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Original article

Wild and managed bee communities in canola respond to landscape context and farm management

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Abstract – Pollinating bees promote greater yield and quality of oilseed crops like canola. Canola acreage has grown over 300% in the past decade in the Pacific Northwest region of the US, providing seasonal pulses of nectar and pollen resources that may affect bee abundance and community structure. However, because pollination by insects does not limit canola seed production, few studies have examined the biodiversity of pollinators that use these resources, or the floral traits of canola that affect pollinators. Here, we conducted surveys at canola farms across the inland Northwest USA to assess how bee biodiversity and abundance varied based on canola production practices and floral traits of canola varieties. We show that mining bees (Adrenidae) were more abundant earlier in the season and sweat bees (Halictidae) later in the season, and that bees were more abundant on farms with less floral nectar and on those in less developed landscapes. Floral traits such as larger petal size and increased nectar were correlated with lower bee abundance and diversity. However, this may reflect that petal size was associated with canola type, and that more abundant and diverse bee communities may have been more effective at removing floral nectar. While we did not find a direct effect of canola type on bees, we did find that winter canola had larger petals but lower nectar volume, which indirectly affected bee diversity and abundance. This research provides information for canola growers and land managers interested in pollinator conservation and offers a framework for future research in pollinator management.

Pollination / Canola / Andrenidae / Halictidae / Unmanaged bees / Environmental influence / Floral resources

1. INTRODUCTION

Communities of bees include generalist and specialist foragers (Cane et al. 2006; Klein et al. 2007; Jha et al. 2013), and variation in resource availability within a landscape can shape the structure of bee communities (Eberle et al. 2015; Tscharntke et al. 2005). In agroecosystems, the availability of floral resources is affected by farm management and habitat near farms (Kennedy et al. 2013; Goulson et al. 2015; Lichtenberg et al. 2017). Globally, conversion of natural habitat to agriculture has led to dramatic declines in floral resources for bee populations, threatening many species (Goulson et al. 2015). However, negative effects of agricultural intensification on bees, such as destruction of ground-nesting habitat by tillage (Ullmann et al. 2016), can be heightened or ameliorated by local practices on farms, such as whether farmers increase floral diversity or practice organic agriculture (Kennedy et al. 2013; Lichtenberg et al. 2017).

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Agricultural ecosystems offer a model to assess how landscape intensification, and shifts in resource availability, may impact bee communities. In the Palouse region of eastern Washington and northern Idaho USA, over 99% of the native prairie has converted to dryland farms in the last century (Black et al. 1998; Looney et al. 2009). While the Palouse supports at least 170 wild bee species, shifts to cereal and legume crops that provide scant nectar and pollen resources have reduced the overall forage available for wild bees (Looney et al. 2009; Looney and Eigenbrode 2012; Rhoades et al. 2017). Yet, over the past decade, acreage of canola has increased from 20 K to over 70 K hectares in Idaho and Washington (USDA NASS 2019), providing vast pollen and nectar resources (Paulitz et al. 2010; Thorup-Kristensen et al. 2012; Pan et al. 2016; Olsson et al. 2021). Although canola does not require insect pollination, studies show that yield can increase by up to 40% when insect pollinators are present, and canola may in turn support wild bee populations (Morandin and Winston 2005; Bommarco et al. 2012).

Effects of canola on bees may be mediated by habitat around farms, the variety and type (winter vs. spring), and management tactics. Canola can be grown as a fall- or spring-planted crop, providing a pulse of resources for months (Esser and Hennings 2012; Pan et al. 2016; Bjerke et al. 2019; Olsson et al. 2021). However, the impact of these resources on bees will likely depend on floral resources in the landscape and the community of bee species (Kennedy et al. 2013; Lichtenberg et al. 2017). As canola bloom often coincides with emergence of bumble bee queens and solitary bees, nectar and pollen could be available throughout bees' entire cycle. Conversely, canola could be a sink for bumble bees if blooming fields attract nesting queens from other habitats, but when flowers senesce colonies have few resources at the end of the season (Galpern et al. 2017). It is also unknown how practices such as tillage or irrigation, which can cause compaction or disturbance, may affect bee communities (Ullmann et al. 2016).

Here, we conducted a study across Palouse landscapes to identify which bee groups use canola, and which traits and varieties of canola attract specific bee groups. We predicted that bee communities would be more abundant and diverse in canola fields with more nectar and sugar, and in fields with larger flowers (Carruthers et al. 2017; O'Brien and Arathi 2018; Adamidis et al. 2019). We also predicted that bees would be less abundant on fields that use tillage because it disrupts ground nests, although irrigation may have positive effects by promoting higher soil quality (Ullmann et al. 2016). As canola is grown throughout landscapes that vary in habitat availability, our study also assessed whether landcover surrounding fields correlated with differences in bee communities. Overall, our study provides a better understanding of how crops like canola, which provide large pulses of resources in otherwise simple floral landscapes, can affect bee communities across fields with variable production practices and landscapes.

