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Are broad sustainability practices sufficient to support wild bees? A case study in cool-climate vineyards

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Research Paper

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Abstract

Wild bees in agricultural landscapes face multiple stressors, including habitat loss and pesticide exposure. As demand for sustainably produced agricultural products increases, it is essential to understand how sustainable practices influence wild bee communities. Bee responses to such practices were assessed across 26 vineyards in Canada over 2 years. Wild bees were sampled alongside vegetation and floral resources to evaluate the effects of cover cropping, mowing frequency, alternate row management, organic farming, and certified sustainable management on bee abundance, diversity, and community composition. Vegetation height between vine rows was the strongest positive predictor of both bee abundance and diversity, while vegetation cover and floral abundance also had positive associations. A higher proportion of flowers from cover crop species was negatively associated with bee abundance, specifically for pan-trap collected bees. Alternate row and organic management had limited effects on bee abundance and diversity, while certified sustainable management showed a slight negative impact on bee diversity, as well as reduced floral richness and vegetation height. Community composition analyses revealed that both the bee communities and flower communities differed between vineyard management types, though the use of cover cropping and alternate row management did not differ between organic, certified sustainable, and conventional sites. These findings suggest that reduced mowing frequency may be an effective strategy for supporting wild bees, while other sustainable practices, such as cover cropping, organic farming, and certified sustainable management, may require enhanced research approaches to detect effects or further refinements to improve their conservation outcomes.

Introduction

Despite their importance as key pollinators for most wild flowering plants and for many important global food crops, increasing evidence is demonstrating that bee diversity is declining (Vanbergen and The Insect Pollinators Initiative, 2013; Zattara and Aizen, 2021). Bees face several threats in agricultural lands, especially in conventional, monoculture crop production, including pesticide exposure, habitat loss, and negative interactions with non-native species (Vanbergen and The Insect Pollinators Initiative, 2013; Goulson et al., 2015). Pesticides (e.g., insecticides, herbicides, and fungicides) are applied to seeds and/or crops across the growing season, and the types and frequencies of pesticides vary greatly among crop systems and farmer practices (Jorge et al., 2014; Rosenheim et al., 2020; Raine and Rundlöf, 2024). As natural lands are turned into monocultures for crop production, resources such as flowers that provide pollen and nectar foraging sources, pithy stems for cavity nesting bees, and undisturbed soil for ground nesting bees are removed or largely diminished from the environment (Kline and Joshi, 2020; Requier and Leonhardt, 2020). Native bee species in agricultural lands interact with non-native plants, pathogens, or animals such as the European honey bee (*Apis mellifera* L.) in North America, which is often used for crop pollination in several crops (Williams et al., 2011; Mallinger, Gaines-Day, and Gratton, 2017). These threats will likely persist as global agricultural production intensifies and expands (Lanz, Dietz, and Swanson, 2018), prompting continued research into how to protect and conserve pollinators within farmlands (Kremen and Miles, 2012; Nicholls and Altieri, 2013; Bretagnolle and Gaba, 2015; Kovács-Hostyánszki et al., 2017; Zamorano et al., 2020). Various agri-environmental solutions have been proposed and investigated to protect and promote pollinators and wild bees in agricultural lands (Dicks et al., 2016). This includes practices that reduce pesticide exposure and/or toxicity for pollinators, including changes to pesticide types and frequencies, application methods, and using integrated pest and pollinator management (IPPM; Lundin et al., 2021). Additionally, various practices may add or enhance important habitat features for bees and pollinators, including flower strips, cover crops, crop rotations, hedgerows, shelterbelts, and other natural and semi-natural land features (Cole et al., 2020). Approaches that limit the negative impact of honey bee colonies on wild bees have also been proposed, such as healthy beekeeping and limiting disease pressure or methods to

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regulate their usage and movement (Decourtye et al., 2019). Still, there are many knowledge gaps surrounding pollinator conservation in agricultural lands, including the crops that have been studied, the geographic locations of studies, the crop management practices that are investigated, and the pollinators under investigation.

Vineyards represent a unique crop system as they are cultivated globally across a multitude of environments (Daane et al., 2018; OIV, 2019) and are considered one of the most intensively managed crop systems (Popescu et al., 2019). The wine grape (*Vitis vinifera* L.) does not require animal pollination, and wild bee use of wine grape flowers as forage is limited (Dorin and Colla, 2024). Thus, in vineyard-dominated landscapes, providing other forage resources is likely important to support wild bees, particularly for growers who produce sustainable grape products (Daane et al., 2018). Several sustainable vineyard management practices may benefit bees, including cover cropping, low- or no-till soil management, reduced mowing, organic production, and integrated pest management (IPM; Griffiths-Lee, Goulson, and Nicholls, 2022b). Studies on between-row vegetation and floral resources, which vary as a result of various practices such as cover cropping, tillage, mowing, and alternate row management, have demonstrated varying impacts on bees (Kratschmer et al., 2018, 2019; Popescu et al., 2019; Blaise et al., 2022; Rocher et al., 2024). In general, higher between-row floral cover generally has positive impacts on bee abundance and diversity (Wilson et al., 2018; Blaise et al., 2022; Griffiths-Lee et al., 2022a). Organic vineyard management has shown inconsistent impacts on bees, with some studies demonstrating a positive impact on bee abundance and/or diversity (Uzman et al., 2020; Kratschmer et al., 2021; Kaczmarek, Entling, and Hoffmann, 2024) while others have shown limited effects (Brittain et al., 2010; Kehinde and Samways, 2012; Biella et al., 2025). While some practices, such as floral resource provision, more consistently benefit bees, questions remain, including the impact of floral cover crops not curated for bees, but rather, those used by growers for nutrients, soil, or pest management on bees (Daane et al., 2018). Furthermore, several practices are largely unaddressed, including the impact of mowing frequencies in the between-row spaces, non-organic sustainability certifications, and alternate row management beyond tillage, such as alternate row mowing or cover cropping. Additionally, certain bee taxa may differentially respond to various management practices due to differences in their traits and behaviors, including factors like lecty, pollen collection methods, proboscis length, nesting habitat requirements, or sociality (Kratschmer et al., 2019, 2021).

In studies that collected data across multiple countries, the bee communities and responses to vineyard management differed between geographic locations (Kehinde et al., 2018; Kratschmer et al., 2019). This highlights the importance of replicating this research in various geographies with different environments, bee communities, and grape growing practices. None of the above studies have occurred in Canada, and few have in cool-climate grape growing regions. Another consideration is the vast differences in methodology used among studies, including the bee sampling methods, the number of sampling events within a growing season, and the number of years the study was replicated, factors that can significantly affect the bee communities collected (Schindler et al., 2013; Russo et al., 2015; McCravy, 2018; Hutchinson et al., 2022). Sampling bees using both netting and pan traps across the entire growing season and over a representative number of sites can provide clearer insights into the impacts of vineyard management on entire bee communities across the growing season (Schindler et al., 2013; Olsson et al., 2025). These knowledge gaps support the need for research on bee conservation within Canadian vineyards.

This research aimed to assess how several vineyard management practices influence wild bee communities. Specifically, we investigated the effects of: (1) cover cropping and the extent of between-row vegetation and floral cover; (2) mowing frequency and the height of between-row vegetation; (3) the use of alternate-row management; and (4) sustainable management programs including organic management and sustainability certifications. The hypotheses and predictions were that (1) vineyards that plant flowering cover crops between vine rows, rather than frequent cultivation, herbicide applications, planting only grasses, or relying on natural vegetation, would provide greater floral resources for bees, leading to higher wild bee abundance and diversity. Similarly, (2) vineyards that mow the between-row spaces less frequently would have taller vegetation, which allows more forb species to flower, increasing both flower and bee abundance and diversity. In contrast, (3) alternate-row management practices, such as alternating tillage, mowing, or seeding in every second row, which can leave every second row with low- or no vegetation, were predicted to reduce the total vegetation and floral resources available, negatively impacting bees. It was also hypothesized that (4) conventional pesticide usage for vineyard pest, disease, and weed management, including the use of herbicides and bee-toxic insecticides, would negatively affect both bees and floral resources, lending to higher bee and flower abundance and diversity in organic vineyards, where synthetic pesticides are not allowed, compared to conventional vineyards. Certified sustainable vineyards, which were predicted to be more likely to implement practices such as cover cropping and IPM, would also support higher floral resources and bee abundance and diversity than conventional systems. Finally, it was also expected that the above management practices would influence the community composition of wild bees, potentially favoring certain taxa over others due to differences in natural histories, life cycles, and behaviors that shape how species interact with their environments.

Methods

Site selection

Grapes are the third largest fruit crop grown in Canada by total acreage (Agriculture and Agri-Food Canada, 2021), and the Niagara Region is the largest planted area with vines covering 13,600 acres (VQA, 2025). Commercial vineyard blocks of *Vitis vinifera* were selected across the Niagara Region that were managed conventionally, organically, or certified sustainably per the Sustainable Winegrowing Ontario (SWO) certification program (SWO, 2025). Organic management in Canada is informed by federal legislation and subsequent industry rules and standards, which outline permissible substances and activities (The Organic Council of Ontario, 2026). Organic grape production prohibits the use of synthetic substances, such as pesticides, instead relying on various cultural practices (e.g., leaf removal), physical controls (e.g., netting), biological controls (e.g., pest predators), semiochemicals (e.g., pheromones), and organic chemicals (e.g., copper; Provost and Pedneault, 2016; Baiano, 2021). The SWO program is a third-party audited certification for both wineries and vineyards, accounting for environmental, economic, and social sustainability (SWO, 2025). For grape production, the program does not prohibit any substances; instead encouraging growers to consider factors such as biodiversity, water use, and soil health in their management (SWO, 2025). SWO recommends growers implement practices, such as cover cropping, IPM, providing

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wildlife habitat (e.g., brush, wetlands), composting and using organic soil amendments, practicing responsible irrigation (e.g., drip), and employing animals in the vineyard. For this study, due to the stricter regulations around organic production, sites that were managed organically and were also certified sustainable (i.e., growers that had both certifications) were categorized as organic—enabling investigation into the sustainability certification in isolation (Seufert, Ramankutty, and Mayerhofer, 2017). In Year 1, 20 sites were sampled: 10 organic, five conventional, and five certified sustainable. In Year 2, two organic sites were removed, and six new sites were added —three certified sustainable and three conventional. Thus, in Year 2, 24 sites were sampled, eight organic, eight conventional, and eight certified sustainable (Supplementary Table 1). Eight sites were sampled for only 1 year (Supplementary Table 1). Sites covered the various grape growing sub-appellations of the region (VQA, 2025) and were at a minimum 600 m apart to sample independent bee communities (Gathmann and Tscharntke, 2002; Knight et al., 2005; Zurbuchen et al., 2010; Fig. 1). This minimum distance represents the closest centroid-to-centroid linear distance between two sites transects; most sites were at least 1 km + apart. This distance between sites accounts for the typical foraging ranges of wild bees, which are ~110 m for solitary species and ~ 450 for primitively eusocial species (Kendall et al., 2022).

