 0.2) and did not change any other results (seed fields all had identical HB stocking rates). LCBs were seen directly harassing HBs during the plot-level observations (also observed by Batra, 1978 and Waytes et al., 2022), but HBs were never the aggressor in these interactions, so we treated LCB visitation as a potential cause of HB visitation (Fig. 1). Pod 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 pod set to flower production to approximate this process. The direction of the path could be reversed, implying that large flower production reduces the proportion of pod set, but we considered only the first scenario, as Sabbahi et al. (2006) showed that low pod set increases flower production. There were no large differences in visitation rates for HBs or LCBs (p = 0.32, 0.72, respectively) between male and female bays in seed fields, so bay was excluded from further analysis (plants and stigmas were not collected from male bays). Finally, we also ran models with each year's worth of data to test for between-year differences, and found that most terms were similar in effect size and directly between years (Table S4 and S5).

Structural equation models do not have paths between all variables, which may bias the model results if this independence assumption is incorrect; this requires testing a "basis set" of independence claims using Shipley's ᴅ-separation criteria (Shipley, 2000, 2009). The initial commodity canola pSEM was misspecfied, as several missing paths were identified (Fisher's C = 167.5, df = 64, p < < 0.001), but the updated pSEM was deemed adequate (C = 52.0, df = 48, p = 0.32). Similarly, the initial seed field pSEM also had several missing paths (C = 105.6, df = 76, p = 0.01), which were added, making the updated pSEM adequate (C = 72.2, k = 72, p = 0.47). Basis sets were generated using the `dagitty` library (Textor et al., 2016).

All component GLMMs of the pSEM were written in Stan 2.18.1 and run using `rstan` 2.26.13 (Gelman et al., 2015; Stan Development Team 2023). We used weakly informative normal priors ($\mu = 0$, $\sigma = 5$) for fixed effects and gamma priors ($\alpha = 1$, $\beta = 1$) for the variance components. Four separate chains were run with an adaptive phase of 1000 iterations, and a sampling phase of 1000 iterations, then checked for convergence of the chains ($\widehat{R} \approx 1$) and low autocorrelation within chains (high N_{eff}). We assessed the underlying probability distribution functions of each model using posterior predictive checks (Gelman et al., 2013). p-values were calculated using the Z-scores (mean/SD) of the sampled posterior distributions, predictions from models were calculated using the posterior median, and uncertainty was derived from the 95% credible intervals (CIs). Unless otherwise specified, listed model coefficents have a p-value less than 0.05, and are considered "strong" effects where p-values are < 0.01 (see Table S4 and S5 for detailed model summaries). Figures were made using `ggplot2` and `ggpubr` (Wickham, 2016; Kassambara, 2020).

3. Results

3.1. Path analyses

Plant size and pollen deposition were the main drivers of seed and pod production in seed canola, while plant size was the main driver in commodity canola (see Fig. 1 for paths and effect sizes). LCB visitation strongly increased pollen deposition in seed canola, but there was no effect of HB visitation in either seed or commodity canola. Plant size increased with distance from the edge of the field in both crops, as well as plant density in seed fields. Plant size strongly increased the number of flowers per plant in both crops, and pods per plant strongly reduced flowers per plant, indicating that high flower survival suppressed flower production in both crops. Plant size increased pod set and seeds per pod in both crop types, and also increased seed size in seed canola plants. Pollen deposition increased pod set and seeds per pod in seed canola, but had no effect in commodity canola, showing that plant resources matter strongly for both crops, but that pollen limitation matters only in seed canola. Finally, there was a direct effect (not mediated by visitation) of bay centre, distance from edge, and distance from LCB shelter on pollen count and pod set in seed fields, pointing to possible differences in pollen transfer even at the same rate of visitation. We consider each component of each path analysis in greater detail below:

3.2. Flower visitation

HB flower visitation (per plot) decreased with distance away from the edge of the field in both commodity and seed canola fields. In commodity fields, HB visitation decreased from 12 visits/hr per plot at the field edge to 1.8 visits/hr at 400 m into the field (Fig. 2a, apiary of 40 hives = 0.625 hives/ha in a 64 ha quarter-section). Lower stocking rates decreased HB visitation at the edge of the field to 7.4 visits/hr at 20 hives, while unstocked field edges had an average of 0.8 visits/hr. Unsurprisingly (given the higher stocking rate of 160 hives per field), HB visitation was much higher in seed canola fields, and decreased from 96.4 visits/hr at edge to 85.7 visits/hr at the centre of the field (Fig. 2a). HB visitation was also much lower near LCB shelters, dropping from 81 visits/hr at 20 m to 31 at 2 m (Fig. 2b), likely due to competition or aggression from LCBs; the direct effect of LCB visitation on HB visitation was weak (p = 0.73, after accounting for LCB distance effect).