2. MATERIALS AND METHODS

2.1. Collecting bees

We sampled pollinators at canola farms across eastern Washington, northern Idaho, and northeastern Oregon in 2018 (10 farms) and 2019 (9 farms) (Figure 1, Table I). All farms were separated by more than 5 km, which is outside of the flight range of most, to limit spatial autocorrelation. Since canola is grown in rotation, not all sites were the same each year, though many growers provided sites both years, and thus year was not included in the statistical analysis. We visited farms when growers determined "peak flowering" was occurring. To establish what "peak flowering" meant to growers, we conducted an informal survey at the PNW Canola Growers Association meeting in January 2018 as to when they see the highest percentage of open flowers. The majority of growers indicated that 5 to 7 days after the first flowers open is when they see the most open flowers. We used this to designate our field days by asking growers when they witnessed "first bloom" and scheduling our visit for 4 to 6 days later.

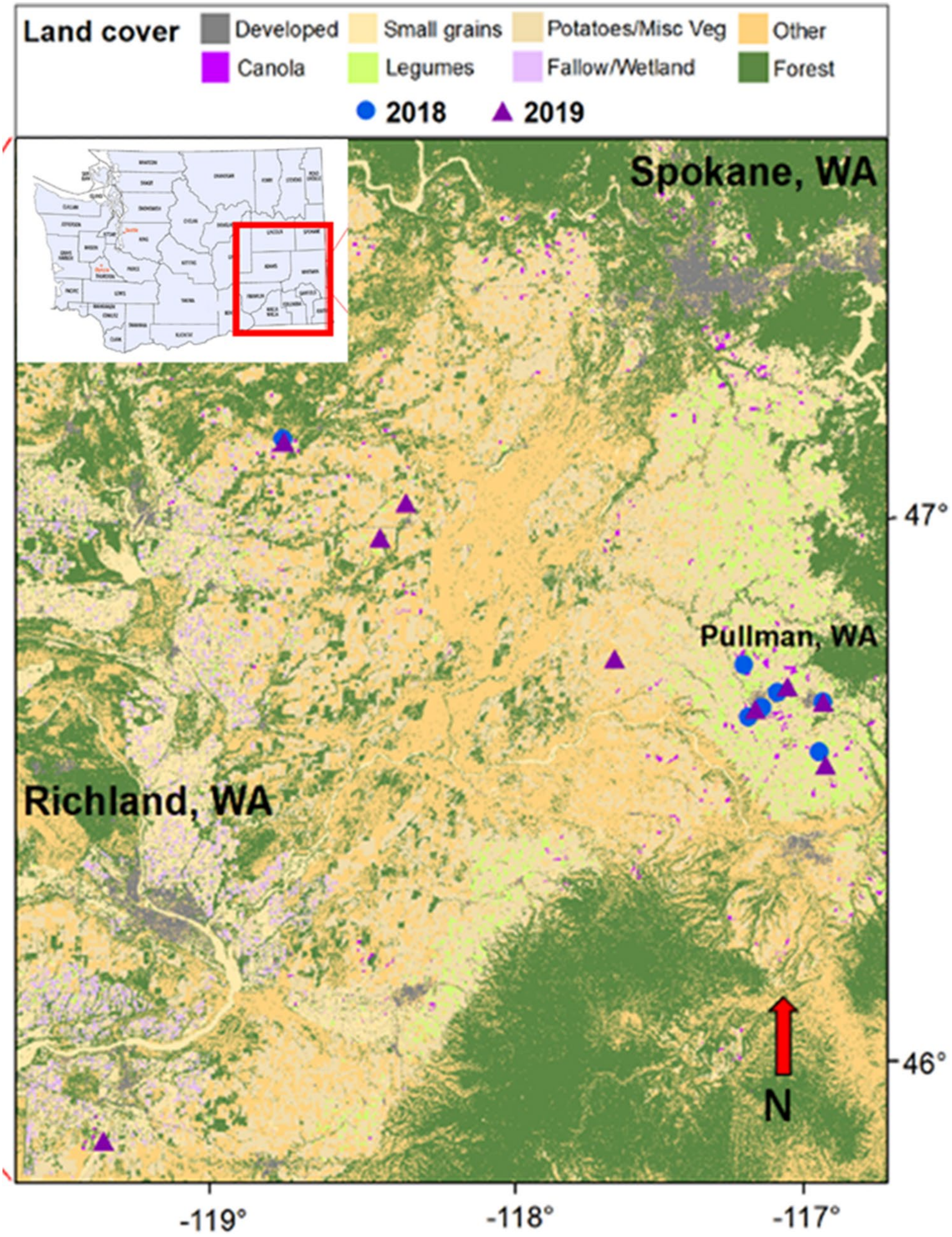


Figure 1. Map showing farm locations in 2018 and 2019 with landscape types across the range of our study system (Oregon, Washington, Idaho)