Bee and vegetation surveys

Wild bee and vegetation sampling occurred every 4 weeks from May through August in 2021 and 2022, corresponding roughly with the grape phenology stages of leaf out, flowering, bunch closure, and veraison (color development; Schindler et al., 2013). Sites were sampled in a semi-random order during each sampling period, which was in accordance with weather forecasts and vineyard management schedules at each site. Bees were sampled using both pan traps and aerial netting on precipitation-free days. A 400 m^2 area was marked out in the center of each vineyard block spanning two neighboring between-row spaces (Kratschmer et al., 2018). The transects were ~ 80 m long along the central vine row and 5 m wide across three neighboring vine rows, with the length adjusted to account for varying row spacing across sites. Aerial netting was performed for 30 minutes in the morning and afternoon, 15 minutes per alternate row, using collecting jars with ethyl acetate (BioQuip 1121 Series Collecting Jars). To focus the sampling effort on wild bee communities, active netting prioritized the collection of non-honey bees during surveys. Twenty-four 3.25 oz (96 mL) pan traps painted fluorescent yellow, blue, or white (New Horizons bee bowls, Maryland) were filled with soapy water and placed on the ground underneath the central vine row spaced ~3 m apart, with alternating colors, before 9:00 am and collected after 5:00 pm. If the under-vine area consisted of tall vegetation, then traps were raised using commercial garden stakes, which were dark green in color, to the height of the vegetation, which was ~15–30 cm (Krahner et al., 2024).

On the same days of bee sampling, vineyard floral resources and vegetation characteristics were also recorded. A 1 m^2 quadrat was semi-randomly placed eight times along the 400 m^2 sampling area. To capture all blooming flowers, half of the quadrats were positioned centrally in the between-row space while the other half were placed closer to the vine rows. Flower species and their abundances were documented for all open flowers (excluding grasses, rushes, and sedges) inside the quadrat (Carvell et al., 2004; Baldock et al., 2019) such that one flower unit was defined as a single capitulum (ex. *Taraxacum officinale*), umbel (ex. *Daucus carota*), head (ex. *Trifolium* spp.), single flower (ex. *Convolvulus arvensis*), single spike (ex. *Plantago major*), or single raceme (ex. *Polygonum aviculare*). Abundances were recorded as the number of open

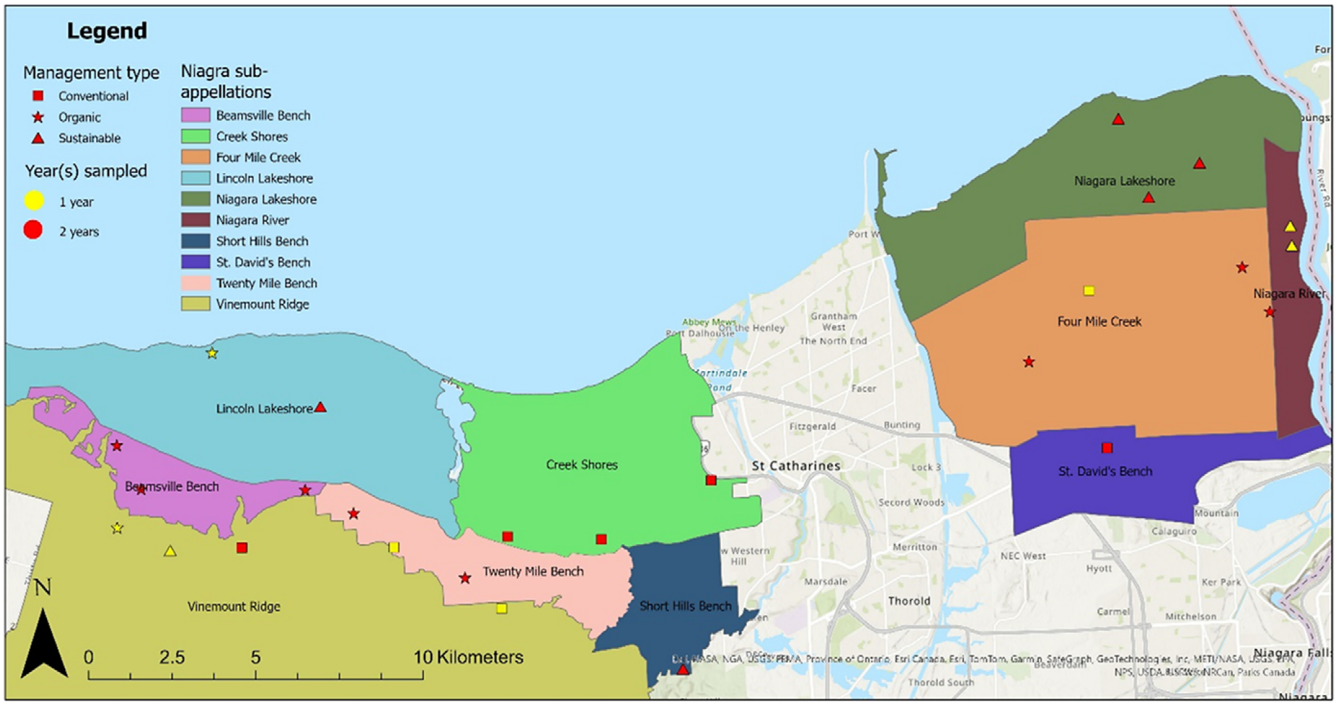


Figure 1. Vineyard sites for bee sampling across the Niagara Region, ON created in ArcMap Pro 3.0.2 (Esri, Redlands, CA) with the World Topographic and World Hillshade basemaps. Sites were overlaid on the VQA map of sub-appellations for wine growing (Brock University Maps, Data & GIS. Niagara Sub-Appellations. 2016 [GIS Data]. Scale unknown. 'Historical Maps of Niagara' http://hdl.handle.net/10464/13712).

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flowering units following Carvell et al. (2004). For highly abundant and dense species (ex. prostrate knotweed (*Polygonum aviculare*)), flower abundance was counted for a smaller area and extrapolated for the entire quadrat based on the visual cover of the species. Flowers were identified using the Newcomb's Wildflower Guide (Newcomb, 1989) and the Ontario Ministry of Agriculture, Food, and Rural Affairs (OMAFRA) resources (OMAFRA, 2009, 2023a). Vegetation cover was visually estimated using a modified DAFOR scale (Rare <10%, Occasional 11%–25%, Frequent 26%–50%, Abundant 51%–75%, Dominant >76%). Vegetation height, a proxy for mowing frequency, was recorded by dividing each quadrat into four equal sections and measuring the tallest piece of vegetation in each section. The means of vegetation and floral data were calculated per site and sampling round, using the median value of the DAFOR scale for vegetation cover. Flowering species were later classified as either weeds or cover crops, the latter representing flowers intentionally planted by growers in the between-row spaces, based on OMAFRA resources and grower insights (OMAFRA, 2023a, 2023b; Supplementary Table 2). The percentage of flowers belonging to cover crop species was then calculated. A vegetation height ratio between adjacent rows was used as a proxy for alternate row management, with a ratio ≥ 2:1 classified as 'yes'. This pattern could result from practices such as alternate row tillage, seeding, mowing, or any other management practice that produced taller vegetation in every second row.

Bee identifications

Washed and pinned bees were identified using a dissecting microscope and several identification guides and keys (see Appendix for a list of identification guides and resources used), as well as the Discover Life bee species and genera guides (Ascher and Pickering, 2022). Some groups of bees were not identified to species level due to difficulty in accurate species identifications: *Lasioglossum* subgenus Dialictus, *Hylaeus affinis/modesutus/illinoinesis*, *Sphecodes atlantis/cressonii*, and one distinct morphospecies of *Sphecodes* sp. All results and discussion at the 'species' level hereafter include these sub-genus level identifications unless otherwise specified. A subset of identifications, per species, was verified by fellow graduate students in York University's Centre for Bee Ecology, Evolution, and Conservation.