LCB flower visitation was much higher close to their shelters, and surprisingly, was also higher at the edge of the field than the centre. Flower density was higher at further distances into the field in both field types, and had a positive effect on LCB visitation (but not HB visitation) in seed fields. LCB visitation dropped from 350 visits/hr at 2 m from the shelter to 50 visits/hr at 20 m (Fig. 2b), and also decreased from 119 visits/hr at the edge of the field to 25 at the centre (Fig. 2a, b). There was no large difference in LCB visitation between the edge and centre of the female bays, but HB visitation was higher at the centre of the bay (88 vs. 139 visits/hr, Fig. 2c). Together, our results indicate that pollination is likely accomplished by different species in different parts of the field.

3.3. Pollen deposition

LCB visitation increased pollen deposition in seed canola, but HB visitation did not increase pollen deposition in commodity or seed canola (Fig. 3a). Pollen deposition on stigmas was high in commodity canola (mean: 293 grains/stigma, SD: 385, range: 0–3981), but HB visitation had no effect. Pollen deposition declined weakly with distance from the edge of the field (p = 0.09), but this only amounted to a 6% average decrease (290 grains/stigma at the field edge vs. 240 at field centre, Fig. 3b). In seed canola, pollen deposition was much lower overall (mean: 22 grains/stigma, SD: 43, range: 0–578), and decreased from 26.3 grains/stigma at the edge to 11.5 at the centre of the field (Fig. 3b), independent of bee visitation. LCB visitation increased pollen deposition from 13 grains/stigma at 0 visits/hr to 25 pollen grains at 100 visits/hr (Fig. 3a), but there was no effect of HB visitation (p = 0.20), implying that most of the pollen deposition in seed fields is the result of LCB visitation. Pollen deposition also decreased from 15 grains/stigma at the edge of the female bay to 9 at the centre of the bay independent of visitation (Fig. 3c), suggesting that bees crossing over into male bays may deposit less pollen as they move towards the centre.

3.4. Seed production

Commodity canola produced fewer flowers per plant than seed canola (mean: 196 vs. 461), and also produced fewer pods per plant (143 vs. 299, Table S1). Commodity canola also produced more seeds per pod than seed canola plants (mean: 23 vs. 16), but seed size was lower than seed canola (2.74 vs. 3.43 mg/seed). Finally, commodity plants had lower plant yields than seed canola plants (mean: 6.8 vs. 9.5 g seed per plant), but had a lower harvest index (g seed per g vegetative biomass) than seed canola plants (0.38 vs. 0.32 g/g), likely due to lower pollen limitation.

Plant size had by far the strongest positive effect on the number of pods produced, and there was evidence of pod set suppressing flower production (Fig. 1). However, pollen deposition did not alter seed or pod production in commodity canola (Fig. 4a,b,c), nor was there a direct effect of HB visitation or distance from field edge, at least at the levels we observed. In both commodity and seed canola, plant size had a strong positive effect on pod set and seeds per pod, but did not increase seed size in commodity canola (Fig. 4d,e,f). Pod set in seed canola decreased with distance away from the field edge and LCB shelters, and was also lower at the centre of the female bay (independent of visitation and pollen deposition). This distance effect was not seen in commodity canola, suggesting a long-term pollen limitation effect in seed canola that was not captured by our snapshot of pollen and visitation. Plant density also had a positive direct effect on seed size in both crops; this likely indicates field areas with better microclimate or soil resources rather than density effects per se, as plants at the edges of the field are typically both smaller and fewer. Finally, pod set also had a strong negative influence on flowers per plant in both crop types, indicating that high pod set suppresses future flower production.