We collected bees using (i) blue vane traps (BanfieldBio, Woodinville, WA), (ii) bowl traps (3.25 oz plastic portion cups painted yellow, blue, or white), and (iii) aerial netting (30 cm diameter net, 0.6 mm × 0.8 mm mesh opening). Three blue vane traps were placed 10 m apart along a field edge, suspended by twine from a bamboo tripod so the trap was at the level of

Table I Number of replicates per variety grown by season across 2018 and 2019. Total farms were 18, but some farms grew multiple varieties

Canola variety	Winter	Spring
HyClass930	2	5
WC.34.5	2	0
46 W94	2	2
930/955 Winfield/Hyclass mix	0	2
Amanda	1	0
Edimax	3	0
InVigor.L233.PL	0	3

flowers. Six bowl traps (two blue, two white, two yellow) were placed between blue vane traps in randomized pairs. Bowls and blue vane traps contained soapy water and were placed between 08:30 and 09:00 and removed 6 h later. All contents of traps were strained through a mesh filter, rinsed with water, and placed in bags with 70% ethanol. When combined, bowl traps and blue vane traps attract a majority of bee families present in the region (Rhoades et al. 2017), but our sampling also included two 15-min bouts of aerial netting at each site (one in the morning and one in the afternoon). For each netting bout, we walked along the field edge and between rows, netting every bee seen on a flower. Bees were moved from the net into a 50-mL vial filled with 70% ethanol for storage until later identification.

To complement our sampling, we made visual observations of bees visiting flowers to see which bees were actively visiting canola flowers. We walked between field rows, stopping every 5 m to cast a 1 × 1 m visual square over a patch of flowers. We then spent 30 s noting every bee that visited the flower in that square. On-the-wing identification to species was infeasible, so we visually identified bees to morphotype including (i) mining bees (Andrenidae), (ii) bumble bees (Apidae), (iii) carpenter bees (Apidae), (iv) green sweat bees (Halictidae), (v) honey bees (Apidae), (vi) longhorned bees (Apidae), (vii) masked bees (Colletidae), (viii) megachilid bees (excluding blue orchard bee; Megachilidae), (ix) blue orchard bees (Megachilidae), (x) medium to large sweat bees (Halictidae), and (xi) small sweat bees (Halictidae).

2.2. Processing and identification

Once returned to the lab, all collected bees were rinsed in ethanol, dried, and then pinned for later identification. Bees were sorted based on data and sampling location, as well as by method of collection. Bees were then identified to morphotype using the same broad groupings that had been used during the visual field observations (Michener 2007).

2.3. Canola petal measurements

During field sampling, we took samples of canola petals to assess the average petal area on blooming flowers. For each of eight plants randomly selected in the field, we took two petals from each of three flowers at various heights on the plant, totaling six petals per plant, and 48 petals per field. We taped these petals to a data sheet that included a size standard black box printed on it. This box measured 46 × 31 mm, or 1426 mm^2. We scanned the data sheets and used ImageJ software (Ferreira and Rasband 2012) to measure the size of each individual petal in pixels, and used the size standard to calculate the area in mm^2 of each petal (Albrechtová et al. 2014).

2.4. Canola nectar measurements

We took nectar from six random flowering plants after placing traps. Plants were selected by tossing a pin flag back over the head of the sampler and collecting nectar from flowers on the closest plant to the flag. We did not bag flowers prior to sampling to exclude nectar foraging because our sampling window was short and the distance between sites made multiple visits in that short window impossible. Thus, bees or other nectar foragers may have reduced the nectar in flowers before we accessed plants. Using a 10-µL microcapillary tube, we extracted nectar from six flowers on a single plant, drawing nectar from each nectary, and then measuring the length of the nectar in the tube using digital calipers as a proxy for volume. We added 4 µL of deionized water to dilute samples for sugar concentration measurements with a refractometer (Farkas et al. 2012).