Statistical analyses

All analyses were performed in R v.4.4.2 (R Core Team, 2024) using all bees collected (pan trap and netted bees combined), unless otherwise specified. Honey bees were removed from analyses due to our focus on wild bees and a lack of knowledge on surrounding hive densities (Kratschmer et al., 2018). This includes an inability to track the use and movement of hives for crop pollination throughout the region—which grows several pollinator-dependent crops, including various fruit trees (Ontario Beekeepers' Association, 2026; OMAFRA, 2024). To determine which vineyard management variables influence bee abundance, species richness, and Shannon diversity index, Generalized Linear Mixed Models (GLMM) were run using the packages 'lme4' (Bates et al., 2015), 'lmerTest' (Kuznetsova, Brockhoff, and Christensen, 2017), 'glmmTMB' (Brooks et al., 2017), and 'MuMIn' (Bartoń, 2024) following Zuur and Ieno (2016) and Harrison et al. (2018). Models included fixed effects for management type, floral abundance, floral richness, vegetation height, vegetation cover, month, and year, with site as a random intercept to account for the non-independent repeat sampling of sites over time and unmeasured site-level variation (Supplementary Table 3; Bolker, 2015). All numeric explanatory variables were scaled and centered, and one variable, floral abundance, was log(x + 1) transformed (Zuur, Ieno, and Elphick, 2010; Harrison et al., 2018). Multicollinearity was checked using variance inflation factors (VIF) with the package 'car' (Fox and Weisberg, 2019). Co-plots were used to visualize interactions with month using the package 'ggplot2' (Wickham, 2016), and interactions were included in model selection when relationships varied substantially over time (Zuur et al., 2010; Harrison et al., 2018). Global models were fitted with the appropriate family and link function and were assessed for model fit and diagnostics by plotting Pearson's residuals against fitted values and using the package 'performance' (Lüdecke et al., 2021) as well as the packages 'gstat' (Gräler, Pebesma, and Heuvelink, 2016) and 'sp' (Bivand, Pebesma, and Gomez-Rubio, 2013) for spatial variograms of model residuals (Zuur and Ieno, 2016; Harrison et al., 2018).

Model selection was based on the second-order Akaike Information Criterion (AICc) using the function *dredge* to rank all possible models and perform model averaging when multiple top models had delta AICc<2 (Harrison et al., 2018; Kratschmer et al., 2018; Biella et al., 2025). Both the zero method, which uses the 'full model' and sets predictor coefficients to '0' for any models where that predictor is not included, and the 'conditional model', which calculates the average predictor coefficients only from models where that predictor is included, were used. The former uses a more conservative approach when model uncertainty is high. To get final model R^2 values for averaged models, a GLMM was run with all fixed effects included in the final averaged model, significant or not. Final averaged models were assessed using the 'DHARMa' package (Hartig, 2024). For significant categorical variables, the 'emmeans' package (Lenth, 2024) was used to obtain back-transformed estimated marginal means and conduct Tukey-adjusted pairwise comparisons.

To assess the effects of cover cropping and alternate row management on bees, mid-summer models using only June and July data were run—which is when these practices were most evident. Due to some bee groups not being identified to species level, three further groups of bee data were modeled as above. First, models were run with genus-level bee richness and the Shannon diversity index. Second, the abundance of *Lasioglossum* (*Dialictus*) bees, which were highly abundant and not identified to species level, was modeled separately. Lastly, bee abundance models were also run separately for bees collected by pan trap and those collected by netting to investigate potential differences in bee responses based on sampling method (Portman, Bruninga-Socolar, and Cariveau, 2020; Supplementary Table 3).

GLMMs were also used to test how floral and vegetation characteristics varied by management type, with floral abundance, floral richness, vegetation cover, and vegetation height as the response variables, vineyard management, month, and year as fixed effects, and site as the random effect, following similar procedures as above. To investigate relationships between floral and vegetation variables themselves, a Spearman's correlation matrix was run on these variables averaged across months and years, with cover crop percentage and vegetation height ratio (a quantitative proxy for alternate row management) averaged across June and July months only. Similarly, to see if vineyard management types differed in their use of cover cropping or alternate row management, the aggregated cover crop percentage and the frequency of alternate row management were compared between the management categories of organic, sustainable, and conventional using a one-way analysis of variance (ANOVA) and Fisher's Exact test, respectively.

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To examine how vineyard management influenced bee community composition, bee species abundances per site were averaged over years, and Hellinger transformations were applied (Zuur, Ieno, and Smith, 2007). Non-metric multidimensional scaling (NMDS) using the 'vegan' package (Oksanen et al., 2024) was run on these data, and permutational multivariate analysis of variance (PERMANOVA) tested differences across management types. Individual bee species, as well as floral and vegetation variables that were correlated with the NMDS, were determined using the *envfit* function with random permutations (n = 999; Kratschmer et al., 2018). To further examine how bee communities varied among management types, negative binomial Generalized Linear Models (GLMs) were run using the 'MASS' package (Venables and Ripley, 2002) for select genera. Models were run for *Andrena, Agapostemon, Augochlorella, Bombus, Ceratina, Halictus, Hylaeus*, and *Lasioglossum* as these genera were the most widespread and abundant genera across sites (Supplementary Table 4) and had at least one species associated with the NMDS of bee community composition. Models were run separately for each year, with management type as the fixed effect, on the total abundance per genus. For each model, we tested the overall effect of management type using likelihood ratio tests comparing a null model (intercept-only) to a model including management type (Bolker, 2008). The resulting p-values were adjusted for multiple testing using the Benjamini–Hochberg false discovery rate procedure. Lastly, NMDS was also performed on Hellinger-transformed floral species data to assess floral community differences by management type, adding floral and vegetation variables as well as individual flower species that were correlated with the NMDS, following similar procedures as above.

Results

In total, 4,490 bees from 27 genera and 95 species or species groups were collected across both years; collecting 2,510 bees, 25 genera, and 73 species in 2021 and 1,980 bees, 24 genera, and 73 species in 2022 (Table 1). The most abundant and widespread genera were *Lasioglossum* collected in 26 of 26 sites; *Agapostemon, Andrena, Augochlorella, Bombus*, and *Halictus* collected in 25 of 26 sites; *Ceratina* collected in 23 of 26 sites; and *Hylaeus* collected in 21 of 26 sites (Supplementary Table 4).

Modeling of bee responses to vineyard management practices and temporal variables displayed relationships with months and years for both bee abundance and diversity (richness and Shannon diversity). Sampling year and months were retained in the final models for all bee response variables, often being significant ($p < 0.05$) in both the conditional and full models. In general, bee abundance and diversity were highest in midsummer months (June and July), lowest in May, and higher in 2021 than in 2022 (Table 2). Multiple vineyard management variables also influenced bee abundance and diversity. Bee abundance had a positive relationship with vegetation height (estimate = 0.12, Z = 2.00, p = 0.046; Fig. 2A) as did bee species richness (estimate = 0.076, Z = 2.03, p = 0.043; Fig. 2B). Bee species richness was also negatively associated with certified sustainable management, though this was not significant at $p < 0.05$ (estimate = −0.21, Z = 1.88, p = 0.061). Shannon diversity index (H) had a positive relationship with floral abundance (estimate = 0.091, Z = 2.66, p = 0.0078; Fig. 2C) and was also negatively associated with certified sustainable management (estimate = −0.26, Z = 2.34, p = 0.019). Post hoc testing showed there was a higher H in organic vineyards compared to certified sustainable vineyards, while conventional vineyards did not significantly differ from either management type (Fig. 2D). Genus-level results were generally similar to species-level but with less significance (Supplementary Table 5). Interestingly, bee genus richness was most impacted by floral richness, with a positive but not significant relationship (estimate = 0.064, Z = 1.93, p = 0.055). For Shannon genus diversity (H′), results were similar to species-level but were no longer significant at $p < 0.05$. Floral abundance had a positive influence on H′ (estimate = 0.066, Z = 1.93, p = 0.054) while certified sustainable vineyards had lower H′ (estimate = −0.21, Z = 1.80, p = 0.072).

The mid-summer models, which included cover cropping and alternate row management, were largely similar to those from the entire growing season (Table 3 and Supplementary Table 6). Alternate row management did not have a significant impact on bee abundance or diversity in any models. However, the percentage of flowers that came from cover crop species had a negative relationship with bee abundance (estimate = −0.12, Z = 2.64, p = 0.008; Fig. 3A) and no significant relationship with species or genus level richness or diversity. Specific to mid-summer months, a positive relationship was seen between vegetation cover and bee abundance (estimate = 0.19, Z = 2.92, p = 0.004; Fig. 3B) as well as between vegetation height and Shannon diversity index (estimate = 0.15, Z = 3.48, p = 0.0005; Fig. 3C) as well as Shannon genus diversity index (estimate = 0.11, Z = 2.28, p = 0.023). Bee species richness was negatively associated with sustainable management in mid-

Table 1. Summary of bees collected across all vineyard sites for each year, excluding honey bees

Year	Month	Bee abundance	Genera richness	Species richness	Mean temperature (°C)	Total precipitation (mm)
2021 - 2,510 bees, 25 genera, 73 species	May	493	14	37	13.2	16.2
	June	637	20	46	20.8	53.2
	July	961	18	39	21.7	59.9
	August	419	16	33	24.4	10.2
2022 - 1,980 bees, 24 genera, 73 species	May	348	11	35	13.8	46.77
	June	386	18	39	19.5	74.7
	July	673	22	39	22.6	33.1
	August	573	13	30	23.1	33.6

Note: Species richness includes specimens identified to subgenera levels (ex. *Lasioglossum* (*Dialictus*)). Weather data were taken from the Port Weller (AUT), Ontario station (Government of Canada, 2024).