3.5. Yield simulations

Our simulations further confirmed the results of the analysis: HB visitation had little effect on total yield in either crop type, but LCB visitation improved total yield in seed crops. The simulations showed no

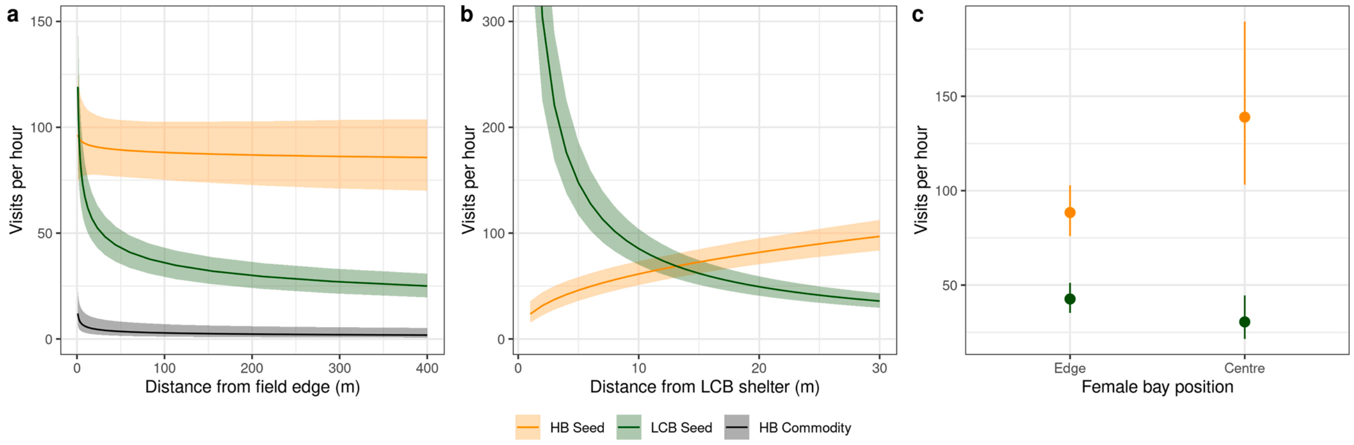

Fig. 2. Partial effect of distance from a) honey bee apiaries (at edge of the field), b) leafcutter shelters, and c) female bay position on visitation rates, with shaded regions and line ranges showing 95% CIs. Commodity fields are shown at a stocking rate of 40 hives (black line), while stocking rates are at 160 hives in seed fields (yellow line).

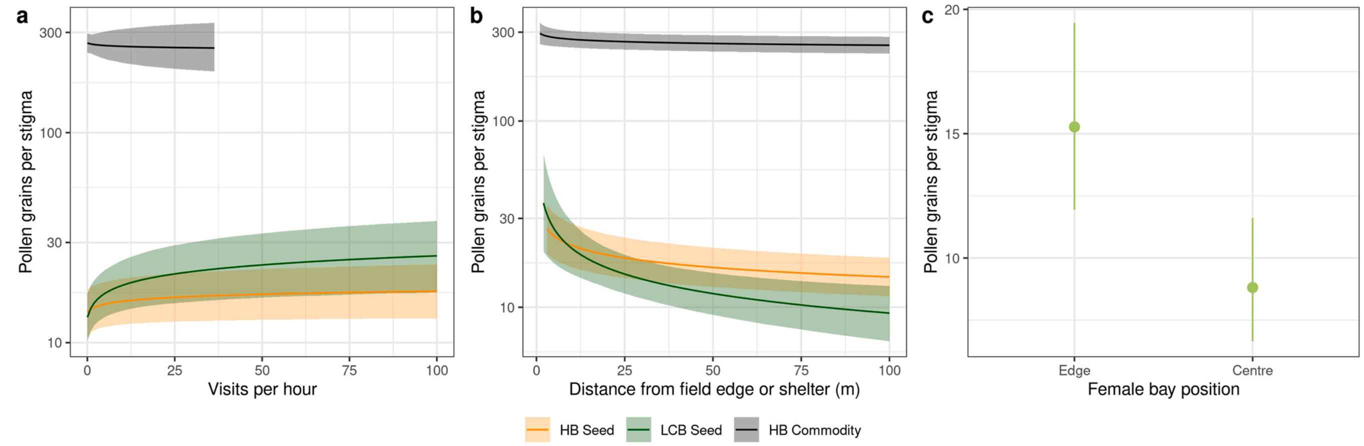

Fig. 3. Partial effect of a) visitation rate, b) distance from apiary (HB) or shelter (LCB), and c) female bay position on pollen deposition, with shaded regions and line ranges showing 95% CIs.