2.5. Landcover analysis

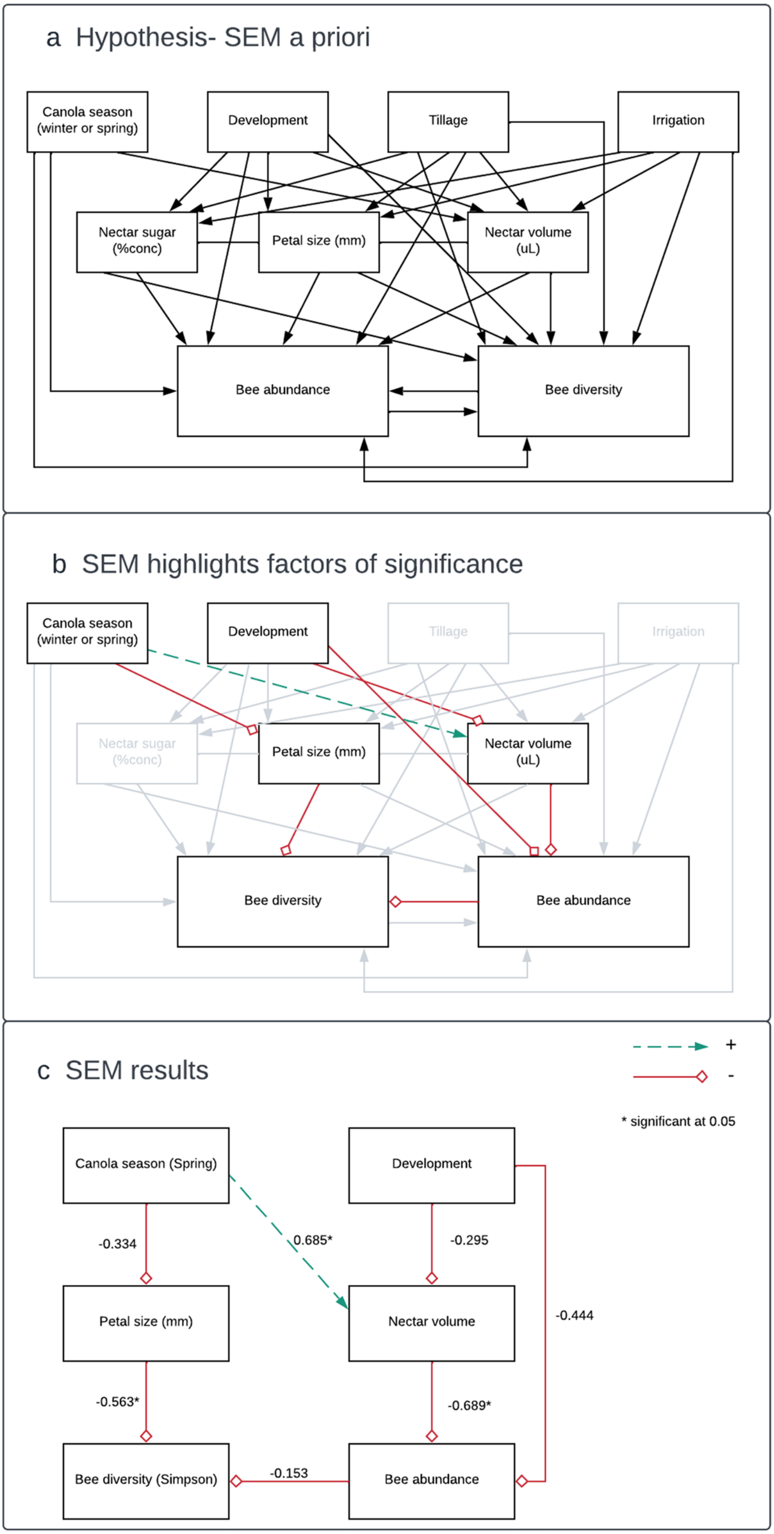
We extracted landscape data from the USGS Cropland Datalayer using 2 km buffers around our study sites and used the ArcGIS zonal metrics package to calculate class area, percentage, and number of patches (Mohler and Johnson 2009) (Figure 1). We simplified landcover area to the following categories: developed (low, medium, and high), small grains, potatoes/mixed veg, canola, legumes, fallow/wetland, forest, and other. Each of these landcover types has over 90% accuracy in estimation. The only four categories with greater than 3% of landscape were developed, canola, legumes, and small grains, with small grain and legume acreage 95% correlated. In turn, only developed, canola, and legume acreage were used in further analysis.

2.6. Data analysis

All data were analyzed using R Statistical software (R Core Team 2019). Figures were generated using the "ggplot2" and "ggmap" packages (Kahle and Wickham 2013; Wickham 2016) and the "viridis" color package (Garnier 2021. Community ecology (Shannon and Simpson Diversity) analyses were performed using the "vegan" package (Oksanen et al. 2019).

For analyses, we first used linear mixed effects models to examine effects of canola type (winter or spring) and variety (HyClass930, WC.34.5, 46 W94, 930/955 Winfield/HyClass mix, Amanda, Edimax, InVigor.L233.PL, nested within canola type) on petal size, nectar volume, and nectar sugar concentration. These variables were nested because some varieties were associated with only winter or spring canola, while other varieties were used in both winter and spring cropping systems. In each analysis, farm site was included as a random effect. At many of our sites, we were unable to collect nectar. For these sites, nectar volume was reported to be 0. Second, we used generalized linear mixed models with a Poisson transformation to measure effects of tillage, irrigation, canola type (winter or spring), canola variety (nested within type), canola petal size, nectar volume, and area of three major landcover types (canola, developed, and legumes) on bee abundance (Chambó et al. 2017); farm was included as a random effect. The final Poisson model had considerably lower deviance residuals (3.08) than numerator degrees of freedom (13), indicating a good fit. Moreover, variance inflation factors showed that all variables included in the model had values <4, indicating collinearity was not a major issue. Final models are presented with variables listed as the section subheaders in the "Results" section.