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Table 2. Generalized linear mixed model (GLMM) summaries for each bee response variable with site as a random effect

Predictor(s)	Estimate	Standard error	*z*-Value	*p*-Value	AICc range	No. models	R2m	R2c
Bee abundance								
Intercept	**3.29**	**0.11**	**30.65**	**< 2e–16 ****	1411.39–1413.25	8	0.33	0.52
Year—2022	**−0.37**	**0.087**	**4.21**	**2.60e–05 ****				
Month—May	**−0.28**	**0.13**	**2.22**	**0.0261 ****				
Month—June	0.029	0.12	0.23	0.8162				
Month—July	**0.47**	**0.11**	**4.25**	**2.11e–05 ****				
Vegetation height	***0.12***	***0.061***	***2.00***	***0.0459 *****				
Floral abundance (log)	−0.078	0.051	1.54	0.1248				
Vegetation cover	0.092	0.060	1.52	0.1289				
Floral richness	−0.033	0.056	0.59	0.5526				
May: Vegetation height	−0.11	0.13	0.86	0.3876				
June: Vegetation height	−0.11	0.10	1.06	0.2880				
July: Vegetation height	0.077	0.091	0.85	0.3947				
Bee species richness								
Intercept	**2.012**	**0.091**	**22.06**	**< 2e–16 ****	850.74–852.68	7	0.30	0.41
Year—2022	**−0.22**	**0.062**	**3.52**	**0.000429 ****				
Month—May	**−0.16**	**0.092**	**1.77**	**0.077143 ***				
Month—June	**0.17**	**0.087**	**1.96**	**0.050125 ***				
Month—July	**0.31**	**0.080**	**3.89**	**0.000100 ****				
Vegetation height	***0.076***	***0.038***	***2.03***	***0.042837 *****				
Management—Organic	−0.022	0.11	0.21	0.834585				
Management—Sustainable	***−0.21***	***0.11***	***1.88***	***0.060859 ****				
Floral abundance (log)	0.033	0.035	0.96	0.335865				
Vegetation cover	0.020	0.040	0.50	0.615488				
Floral richness	0.054	0.041	1.34	0.181979				
Shannon diversity index (H)								
Intercept	**1.42**	**0.10**	**13.65**	**< 2e–16 ****	194.47–195.68	4	0.33	0.44
Year—2022	***−0.10***	***0.060***	***1.74***	***0.081512 ****				
Month—May	−0.12	0.081	1.41	0.157725				
Month—June	**0.32**	**0.082**	**3.86**	**0.000113 ****				
Month—July	**0.25**	**0.082**	**3.04**	**0.002359 ****				
Floral abundance (log)	**0.091**	**0.034**	**2.66**	**0.007773 ****				
Management—Organic	0.16	0.11	1.47	0.141901				
Management—Sustainable	**−0.26**	**0.11**	**2.34**	**0.019459 ****				
Vegetation height	0.053	0.040	1.34	0.180043				

Note: Model summaries are from model averaging of the top models (ΔAICc<2). On the left are predictors included in the conditional averaged models alongside their estimates, standard errors (adjusted for averaged models), *z*-values, and *p*-values. All continuous predictor variables were standardized (*z*-scored) before analyses. Interactions are denoted by 'X:X'. Significant predictors are shown at $p < 0.05$ (**) and nearly significant at $p < 0.1$ (*). Bolded predictors are significant in both the full and conditional models, while bolded and italicized predictors are significant only in the conditional model. For categorical variables, reference values are those not shown: 'Conventional' for Management, '2021' for Year, and 'August' for Month. Also shown is the range of AICc values across the top models included in model averaging, as well as the number of models included in the final averaged model. The marginal R2 (R2m, variance explained by fixed effects) and conditional R2 (R2c, variance explained by fixed and random effects) are shown for a model run with all variables included in the averaged model (significant or not).

summer (estimate = −0.23, $Z = 2.04$, $p = 0.042$); however, post-hoc comparisons were not significant (Fig. 3D).

Models examining distinct groups of collected bees produced differing results. Models specifically examining *Lasioglossum* (Dialictus) abundance revealed a negative relationship with floral abundance (estimate = −0.17, $Z = 2.06$, $p = 0.040$; Supplementary Table 7) and in mid-summer, a positive relationship with vegetation cover (estimate = 0.24, $Z = 2.18$, $p = 0.030$) and negative association with organic management (estimate = −0.66, $Z = 2.37$, $p = 0.018$). Furthermore, models of the abundance of bees collected

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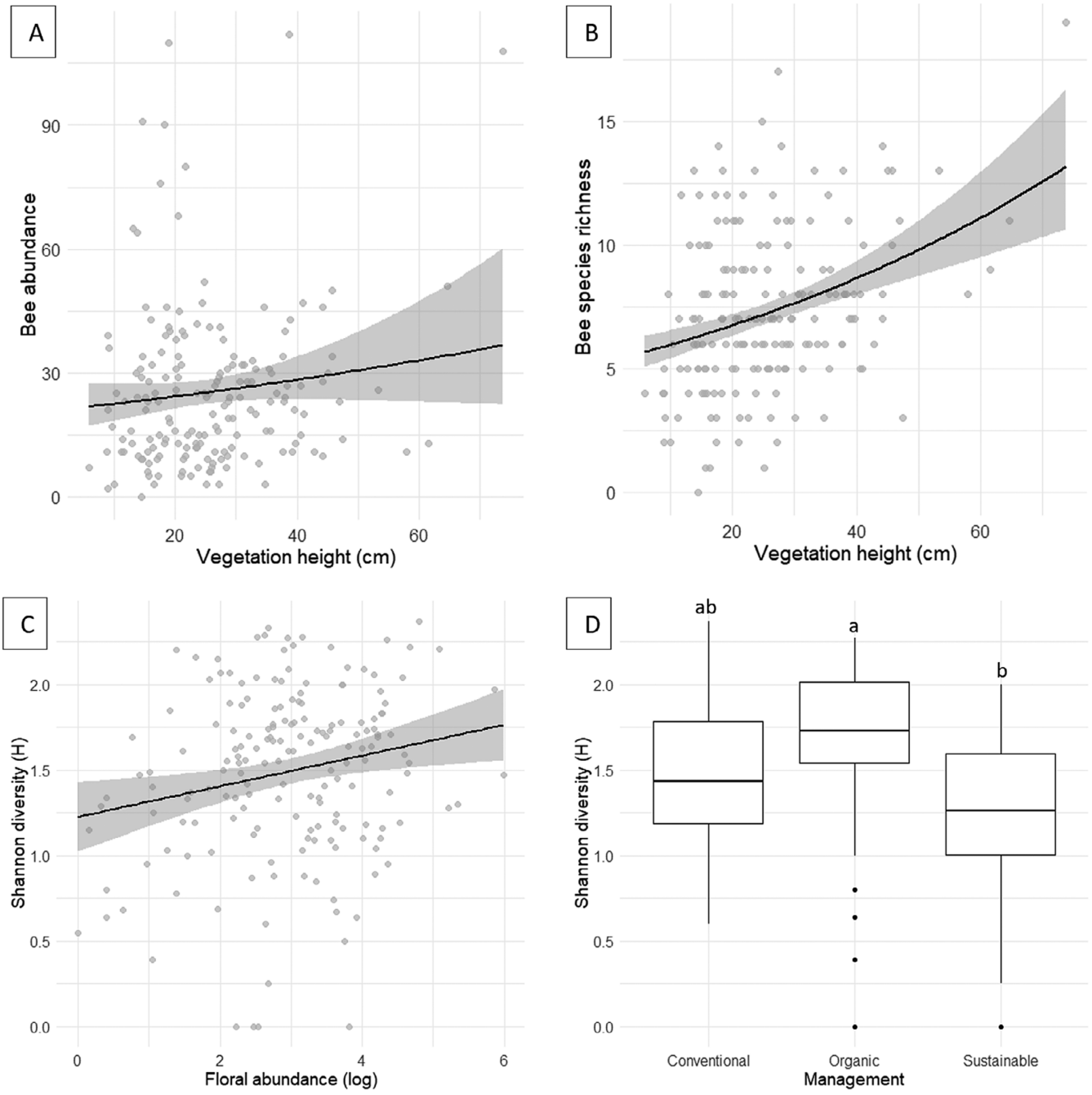


Figure 2. Significant ($p < 0.05$) vineyard management predictors from the Generalized Linear Mixed Models (GLMM) of bee response variables: bee abundance (A), bee species richness (B), and Shannon diversity index (C, D). Final GLMMs were averaged from the top models using delta AICc <2. Graphs show the raw data points. For categorical variables, Tukey post hoc tests from model-estimated marginal means are shown with different letters denoting significantly different categories ($p < 0.05$).

by netting showed that netted bees were positively associated with vegetation height (estimate = 0.24, $Z = 3.57$, $p = 0.0004$) and floral richness (estimate = 0.23, $Z = 3.82$, $p = 0.0001$) and slightly negatively associated with sustainable management, though this was not significant (estimate = −0.38, $Z = 1.86$, $p = 0.0630$; Supplementary Table 8). In mid-summer, similar relationships existed with vegetation height and floral richness, while a nearly significant positive relationship with floral abundance was also seen (estimate = 0.17, $Z = 1.82$, $p = 0.069$). Pan trapped bee abundance, oppositely, had a negative relationship with floral richness (estimate = −0.17, $Z = 2.10$, $p = 0.036$) and a positive relationship with vegetation height in July only (estimate = 0.29, $Z = 2.46$, $p = 0.014$) and a nearly significant positive relationship with vegetation cover (estimate = 0.14, $Z = 1.94$, $p = 0.0519$). In mid-summer, similar relationships were seen with floral richness and vegetation cover, as well as a negative relationship with the percentage of flowers from cover crops (estimate = −0.22, $Z = 4.12$, $p = 0.000$).