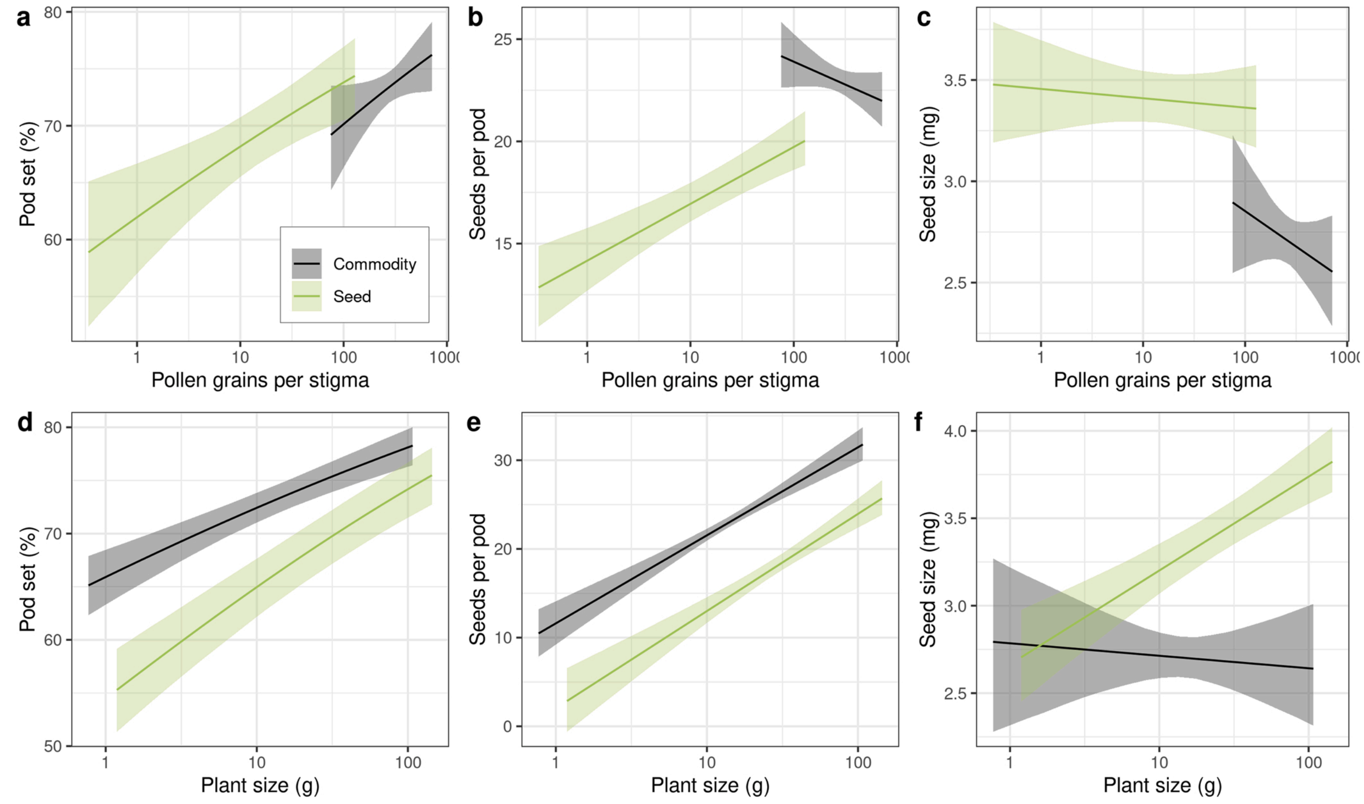

Fig. 4. Partial effect of pollen deposition (top row) and plant size (bottom row) on flower survival, seeds per pod, and seed size, with shaded regions showing 95% CIs.