As bee communities respond to landscape context, agronomic practices, and canola traits through direct and indirect pathways, we used path analysis to test the strength of relationships between these attributes and bee abundance and diversity (Figure 2a). We assumed canola type (winter, summer), tillage (conventional, conservation, no-till), and irrigation (present, absent) could directly affect nectar sugar content, nectar volume, and petal size (Pan et al. 2016; Adamidis et al. 2019). We also assumed canola type, tillage, irrigation, and traits (nectar sugar content, nectar volume, petal size) could affect bee abundance and diversity by affecting habitat and resource availability (Ullmann et al. 2016). Based on many studies, we predicted that landscape context could affect bee abundance and diversity (Kennedy et al. 2013; Torné-Noguera et al. 2014; Lichtenberg et al. 2017). As sugar concentration was related to the amount of water in our samples, and the weather and exact time of day of sample collection could have affected the amount of water evaporation


a Hypothesis- SEM a priori
Canola season (winter or spring)
Development
Tillage
Irrigation
Nectar sugar (%conc)
Petal size (mm)
Nectar volume (uL)
Bee abundance
Bee diversity
b SEM highlights factors of significance
Canola season (winter or spring)
Development
Tillage
Irrigation
Nectar sugar (%conc)
Petal size (mm)
Nectar volume (uL)
Bee diversity
Bee abundance
c SEM results
+
-
* significant at 0.05
Canola season (Spring)
Development
-0.334
0.685*
-0.295
Petal size (mm)
Nectar volume
-0.444
-0.563*
-0.689*
Bee diversity (Simpson)
-0.153
Bee abundance

◂**Figure 2.** **a** A priori structural equation model showing hypothesized relationships among factors and results showing **b** whether factors and pathways were retained or not in the final path analysis and **c** the relative magnitude and direction of effects in the final path analysis

from nectar before our extraction, in our models we assumed nectar sugar content and volume were correlated traits, where we could not assume a particular direction of the effect (Figure 2a) (Wiemer et al. 2012). We built the a priori model with a series of linear regression models in R and used the "piecewiseSEM" package to construct the final path model (Lefcheck 2016). For analysis, nonsignificant paths that reduced model fit were dropped (measured as increase in AIC > 2), and paths were added if models without them were rejected via directed separation tests and the relationships were biologically feasible (Lefcheck 2016). Final standardized path coefficients and significance tests are reported in Table II.

3. RESULTS

3.1. Bees collected

Across the 2 years of sampling, we collected 3287 bees in 5 families and 13 genera (Figure 3). The majority of bees (over 1700) were collected at a single farm in the earlier part of the season in 2018 (site Du18w, Figure 3). We recognize this outlier might exert high leverage on the overall results, so we analyzed all data with and without that site. However, we observed the same trends when data were excluded or included, so the site was included. Across both years, the most abundant bees were green sweat bees and small black sweat bees ($F_{10,198} = 2.21$, $P = 0.01$) (Figure 3), but there were no differences in abundance between the other bee taxonomic groups (Figure 3).

3.2. Petal size and nectar

Canola petal size varied significantly across varieties ($\chi^2 = 32.5$, df = 7, $P < 0.0001$) (Figure 4a). Edimax had the largest petals (98.4 ± 1.99 mm^2), followed by 05.WC.34.5 (74.8 ± 1.99 mm^2) and InVigorL233P (75.3 ± 1.99 mm^2). These varieties had petals significantly larger than the most common variety, HyClass930 (70.6 ± 0.94 mm^2), Winfield-Hyclass (72.4 ± 1.77 mm^2), and 46 W94 (65.6 ± 1.99 mm^2) (Figure 4a). Nectar volume varied across sites and varieties, but there were no statistically significant trends ($\chi^2 = 5.23$, df = 6, $P = 0.52$), and five sites did not have measurable nectar on the day of collection (Figure 4b). Nectar sugar concentration varied between 50 and 75% for most varieties, and there was a significant effect of canola variety on this metric ($\chi^2 = 12.9$, df = 6, $P = 0.044$) (Figure 4c). The HyClass930 variety had the highest nectar sugar concentration,

Table II Standardized path coefficients and significance tests from accepted path model. Standardized coefficients (βstd) indicate relative magnitude and direction of effect

Path coefficients

Response	Predictor	βstd	DF	*P*-value
Nectar volume	Spring variety	0.68	14	0.0047
	Prop. developed landscape	− 0.30	14	0.17
Petal size (mm)	Spring variety	− 0.33	13	0.22
Simpson diversity	Bee abundance	− 0.15	12	0.55
	Petal size (mm)	− 0.56	12	0.05
Bee abundance	Prop. developed landscape	− 0.44	14	0.04
	Nectar volume	− 0.69	14	0.0029