Overall, between-row vegetation characteristics were important predictors of multiple bee response variables, with vegetation height emerging as the most influential factor. Across the full

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Table 3. Generalized linear mixed model (GLMM) summaries for each bee response variable for mid-summer models run with June and July data only, to include cover crop percentage and alternate row management as additional predictors

Predictor(s)	Estimate	Standard error	*z*-Value	*p*-Value	AICc range	No. models	R2m	R2c
Bee abundance								
Intercept	**3.92**	**0.091**	**43.22**	**< 2e–16 ****	698.07–700.03	5	0.33	0.46
Year—2022	**−0.65**	**0.092**	**7.03**	**< 2e–16 ****				
Month—June	**−0.38**	**0.086**	**4.42**	**1e–05 ****				
Vegetation cover	**0.19**	**0.066**	**2.92**	**0.0035 ****				
Cover crop %	**−0.12**	**0.045**	**2.64**	**0.0084 ****				
Floral richness	−0.087	0.067	1.30	0.19344				
Vegetation height	0.065	0.061	1.07	0.28289				
Alternate row—Yes	0.097	0.141	0.68	0.49761				
Bee species richness								
Intercept	**2.30**	**0.090**	**25.48**	**< 2e–16 ****	442.18–444.15	7	0.25	0.32
Year—2022	**−0.18**	**0.080**	**2.22**	**0.0267 ****				
Month—June	***−0.15***	***0.075***	***1.97***	***0.0493 *****				
Vegetation height	**0.11**	**0.043**	**2.52**	**0.0116 ****				
Management—Organic	−0.11	0.11	1.01	0.3124				
Management—Sustainable	***−0.23***	***0.11***	***2.04***	***0.0416 *****				
Vegetation cover	0.077	0.052	1.50	0.1336				
Floral abundance (log)	0.036	0.047	0.76	0.4504				
Alternate row—Yes	−0.058	0.095	0.61	0.5429				
Shannon diversity index (H)								
Intercept	**1.66**	**0.070**	**23.67**	**< 2e–16 ****	75.93–77.91	6	0.25	0.42
Month—June	0.057	0.069	0.83	0.406942				
Vegetation height	**0.15**	**0.044**	**3.48**	**0.000503 ****				
Management—Organic	0.041	0.12	0.34	0.732718				
Management—Sustainable	−0.19	0.12	1.59	0.111647				
Floral abundance (log)	0.041	0.046	0.89	0.371656				
Vegetation cover	−0.025	0.048	0.52	0.606466				

Note: All models had site as a random effect. Model summaries are from model averaging of the top models (ΔAICc<2). On the left are predictors included in the conditional averaged model alongside their estimates, standard errors (adjusted for averaged models), z-values, and p-values. All continuous predictor variables were standardized (z-scored) before analyses. Interactions are denoted by 'X:X'. Significant predictors are shown at $p < 0.05$ (**) and nearly significant at $p < 0.1$ (*). Bolded predictors are significant in both the full and conditional models, while bolded and italicized predictors are significant only in the conditional model. For categorical variables, reference values are those not shown: 'Conventional' for Management, '2021' for Year, 'June' for Month, 'No' for Alternate row. Also shown is the range of AICc values across the top models included in model averaging, as well as the number of models included in the final averaged model. The marginal R2 (R2m, variance explained by fixed effects) and conditional R2 (R2c, variance explained by fixed and random effects) are shown for a model run with all variables included in the averaged model (significant or not).

growing season (Table 4), bee abundance, netted bee abundance, and bee species richness all increased with greater vegetation height. During mid-summer (Table 5), vegetation height was also positively associated with netted bee abundance, bee species richness, and Shannon diversity at both the species and genus levels. Vegetation cover showed fewer significant relationships and only during mid-summer, where it was positively associated with total bee abundance, pan-trapped bee abundance, and *Lasioglossum* (*Dialictus*) abundance. Floral resources exhibited mixed effects; floral richness was positively associated with netted bee abundance but negatively associated with pan-trapped bee abundance, while floral abundance was positively related to Shannon diversity and negatively related to *Lasioglossum* (*Dialictus*) abundance. In mid-summer, cover cropping was negatively associated with both bee abundance and pan-trapped bee abundance, whereas alternate row management showed no significant relationships. Vineyard management type had modest effects, with sustainable management negatively associated with bee species richness (mid-summer) and Shannon species diversity (full season), while organic management was negatively associated with *Lasioglossum* (*Dialictus*) abundance (mid-summer). Collectively, these results suggest that while some aspects of between-row vegetation structure broadly support bee communities, specific bee taxa may respond differently to particular vegetation characteristics and management practices.

This was further seen with the analysis of the bee species and their abundances across sites, which showed that bee community composition differed significantly between vineyard management categories (PERMANOVA $F = 2.18$, $R^2 = 0.16$, $p = 0.003$; Fig. 4). Certified sustainable sites were associated with *Lasioglossum (Dialictus), Andrena commoda*, and *Agapostemon virescens*, while

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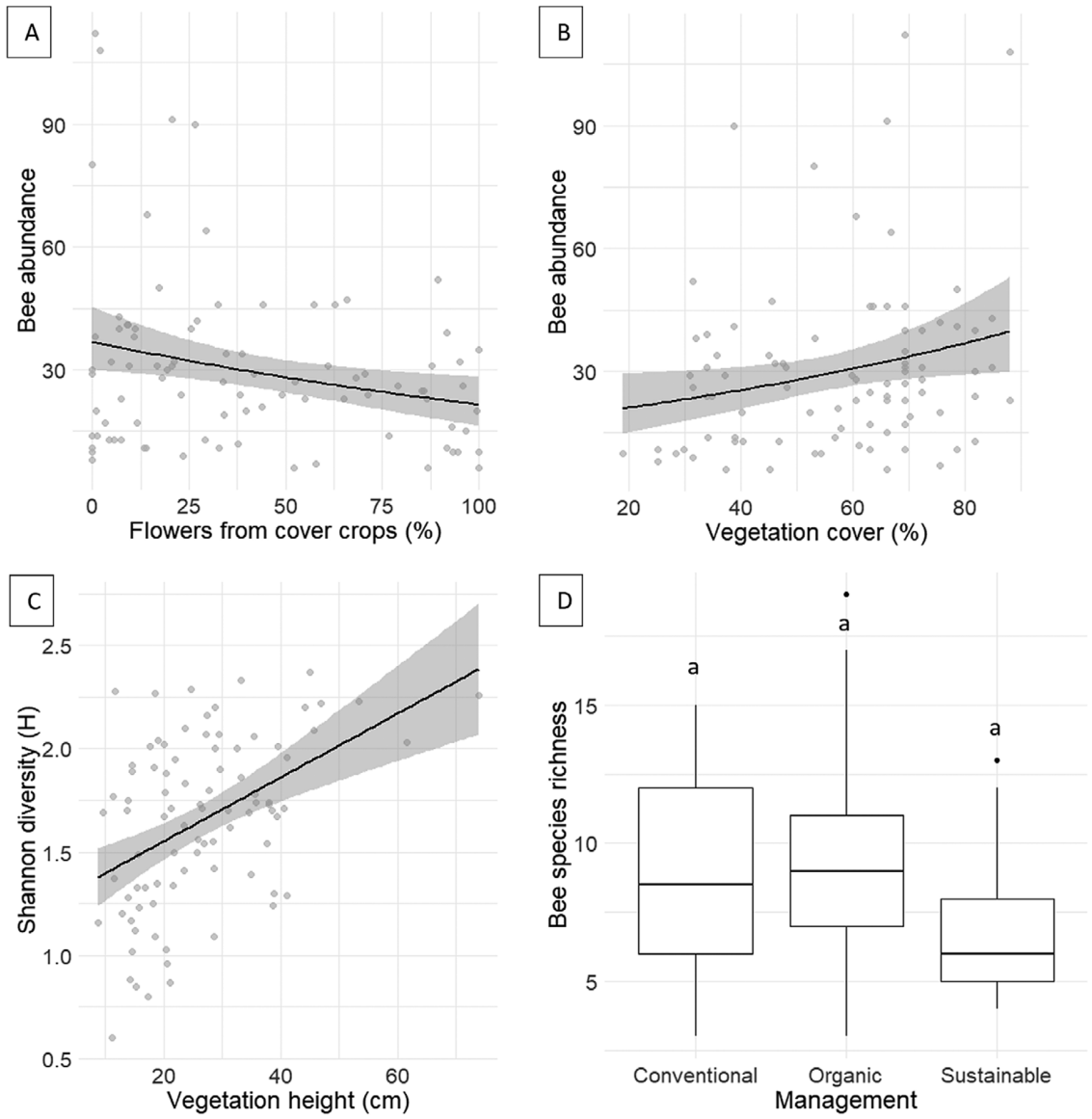


Figure 3. Newly significant ($p < 0.05$) vineyard management predictors from the Generalized Linear Mixed Models (GLMM) for bee response variables from mid-summer months only (June and July) for bee abundance (A, B), Shannon Diversity of bee species (C), and bee species richness (D). Final GLMMs were averaged from the top models using delta AICc <2. Graphs show the raw data points. For categorical variables, Tukey post hoc tests from model-estimated marginal means are shown with different letters denoting significantly different categories ($p < 0.05$).

conventional sites were associated with *Halictus confusus, Halictus rubicundus*, *Osmia conjuncta*, *Melissodes subillatus*, *Ceratina calcarata*, and *Lasioglossum cinctipes.* Organic sites were associated with *Andrena wilkella*, *Augochlorella aurata*, *Megachile mendica*, and *Hylaeus affinis/modestus/illinoisensis. Augochlora pura*, *Bombus bimaculatus*, *Bombus impatiens*, and *Andrena nasonii* were associated with both organic and conventional sites, while *Lasioglossum zonulum* was associated with both sustainable and organic sites. Organic sites were also associated with higher floral richness, vegetation cover, and vegetation height (Fig. 4). Comparisons of the abundance of select genera between management types further highlighted some of these differences in bee community composition, though no genera were significantly different at $p < 0.05$ after false discovery rate adjustments (Supplementary Table 9). However, some trends include, in at least 1 year of the study, Bombus and Hylaeus were less abundant in sustainable sites, Augochlorella and Andrena were more abundant in organic sites, and Lasioglossum were more abundant in sustainable sites.