large effect of HB stocking on seed size or total yield in commodity fields (Fig. 5a and b, respectively), aside from the effect of distance from the edge of the field. Similarly, the simulations for seed fields showed a small increase in seed size and total yield with distance from the HB hives at the field edges, but the effect of distance from the LCB shelters was much more dramatic (compare isoline spacing along the x-axis and y-axis in Fig. 5c and d). Simulations run separately for the edge and centre of the female bay revealed that not only were total seed size and total yield lower at the bay centre, but that the effect of HB distance was effectively *nil* at the bay centre (yield isolines are horizontal in bay centre, and angled at the bay edge, Fig. 5d and f). Interestingly, the simulations also showed evidence of nonlinear behaviour occurring in the centre of seed field bays, where a local minima in total yield appears at approximately 25 m away from HB hives and 45 m away from LCB shelters (Fig. 5f), likely because of an interaction between the components of yield (seeds per pod, pods per plant, and weight per seed).

4. Discussion

Our results showed a strong link between visitation and yield in seed canola, but not in commodity canola. HB visitation had little direct influence on pollen deposition in either crop type, while LCB visitation had a positive effect on pollen deposition in seed canola. We found that crop yield in commodity canola is largely limited by plant size, while seed canola yield is limited by both pollen and plant size; our simulation results from the path analyses further confirmed this, showing the strong