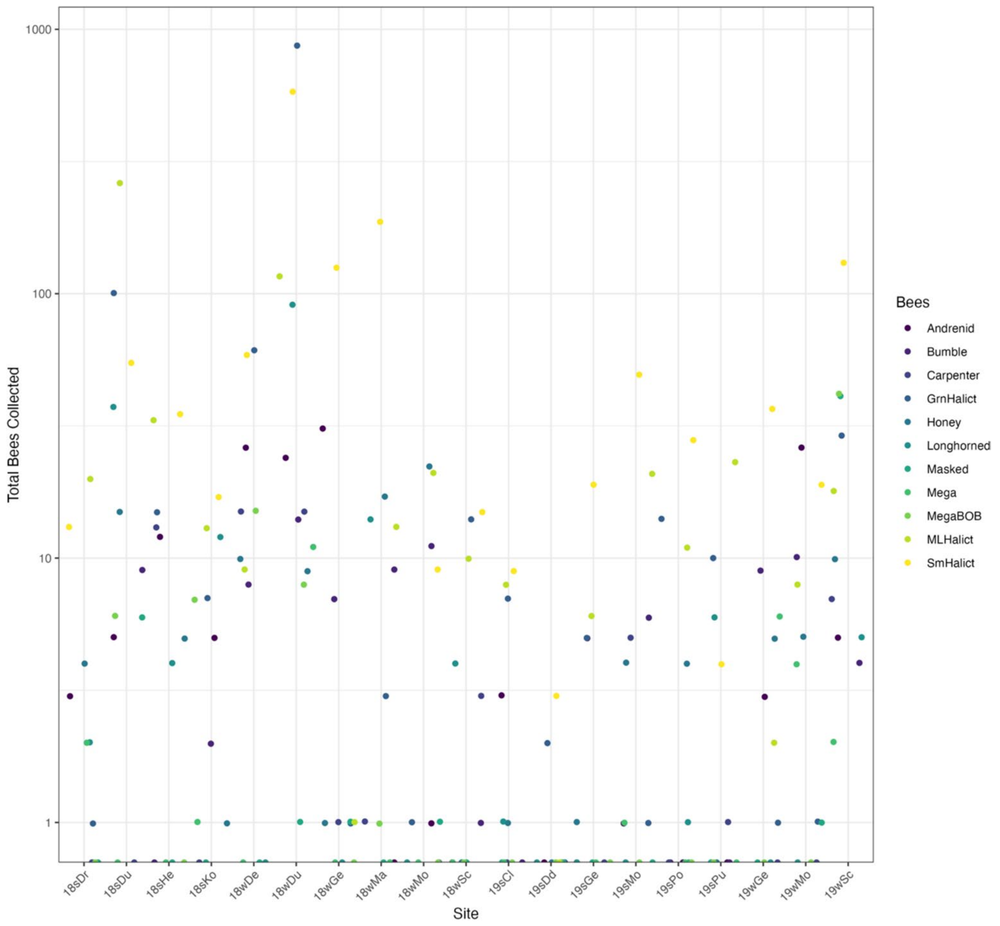


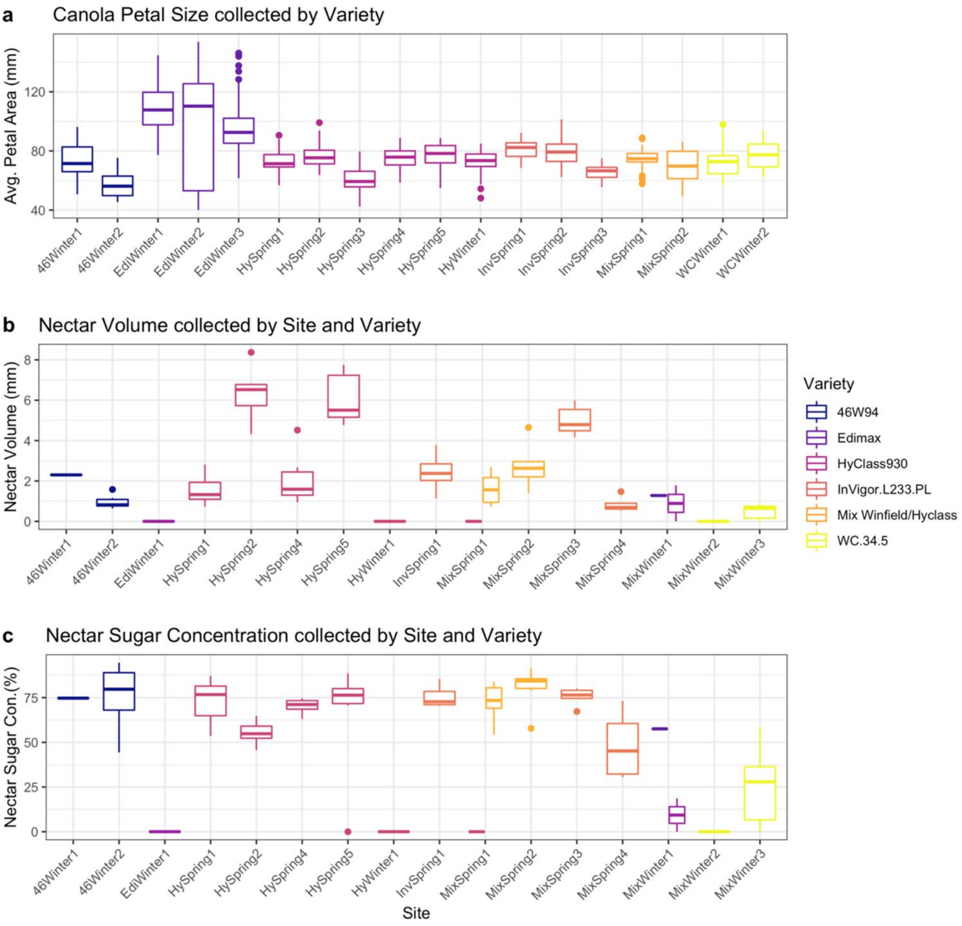
Figure 3. The abundance of bees of each morphotype sampled at each site in 2018 and 2019. Site name follows code to protect anonymity of grower but indicates year and canola season in the code name. Example: 18 sRo refers to data collected in 2018 (18) from spring (s) canola on “Robinson” (Ro) farm. Note: Robinson is not one of our actual farms but used as an example.