Comparison of the local vegetation characteristics and floral resources across vineyard management categories (Supplementary Table 10) revealed that certified sustainable vineyards had the lowest floral richness (estimate = −0.70, $p = 0.02$; Fig. 5A). Vegetation height was slightly positively influenced by organic management (estimate = 6.18, $p = 0.09$), and post hoc testing indicated that vegetation was tallest in organic vineyards and shortest in certified sustainable vineyards, with conventional vineyards not differing significantly from either (Fig. 5B). Furthermore, aggregated floral and vegetation data across months and years showed that several of these variables were significantly correlated with one another ($p < 0.05$; Supplementary Figure 1). Vegetation height, vegetation cover, floral abundance, and floral richness were all positively correlated with one another, while the vegetation height ratio

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Table 4. Summary of the top models for each bee response variable across the entire growing season

	Bee abundance—total	Netted bee abundance	Pan-trapped bee abundance	Bee species richness	Bee genus richness	Shannon Diversity Index—bee species	Shannon Diversity Index—bee genera	Lasioglossum (Dialictus) abundance
	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE
Intercept	**3.29 ± 0.11**	**1.90 ± 0.15**	**2.92 ± 0.13**	**2.012 ± 0.091**	**1.72 ± 0.081**	**1.42 ± 0.10**	**1.21 ± 0.10**	**2.28 ± 0.27**
Year—2022	**−0.37 ± 0.087**		**−0.49 ± 0.10**	**−0.22 ± 0.062**	**−0.20 ± 0.053**	−0.10 ± 0.060	−0.088 ± 0.058	**−0.58 ± 0.14**
Month—May	**−0.28 ± 0.13**	−0.13 ± 0.17	−0.32 ± 0.16	−0.16 ± 0.092	−0.15 ± 0.081	−0.12 ± 0.081	−0.085 ± 0.084	−0.099 ± 0.19
Month—June	0.029 ± 0.12	0.12 ± 0.16	0.09 ± 0.15	0.17 ± 0.087	**0.25 ± 0.073**	**0.32 ± 0.082**	**0.35 ± 0.082**	**−0.45 ± 0.19**
Month—July	**0.47 ± 0.11**	0.22 ± 0.14	**0.61 ± 0.13**	**0.31 ± 0.080**	**0.27 ± 0.068**	**0.25 ± 0.082**	0.13 ± 0.076	**0.62 ± 0.18**
Vegetation cover	0.092 ± 0.060	−0.08 ± 0.08	0.14 ± 0.07	0.020 ± 0.040	−0.017 ± 0.035			0.13 ± 0.096
Vegetation height	**0.12 ± 0.061**	**0.24 ± 0.07**	−0.09 ± 0.12	**0.076 ± 0.038**	0.026 ± 0.035	0.053 ± 0.040		−0.13 ± 0.11
Floral richness	−0.033 ± 0.056	**0.23 ± 0.06**	**−0.17 ± 0.08**	0.054 ± 0.041	0.064 ± 0.033		0.072 ± 0.044	
Floral abundance (log)	−0.078 ± 0.051		−0.11 ± 0.07	0.033 ± 0.035		**0.091 ± 0.034**	0.066 ± 0.034	**−0.17 ± 0.081**
Management—Organic		−0.16 ± 0.17		−0.022 ± 0.11	−0.018 ± 0.11	0.16 ± 0.11	0.12 ± 0.11	−0.41 ± 0.30
Management—Sustainable		−0.38 ± 0.20		−0.21 ± 0.11	−0.18 ± 0.12	**−0.26 ± 0.11**	−0.21 ± 0.12	0.50 ± 0.31
R2m	0.33	0.30	0.39	0.30	0.09	0.33	0.25	0.35
R2c	0.52	0.39	0.61	0.41	0.15	0.44	0.44	0.58

Note: For each model's predictors, the estimate (Est) and adjusted standard error (SE) are shown, as well as the model's marginal R2 (R2m) and conditional R2 (R2c). Empty cells are variables that were not retained in the top-averaged model based on delta AICc. Interaction terms, which were only included in the bee abundance models, are not shown. Orange shading represents a negative relationship with the response variables, and green indicates a positive relationship, while bolded text and darker shading indicate significance at $p < 0.05$. For categorical variables, reference values are those not shown: 'Conventional' for Management, '2021' for Year, and 'August' for Month.

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Table 5. Summary of the top models for each bee response variable across mid-summer months

	Bee abundance—total	Netted bee abundance	Pan-trapped bee abundance	Bee species richness	Bee genus richness	Shannon Diversity Index—bee species	Shannon Diversity Index—bee genera	Lasioglossum (Dialictus) abundance
	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE	Est ± SE
Intercept	**3.92 ± 0.091**	**1.97 ± 0.12**	**3.75 ± 0.10**	**2.30 ± 0.090**	**1.96 ± 0.078**	**1.66 ± 0.070**	**1.31 ± 0.068**	**3.24 ± 0.23**
Year—2022	**−0.65 ± 0.092**	0.13 ± 0.14	**−0.84 ± 0.11**	**−0.18 ± 0.080**	**−0.17 ± 0.072**			**−0.81 ± 0.16**
Month—June	**−0.38 ± 0.086**	−0.24 ± 0.15	**−0.47 ± 0.10**	**−0.15 ± 0.075**	−0.050 ± 0.065	0.057 ± 0.069	**0.19 ± 0.068**	**−1.02 ± 0.15**
Vegetation cover	**0.19 ± 0.066**		**0.24 ± 0.08**	0.077 ± 0.052	0.061 ± 0.046	−0.025 ± 0.048	−0.053 ± 0.052	**0.24 ± 0.11**
Vegetation height	0.065 ± 0.061	**0.22 ± 0.07**		**0.11 ± 0.043**	0.070 ± 0.043	**0.15 ± 0.044**	**0.11 ± 0.046**	−0.14 ± 0.11
Floral richness	−0.087 ± 0.067	**0.18 ± 0.08**	**−0.17 ± 0.08**		0.053 ± 0.045		0.053 ± 0.049	−0.17 ± 0.11
Floral abundance (log)		0.17 ± 0.09		0.036 ± 0.047	0.067 ± 0.045	0.041 ± 0.046	0.082 ± 0.047	−0.13 ± 0.10
Management—Organic				−0.11 ± 0.11	−0.074 ± 0.13	0.041 ± 0.12		**−0.66 ± 0.28**
Management—Sustainable				**−0.23 ± 0.11**	−0.22 ± 0.13	−0.19 ± 0.12		0.12 ± 0.29
Cover crop percentage	**−0.12 ± 0.045**	0.10 ± 0.07	**−0.22 ± 0.05**					−0.11 ± 0.081
Alternate row—yes	0.097 ± 0.141		0.12 ± 0.17	−0.058 ± 0.095				
R2m	0.33	0.19	0.43	0.25	0.04	0.25	0.15	0.56
R2c	0.46	0.28	0.58	0.32	0.09	0.42	0.50	0.70

Note: For each model's predictors, the estimate (Est) and adjusted standard error (SE) are shown, as well as the model's marginal R2 (R2m) and conditional R2 (R2c). Empty cells are variables that were not retained in the top-averaged model based on delta AICc. Orange shading represents a negative relationship with the response variables, and green indicates a positive relationship, while bolded text and darker shading indicate significance at $p < 0.05$. For categorical variables, reference values are those not shown: 'Conventional' for Management, '2021' for Year, 'July' for Month, and 'No' for Alternate row management.

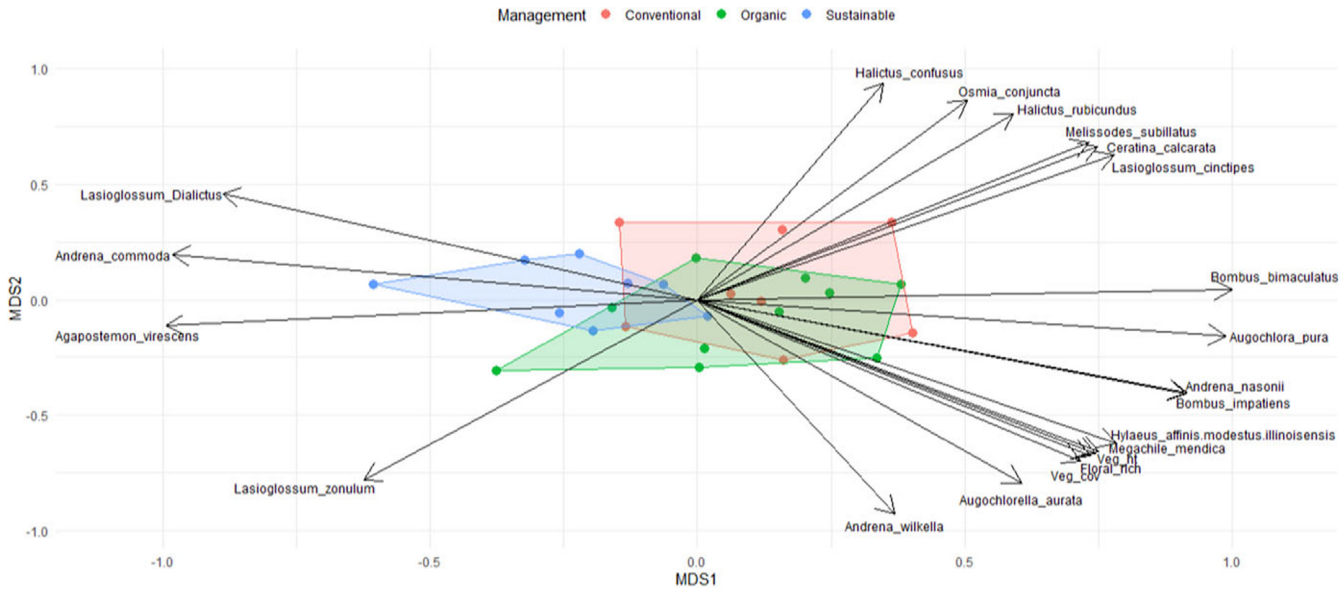


Figure 4. Non-metric multidimensional scaling (NMDS) of bee community composition data aggregated per site across months and years ($n = 26$) using Bray–Curtis dissimilarity of Hellinger-transformed abundance data (stress = 0.20). Convex hulls represent different vineyard management categories (Permutational Multivariate Analysis of Variance $F = 2.18$, $R^2 = 0.16$, $p = 0.003$) as well as vectors for significantly correlated bee species and vegetation and floral variables ($p < 0.05$, based on 999 permutations).