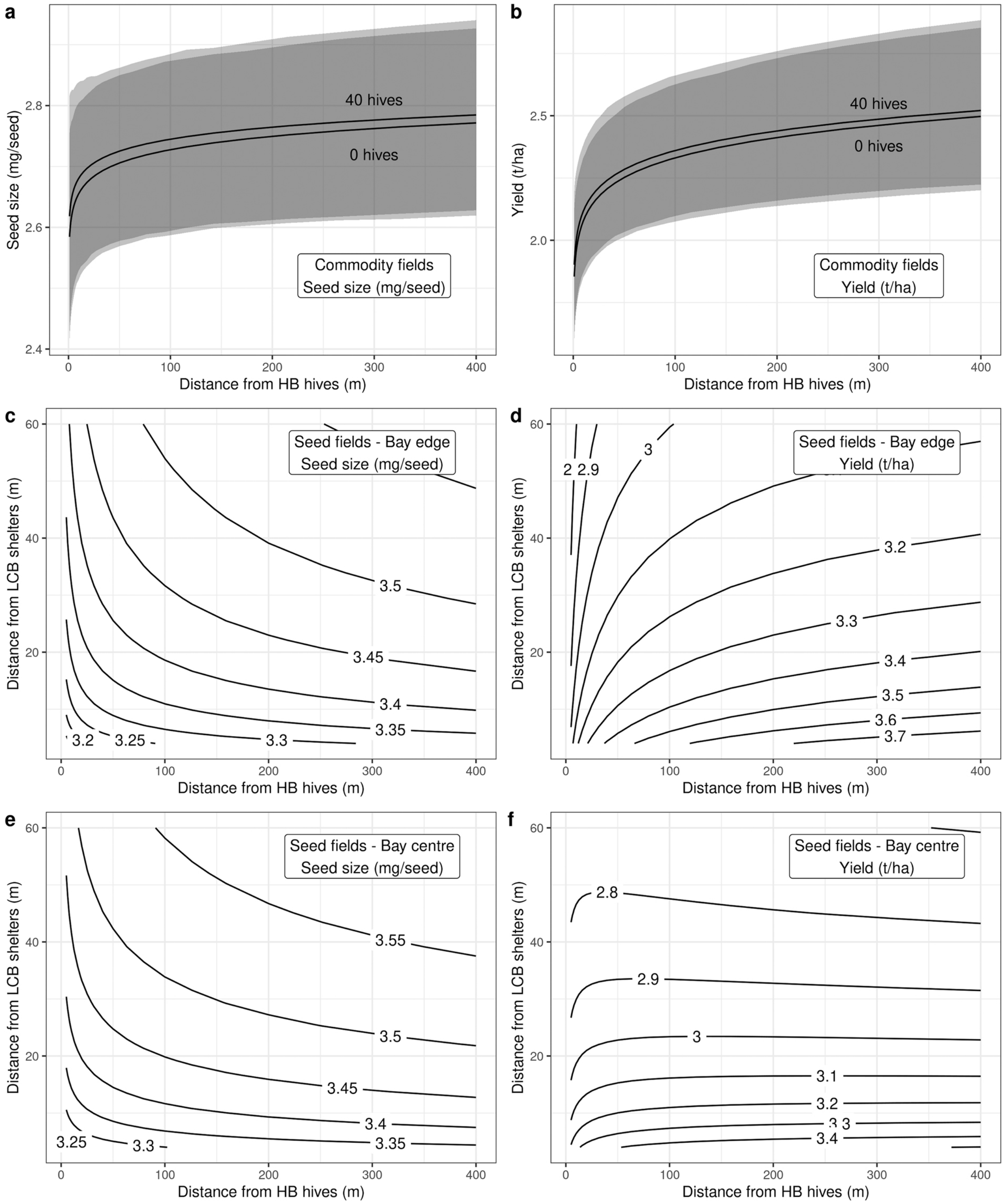

Fig. 5. Simulated effect of honey bee distance and leafcutter distance on seed size (mg/seed, first column) and total yield (tonnes/hectare, second column), using coefficients from paths for simulation. Shaded areas shown in a & b are 95% quantiles for the simulations. Lines on panels c - f are isolines of constant seed size (c, e) or yield (d, f).

influence of LCB visitation on seed size and total yield. These results provide mechanistic information on the value of pollination services in commodity and seed canola crops, and show how a statistical-mechanistic model of seed production provides richer insight into the process of seed production than linear models alone.

4.1. *Bee visitation*

HB visitation was much higher in seed fields than commodity fields due to the higher stocking rate (2.5 vs. 0.6 hives/ha), but HB visitation in both field types declined with distance into the field. This decline was not surprising, since HBs travel from their hive outside the edge of the field (Robinson et al., 2022), but we did not expect a similar decrease in LCB visitation with distance into the field, as their shelters are located *within* the field. This decrease with distance may have been caused by LCBs migrating from shelters at the centre of the field to the edge (Goerzen et al., 1995), as female LCBs 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, LCBs are not as constrained to a single nest and can drift between shelters within a given field (Goerzen et al., 1995; Pitts-Singer, 2013). LCBs must also forage for leaf materials to create cocoons, but prefer leaves other than canola (Sinu and Bronstein, 2018). Since seed canola fields have few weeds within the crop, LCBs at the centre of the field may have few choices of leaf material, or alternative pollen and nectar sources. Therefore, LCBs may move from their natal shelters to the shelters at the edge of the field to gain access to better leaf material or more diverse food sources (Horne, 1995a, 1995b).

In seed fields, HB visitation was correspondingly lower in areas close to LCB shelters, suggesting competition between HBs and LCBs. Lower HB visitation may have been caused by lower nectar and pollen resources, as areas close to LCB shelters can become depleted in nectar and pollen (Currie, 1997). HBs also suffer from direct interference by LCBs near to their shelters; during the study we observed LCBs directly harassing HBs during the plot-level observations, attacking HBs both on the flowers and in the air (Batra, 1978; Waytes et al., 2022). HB visitation and foraging behaviour varied strongly between the edge and centre of the female bays in seed fields, while there was little difference between LCB visitation rates. HB visitation rates were almost twice as high at the centre of the female bay, but there was no difference in LCB visitation between male and female bays; this may reflect a greater need for pollen among LCBs than HBs (Cane et al., 2011), as female canola plants produce only nectar.

Very few HBs in the female bay were pollen foragers (1.4%, see Table S3), meaning that foragers who have recently come into contact with pollen are rare. HBs cross minimally between bays in hybrid crop systems (Gaffney et al., 2019; Waytes et al., 2022), limiting pollen transfer. Side-working was a very common behaviour among HBs in commodity fields (65% of the total visits from HBs during 2015 were side-working), as well as the male bays of seed fields (36%), but not in the female bays (3%, Table S3). 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 HBs avoiding contact with the stigmas to increase ease of access to nectar, or to reduce pollen grooming during a nectar foraging trip. The foragers who were side-working tended to not switch to top-working (anecdotally), so this may be a consistent individual foraging behaviour. Taken together, this suggests that HBs provide limited pollen transfer in both commodity and seed fields, as they commonly engage in side-working behaviour in both field types, and pollen foragers typically avoid female bays in seed canola fields.