with significantly higher levels than Winfield-Hyclass, Amanda, and Edimax (with these three varieties not significantly different from each other) (Figure 4c).

3.3. Environmental factors and bee abundance

There were fewer bees in locations with minimal or no tillage compared to conventional tillage ($Z = -7.34$, $P < 0.001$, $Z = -5.25$, $P < 0.001$, respectively), and at sites with more developed land around the farm ($Z = -14.1$, $P < 0.001$). In contrast, bees were more abundant in irrigated than non-irrigated sites ($Z = 5.81$, $P < 0.001$), at farms with smaller petals ($Z = -9.52$, $P < 0.001$), and at farms with lower nectar volumes ($Z = -2.01$, $P = 0.040$).

Our path analysis retained many of the significant pathways in the linear models, but identified fewer significant factors mediating relationships between environmental factors and floral and bee responses (Fisher’s C = 3.68, $P = 1.0$, Figure 2b, c, Table II). Spring canola positively affected nectar volume (βstd = 0.68, $P = 0.005$), and smaller petals


a Canola Petal Size collected by Variety

b Nectar Volume collected by Site and Variety

c Nectar Sugar Concentration collected by Site and Variety

Figure 4. Canola trait data including **a** average petal size, **b** nectar volume, and **c** nectar sugar concentration (%). Each panel is organized by site code and variety; site codes reflect the dominant variety at the location, but the color codes reflect the actual variety collected in the field. Site codes also indicate the season of canola growth. Ex: 46 Winter1 is a field with the 46 W94 variety, grown as a winter crop, and 1 indicates the site using this variety that year.

were positively correlated with bee diversity (βstd = − 0.56, P = 0.05). Increased developed land around farms negatively correlated with nectar volume (βstd = − 0.29, P = 0.17) and bee abundance (βstd = − 0.69, P = 0.003, Figure 2b, c, Table II).

4. DISCUSSION

We collected many bee taxa, suggesting canola supports diverse pollinator communities, and taxa that were most abundant (green sweat bees, small sweat bees) are smaller bodied bees (Table III). Body size is often associated with foraging distance, where larger bees forage further from their nests than smaller bees (Gathmann and Tscharntke 2002). Given that we collected mostly small bees, our results suggest that many bees nest near canola fields (Greenleaf et al. 2007). Moreover, our study shows that bee diversity increased with smaller petal size, which could lead to greater pollination from small wild pollinators (Halinski et al. 2018). Although some studies show that larger

Table III Total bees collected across all collection sites and dates by bee type

Bee type	Total collected across all sites and dates
Andrenid bee	150
Bumble bee	90
Carpenter bee	61
Green halictid bee	1135
Honey bee	114
Longhorned bee	177
Masked bee	51
Megachilid (not blue orchard bee)	27
Blue orchard bee	79
Medium–large halictid bee	595
Small black halictid bee	1393
Grand total	**3872**

flowers are more attractive in general to bees (Murcia 1990), our results align with other studies that show small bees prefer smaller flowers that are appropriate for their body size (Galen & Newport 1987). Due to the request from canola growers that we stay on field edges to reduce damage to plants, it is possible the pollinators we collected are specialists of field edges, rather than a true representation of the overall pollinator populations. Because body size is correlated with flight distance (Gathmann and Tscharntke 2002), we may have found larger bodied bees in different abundances if we had collected further from the edges.