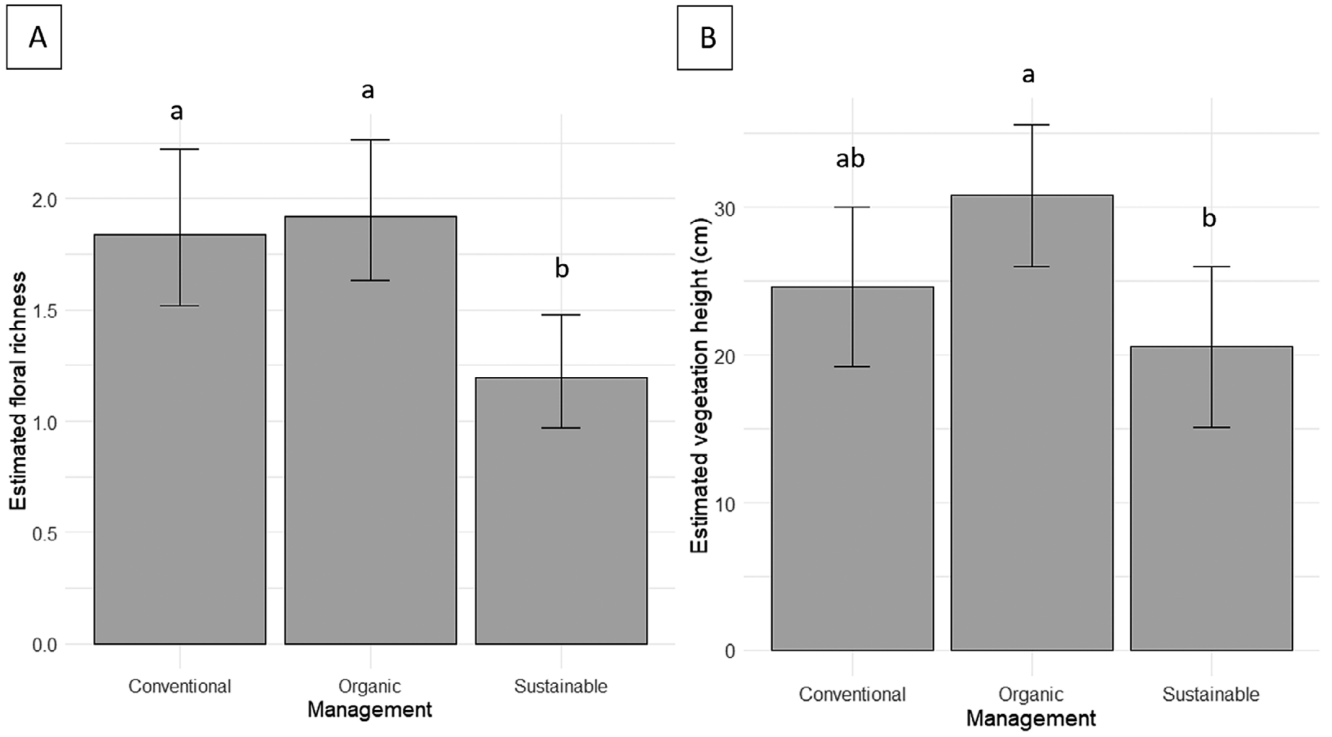


Figure 5. Comparison of floral richness (A) and vegetation height (B) in vineyards under different management types. Graphs show the estimated marginal means from Generalized Linear Mixed Models of each response variable with month, year, and vineyard management as fixed effects and site as a random effect. Letters denote significantly different categories ($p < 0.05$) from Tukey post hoc testing of model-estimated marginal means.

(proxy for alternate row management) was strongly negatively correlated with vegetation cover. When comparing cover cropping and alternate row management across vineyard management categories in mid-summer, there was no difference in the percentage of flowers from cover crops between organic, conventional, or sustainable vineyards (Supplementary Figure 2A) or in the use of alternate row management (Supplementary Figure 2B). Lastly, grouping of sites by their flower species and abundances showed that the floral community composition also differed significantly between vineyard management categories, with organic vineyards

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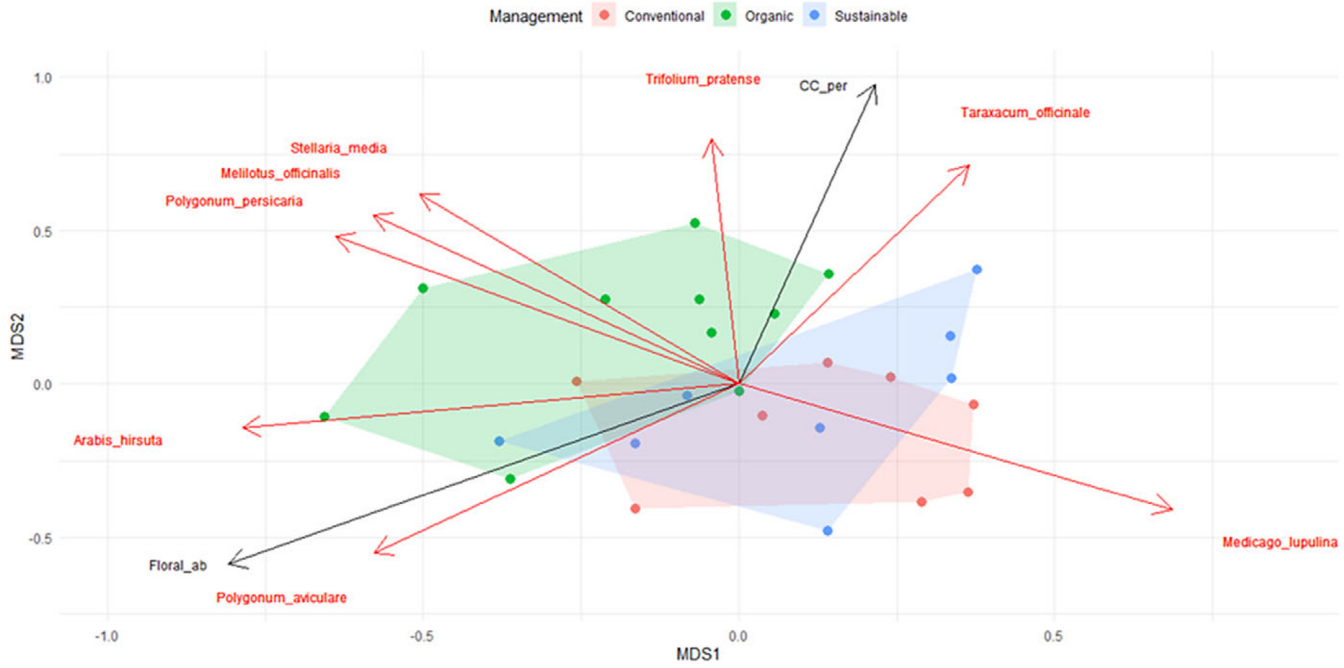


Figure 6. Non-metric multidimensional scaling (NMDS) of flower community composition data aggregated per site ($n = 26$) using Bray–Curtis dissimilarity of Hellinger-transformed abundance data (stress = 0.25). Convex hulls represent vineyard management categories (PERMANOVA F = 1.81, $R^2 = 0.14$, $p = 0.005$). Overlaid are vectors of the most correlated vegetation and floral variables with the ordination ($p < 0.1$, based on 999 permutations, black font); Floral_ab = floral abundance ($r^2 = 0.26$, $p = 0.03$) and CC_per = percentage of flowers from cover crops in mid-summer months ($r^2 = 0.19$, $p = 0.09$). Also shown are the flower species that were significantly correlated with the ordination ($p < 0.05$), highlighting species that largely contribute to community variation (orange font). Redundant species with overlapping vectors were removed for clarity: *Asclepias syriaca*, *Hieracium lachenalii*, and *Linaria vulgaris* (redundant with *Arabis hirsuta*).

being most dissimilar to conventional and certified sustainable vineyards (PERMANOVA $F = 1.81$, $R^2 = 0.14$, $p = 0.005$; Fig. 6). Organic vineyards were associated with species such as common chickweed (*Stellaria media*), yellow sweetclover (*Melilotus officinalis*), and spotted ladysthumb (*Polygonum persicaria*), while sustainable and conventional sites were more associated with black medick (*Medicago lupilina*). Vineyard floral abundance and cover crop percentage were associated with the sorting of sites by floral communities, with cover cropping being associated with sites high in red clover (*Trifolium pratense*) and common dandelion (*T. officinale*), while high floral abundance sites were associated with prostrate knotweed (*P. aviculare*).

Discussion

Of the vineyard management practices investigated in this study, the most consistently impactful variable on bee abundance and diversity was mowing frequency, as measured through between-row vegetation height. We hypothesized that sites with lower mowing frequencies, and thus taller vegetation, would support more abundant and diverse bee communities—consistent with what was found. However, while vegetation height was used as a proxy for mowing frequency, it can also be influenced by factors such as the plant community composition, tillage practices, soils and nutrients, and light and water availability (den Hollander, Bastiaans, and Kropff, 2007). Vegetation height is less frequently recorded in other studies on this topic; however, the positive association with vegetation height in this study is consistent with Biella et al. (2025), who also found a significant positive impact of vegetation height on bee diversity. While vegetation height, floral richness, floral abundance, and vegetation cover were all positively correlated with each other in this study, vegetation height was the most consistently significant predictor of bee abundance and diversity. This suggests that vegetation height may capture additional ecological factors beyond those represented by the other correlated variables. The hypothesis was then that the floral community composition would differ with vegetation height, as taller vegetation would allow certain forbs to reach flowering that otherwise would not be able to flower with constant mowing. However, vegetation height did not significantly correlate with the NMDS of sites by floral composition. Instead, floral abundance and cover crop percentage had a stronger influence. Although the underlying mechanism remains unclear, reducing mowing frequency may benefit bees, and possibly other pollinators, and warrants further investigation with research extending beyond pollinator conservation to include broader vineyard management implications, such as impacts on pest and predator populations, fungal pressure, and other relevant factors (Guerra and Steenwerth, 2012).