4.2. Pollen deposition

HB visitation did not increase pollen deposition in commodity canola fields compared to unstocked fields, meaning that self-pollination is the likely agent of pollen transfer (*Brassica* flowers are not aligned for wind pollination, so cross pollination mainly occurs via insects; Mesquida and Renard, 1982; Cresswell et al., 2004). However, wind-induced self-pollination can increase yield in *Brassica* (Williams et al., 1986; Mesquida et al., 1988), and fields without bee pollination can have outcrossing rates of about 20% within the field (Rakow and Woods, 1987; Becker et al., 1992). HBs 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 et al. (2022) used male-sterile flowers to estimate pollen deposition and found that HB pollen foragers deposited far less outcrossed pollen than previously reported (~ 2 grains per visit), suggesting that much of the pollen deposited on commodity canola stigmas may be self-pollen. Because the overall pollen deposition rates found in this study were high, HB visitation seems to have made little difference in the amount of self-pollination, as large amounts of pollen were present on commodity canola stigmas even at the centre of unstocked fields. This suggests that commodity canola stigmas are largely saturated with self-pollen, effectively "swamping" any extra pollen deposition by HBs.

Our models also revealed that pollen-transferring behaviour of HBs is limited in seed fields, as deposition strongly increased with LCB visitation, but not HB visitation. HBs in seed fields tended to visit more in the centre of the female bay, even close to the edge of the field, yet pollen deposition was still about 40% lower. LCBs switch between male and female flowers more frequently than HBs, travel further between flowers, transport more viable pollen, and tend not to side-work canola flowers (Soroka et al., 2001; Parker et al., 2015; Brunet et al., 2019), all of which may explain their higher pollination efficacy. Pollen deposition in seed fields also decreased with distance from the edge of the field, and was lower in the centre of the female bays independent of visitation, suggesting lower pollen transfer per visit. These may have been caused by low pollen carryover with distance into the female bays or shorter trips between flowers at the centre of the field. Pollen carryover from the edge to the centre of the bay female is likely reduced as LCBs typically visit the edge of the female bay before venturing into the centre (Thomson, 1986; Pinnisch and McVetty, 1990). *Bombus* take shorter trips between flowers under nectar-rich conditions (Pyke, 1978; Heinrich, 1979), suggesting that HBs and LCBs may operate similarly at the centre of seed fields, resulting in lower pollen transfer. While manipulating nectar levels within a field to produce greater travel between flowers could be difficult, this suggests that the optimal width of female bays within seed fields may be lower than is currently practiced.

While we found that HBs have no direct effect on pollen deposition in either crop type, they may have an indirect positive effect caused by: a) increasing airborne pollen from male-fertile flowers (Pierre et al., 2010), b) lowering nectar and pollen standing crop, causing LCBs to travel further (Pyke, 1978; Heinrich, 1979), or c) lowering floral fidelity on higher-rewarding flowers in the male bays (Mesquida and Renard, 1978; Waytes et al., 2022; Gaffney et al., 2019). A simple test of this could be to remove HB hives from a seed field (mid-season) and observe changes in LCB visitation before and after the removal.