Canola has been bred for traits like larger seeds, more oil, and high protein content (Brown and Davis 2020). Canola is commonly self-fertile, so little emphasis has been put into breeding for pollinator attractive traits like flower petal size or nectar content. However, previous studies have demonstrated that even in canola varieties that do not require insect pollination, yields can increase up to 40% when insect pollinators are present (Morandin and Winston 2005; Zou et al. 2017). If bees are attracted to flowers based on body size, a survey of wild pollinators might inform growers of a variety of canola with appropriately sized flowers to best take advantage of the pollinators nearby. We saw low abundances of bumble bees and other large-bodied bees on farms with relatively small petals, even though we witnessed bee activity during the time these flowers were blooming. It is possible that small flowers are not suitable for large bees, and thus are more able to be pollinated by smaller bees. Alternately, if a grower stocks honey bees near their canola field, they may need a large-flowered variety. It is also important to note how much nectar is being produced by the variety; if the flowers do not produce enough nectar to support large honey bee colonies, it could result in bee or honey losses to the beekeeper (Goodrich 2019).

An unexpected finding was higher bee abundances in farms with conventional tillage, as this is the most disruptive type of soil disturbance in canola (Ullmann et al. 2016). However, bees could have established new nests in the canola fields, and the disruption would not occur until the end of the season or the following spring during ground preparation for the next crop. The soil disruption later in the season would impact the bee communities in the following year by damaging nests and offspring that were provisioned during our sampling period. It would be very challenging to suggest a grower alter their tillage schedule around bee nesting periods, due to winter ground freezing and fertilization schedules.

However, frequent farm implement presence in farms could discourage bees from nesting directly in the fields, and drive them to nest in reduced-traffic areas such as nearby fallow fields, field margins, or farm roads, which might act as habitat refugia in these highly disturbed areas (Greenleaf et al. 2007). Another surprising finding was bees were observed in higher abundance in fields that had lower nectar volume. However, high abundances of bees at fields with low nectar values could indicate that since plants were not bagged, bees may have collected nectar before we arrived, actually leading to a negative correlation between bee abundance and nectar volume. We recognize this was a limitation of our study, and that bagging flowers ahead of collection visits to test nectar volume may have allowed us to better infer whether the nectar was the attractive plant trait, or if there was a different attractant, like flower abundance or petal size at our locations.

We expected to see strong positive correlation between the land surrounding the farm site planted in canola or legumes and bee abundance and diversity. Neither of these were predictors of bee abundance, but the amount of land surrounding the site that was developed was a strong negative predictor of bee abundance and diversity. Developed land included buildings, roads, and other human-made structures or impenetrable surfaces. These habitat modifications reduce the suitability for bees by depleting floral resources and nesting sites, so it makes sense that this type of landscape would correlate with low abundance of bees (Goulson et al. 2015). Although canola acreage has increased in the Palouse, it still makes up a small proportion of the landscape (Figure 1). Due to the patchy nature of this crop and limited additional forage available throughout the landscape, without suitable corridors to travel between canola fields, many populations of most bees will be limited to field nearest their nesting site (Greenleaf et al. 2007). We did notice a negative correlation between landcover development and nectar, which could be a response to reduced forage available to bees in the landscape, meaning that it was likely an indirect result mediated by alterations of bee abundance rather than a direct effect of landscape composition on nectar. Previous work shows that it takes years to see changes in pollinator communities as a response to plant landscape change (Petanidou et al. 2008). This understanding might provide support to growers looking to understand their pollination needs and resources, or when it might be useful to seek the services of a beekeeper rather than relying solely on wild pollinators.

Our goal in this study was to understand which pollinators are using canola as a floral resource, and what factors might be influencing the pollinator communities at individual sites. Our research provides data to inform canola growers on potential management practices that could encourage pollinator conservation. Future research should explore whether bee body size is indeed relevant to flower petal size and foraging distance, and if we might use bee size to understand more about where bees are nesting to preserve and improve habitat spaces. We also plan to extend similar methods to explore pollination in other cropping systems in the effort to protect pollinator communities and improve pollination of crops on a larger scale.

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AUTHOR CONTRIBUTIONS

Study conception and design were done by RO and DC. Data collection and preparation were done by RO. Data analysis was done by VP and BL. The first draft of the manuscript was written by RO and DC. Further editing and manuscript preparation were done by LO. All authors read and approved the final manuscript.

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DATA AVAILABILITY

The experimental data and the simulation results that support the findings of this study are available in Figshare with the identifier https://doi.org/10.6084/m9.figshare.26009332. The USDA Cropland Data Layer can be found at https://www.nass.usda.gov/Research_and_Science/Cropland/SARS1a.php.

DECLARATIONS

Competing interests The authors declare no competing interests.

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