4.3. Seed production

Plant size increased the proportion of pod set in commodity canola, but both plant size and pollen deposition increased pod set in seed canola, suggesting that both pollen deposition and plant resources constrain pod production. Other studies have shown that pod set in male-sterile plants responded positively to visitation, while male-fertile plants had no response (Mesquida and Renard, 1981; Steffan-Dewenter, 2003), but see (Adegas and Nogueira Couto, 1992). Both pod set and seeds per pod can increase with extra pollination (Jauker and Wolters, 2008; Sabbahi et al., 2005, 2006; Durán et al., 2010), so the low influence of pollination in commodity fields may be due to a high overall level of pollen deposition (Fig. 3). There was no additional effect of HB visitation on pod set, meaning that HB visitation did not cause more deposition or improve pollen quality through increased outcrossing (Rosa et al., 2011), but this may be variety-dependant (Marini et al., 2015; Adamidis et al., 2019). Flowers per plant was reduced by pod set, implying that high pod set suppresses further flower production or increases competition among pods for plant resources. The first scenario is more likely, 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 per plant (our plants had a mean of 143 and 299 pods per plant in commodity and seed canola, respectively). There were also effects of distance on pod set independent of pollen: pod set decreased with distance from the edge of the field, distance to LCB shelters, and was lower at the centre of the female bays. Mesquida and Renard (1978) also found that pod 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. Finally, the effect of plant size was roughly 6x larger than that of pollen deposition, indicating that the factors controlling plant size (e.g. fertilizer application, soil quality) likely constrain pod production more strongly than pollination alone (Marini et al., 2015; Tamburini et al., 2017, 2019; Gagic et al., 2017).

We found that seeds per pod in commodity canola was mainly influenced by plant size, while both seed size and seeds per pod was influenced by both plant size and pollen deposition in seed canola. Extra pollination generally results in canola plants producing more, smaller-sized seeds (see review in Ouvrard and Jacquemart, 2019), but see also Kołtowski, 2005, as the plant re-allocates resources across a greater number of fertilized ovules. Similarly, canola plants can also increase the number of matured ovules depending on the available plant resources (Bouttier and Morgan, 1992; Kirkegaard et al., 2018). Our results in seed canola fields showed that pollen deposition had a smaller effect than plant size for seeds per pod, suggesting that plant resources limit seed production more strongly than pollen deposition, while plant size was the dominant factor for commodity canola production. Seed size was affected only by plant size in seed canola, and was not affected by pollen or plant size in commodity canola. Plant size is a measure of the source of photosynthates available to the seeds, while fertilized flowers act as sinks of nutrients, but both of these measures are crude, as both sources and sinks of seed nutrients vary across the season (Clarke, 1979; Zhang and Flottmann, 2018). Canola growth is indeterminate, and poorly-pollinated plants respond by making more branches (Mesquida and Renard, 1981; Sabbahi et al., 2006), so it may be that large, poorly-pollinated plants have more resources and low numbers of fertilized ovules per flower at the end of the season. While we did not quantify pod position on branches, the pods at the end of the branches did appear to have fewer seeds, meaning that variation within plants likely occurred because of late-season seed. Unexpectedly, plant density had a *positive* effect on seed size in both crop types, which may be caused by two different processes: a) plant density could be positively related to resource availability if plant survival is higher in plots with better growing conditions (i.e. Berkson's paradox, Snoep et al., 2014) or b) plant density may improve the microclimate conditions of the canola stand, reducing heat or desiccation stress on individual plants. We consider the first process more likely, as planting density under uniform conditions typically has little effect on seed size (Angadi et al., 2003).

4.4. Conclusion

This study has revealed some of the detailed aspects of pollination in commodity and seed canola crops. First, it shows how two important species of commercial pollinators decline with distance from their nesting sites, and how LCBs unexpectedly decline with distance from the edge of the field. Second, it sheds light on the relative importance of HBs and LCBs as pollinators, showing that levels of HB stocking used for honey production do not strongly influence yield in commodity canola crops, and the importance of LCBs as primary pollinators of seed canola. Finally, it contextualizes the value of pollination alongside plant resources (Marini et al., 2015; Tamburini et al., 2017, 2019), showing that plant resources and pollen limit production in seed canola, while only plant resources limit production in commodity fields. Our unique SEM approach serves as an approximation of a dynamic process, but could be extended with dynamic linear models (Iwasa, 2000; Nord et al., 2011; Sáez et al., 2018) to examine how plants respond to changes in pollination over time. 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.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Shelley Hoover reports financial support was provided by the Alberta Crop Industry Development Fund. Samuel Robinson reports financial support was provided by Alfalfa Seed Commission Fund, the Canadian Bee Research Fund, and the Alberta Beekeepers Commission.

Data availability

Data are available at https://doi.org/10.5061/dryad.vhhmgqnvj and https://doi.org/10.5061/dryad.3n5tb2rn6.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.agee.2023.108396.

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