Two other between-row vegetation variables had a positive association with bees—floral abundance had a positive relationship with the Shannon diversity index, and vegetation cover had a positive relationship with bee abundance during mid-summer months. This is consistent with the hypothesis that vineyards with more vegetation cover between vine rows, as opposed to bare soil, and where vegetation consisted of more flowers, as opposed to grasses, would support more abundant and diverse bees. The positive influence of vegetation cover seen in this study is consistent with Popescu et al. (2019) and Kratschmer et al. (2019) and highlights the importance of between-row vegetation cover rather than bare soil for bees. Furthermore, the positive influence of floral abundance on bees emphasizes that floral cover between vine rows, rather than grasses alone, which are also common cover crops

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(Sharifi et al., 2024), is an important consideration for bee conservation in vineyards. Further research should be extended to investigations into floral under-vine cover cropping (Abad et al., 2023), which opposes the common practice of herbicides or tillage, as half the quadrats used in this study were placed toward the vine rows to capture all floral resources within the vineyard. This practice could further extend the cover of vegetation and flowers in vineyards and may be beneficial to bees. Interestingly, while floral richness was not a significant predictor in the bee abundance or diversity models, it was significantly associated with the NMDS of sites by bee community composition. Furthermore, high floral richness was associated with higher bee abundance through netting but lower bee abundance in pan traps. The negative relationship with pan-trapped bees may be explained by the taxonomic bias of pan-trap collections toward certain bees, such as Halictidae, which may not require as diverse a floral resource (Portman et al., 2020). Alternatively, it is possible that bees are more likely to be collected by pan traps in resource-poor environments, though the opposite relationship may also be true as flowers draw in more bees to the area (Portman et al., 2020). Consistent with this uncertainty, a recent systematic review of pan trapping studies by Krahner et al. (2024) found no consistent evidence that surrounding floral abundance or diversity systematically increases or decreases bees captured in pan traps, with correlations being highly variable and often non-significant even among studies using similar methodologies.

During mid-summer months, when cover crop species were primarily in bloom, the cover crop percentage of floral resources was negatively associated with bee abundance and had no association with bee diversity, not supporting the prediction that floral cover crops would positively influence bee communities. These results may be explained by the common cover crop species observed, which were predominantly clover species (*Trifolium sp.*)—with white clover (*Trifolium repens*) being the fourth most abundant flower species recorded occurring in 23 of 26 sites, while both aslike clover (*Trifolium hybridum*) and red clover (*Trifolium pratense*) occurred in 11 and 18 sites, respectively. Clover flowers, with their long corollas, may primarily support certain bees, such as bumble bees and honey bees, while solitary or smaller-bodied bees may be unable or unlikely to utilize these flowers for forage (Harris and Ratnieks, 2022). This is further evidenced by the negative relationship between the percentage of flowers from cover crops and the abundance of pan-trapped bees—a relationship not seen with netted bees. Smaller-bodied pan-trapped bees, such as Lasioglossum, which were primarily collected by pan traps (Supplementary Table 4), may be unable or unlikely to utilize the clover cover crops. In contrast, Wilson et al. (2018) found cover cropping increased both the abundance and diversity of bees in vineyards using a cover crop mixture of *Phacelia tanacetifolia* (purple tansy), *Ammi majus* (Bishop's flower), and *Daucus carota* (wild carrot). Griffiths-Lee et al. (2022a) found that floral plantings specifically formulated for bees had stronger impacts on bee abundance and diversity than natural regeneration or other seed mixes. Thus, more research is needed on cover crop species mixes that are both beneficial to vineyard management (ex. pest suppression, weed competition, soil health and nutrients, water use) and wild bees.

In contrast to the negative association between bee abundance and cover crops observed in this study, there was no significant impact of alternate row management on either bee abundance or diversity. This suggests that alternate row management is not detrimental to bees, opposing the initial prediction that it would negatively affect bees by reducing total floral and vegetation resources. While Kratschmer et al. (2018) reported a positive influence of alternate row tillage on bees and on floral resources, in this study, alternate row was defined as the ratio of vegetation height between alternate rows, reflecting management more broadly; any practice that alters vegetation in one row, such as mowing, seeding, or tilling. These results underscore the need to understand how much flower-rich habitat is required to support pollinators in farmlands (Dicks et al., 2015), as our results suggest that alternate row management could be a cost-effective way to implement practices like mowing or cover cropping, saving both time and costs for growers, without negatively impacting bees. Future research should investigate the impact of alternate row floral plantings or cover cropping and alternate row mowing on bees, as well as on vineyard production.

Opposing our prediction that organic sites would have the highest bee abundance and diversity, there was a limited impact of organic vineyard management on bee abundance or diversity in this study—with only a slightly higher Shannon species diversity index in organic vineyards when compared to sustainable vineyards, and no difference from conventional sites. Additionally, despite organic regulations surrounding herbicide usage, vegetation height was the only vegetation or floral characteristic that differed significantly in organic vineyards, being taller than in sustainable vineyards. The limited effect of organic management on wild bees in this study is consistent with findings from other studies (Brittain et al., 2010; Kehinde and Samways, 2012) and is notable given that organic vineyards avoid synthetic pesticides, many of which are known to be harmful to bees (OMAFRA, 2021; Campani et al., 2025). These results may be attributed, in part, to the fact that several of the organic sites were in close proximity to conventional vineyards or other crop types. Thus, bees, even those with relatively small foraging ranges, may be exposed to pesticides outside of the studied organic blocks by foraging elsewhere. Ostandie et al. (2021) found lower pollinator abundance in organically managed vineyards, associated with increased tillage intensity in organic sites, but found a positive effect from the proportion of organic farming in the surrounding landscape within a 1 km radius. This suggests that landscape-scale adoption of organic farming may be an important consideration for pollinator conservation in farmlands. Ostandie et al. (2021) also found that insecticide use intensity, both organic and conventional, negatively impacted pollinator abundance and richness. Similarly, Zielonka et al. (2024) found that while organic vineyards in the UK tended to apply fewer harmful pesticides, the frequency of their organic agrochemical applications was higher than in non-organic vineyards. This increased frequency of sprays had a stronger negative effect on arthropod diversity than the consideration of frequency and toxicity together. However, Kaczmarek et al. (2024) found no impact of reduced fungicide use on wild bees in vineyards, and they did find a positive influence of organic management on bee abundance. Further research is needed to evaluate how different vineyard spray regimes, including types and frequencies, affect wild bee communities at both field and landscape scales over longer time periods. In this study, organic sites were required to have been managed organically for at least 3 years. The lethal and sub-lethal effects of pesticide exposure may not be immediately evident in metrics such as bee abundance and diversity and likely require longer-term studies to fully capture their population- and community-level impacts (Raine and Rundlöf, 2024). Future research should obtain the length of time under organic management from producers and include this as a factor in models looking at wild bee responses to farm management.

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Opposite to our prediction that certified sustainable sites would have higher bee abundance and diversity than conventional sites, we found that Shannon species diversity was lower in certified sustainable vineyards compared to organic vineyards and did not differ significantly from conventional vineyards. However, *Lasioglossum* (*Dialictus*) bee abundance in mid-summer was oppositely negatively impacted by organic management. Thus, some of the differences in diversity between vineyard management types may be attributed to the fact that *Lasioglossum* (*Dialictus*) bees were not identified to species level and were more abundant in sustainable vineyards than in organic vineyards. It is difficult to estimate the diversity and evenness of *Lasioglossum* (*Dialictus*) bees in these sites, as the range in abundance across sites was extremely large, ranging from 2 to 219 individuals per year. Sites with significantly higher *Lasioglossum* (*Dialictus*) abundances may indicate nearby nest aggregations (Nelson et al., 2023) or may be dominated by highly abundant species. A study of the bees in mowed and unmowed meadow sites in the Niagara Region demonstrated that of the nine *Lasioglossum* (*Dialictus*) species or morphospecies collected, two species (*L. hitchensi* Gibbs and *L. versatum* (Robertson)) represented ~75% of all *Lasioglossum* (*Dialictus*) bees collected (Audet, Romero, and Richards, 2021).

Overall, the genus-level results of this study may be clearer in their interpretation than the species-level results. While the genus level decrease in bee diversity in sustainable sites was only nearly significant ($p < 0.1$), these results indicate that vineyard sustainability certifications may require bee-specific requirements to benefit the diversity of bees in the region. When Zielonka et al. (2024) investigated the arthropods in UK vineyards enrolled in the Sustainable Wines of Great Britain (SWGB) scheme, they found no difference in arthropod abundance or diversity between SWGB-accredited vs. non-SWGB-accredited vineyards. They also calculated an 'ecotoxicity score' based on grower-reported chemical inputs and a 'practice score' rating the sustainability of reported management practices. Interestingly, the ecotoxicity score was higher, and the sustainability practice score was lower in SWGB-accredited sites. Authors discuss that conventional vineyards can still be low-input and harbor more biodiversity than organic or sustainably certified vineyards. Similarly, in this study, there was also no difference in the use of cover cropping or alternate row management between vineyard management categories. This demonstrates that conventional growers in Niagara were also using these practices.

Another important consideration for this study is that the SWO program only began in 2017 (SWO, 2025), and several sites had just begun their certification at the time of this study. Additionally, several sites that were considered 'conventional' for this project were later SWO certified in the following years—suggesting they may have been implementing sustainable practices prior to formal certification. Furthermore, all participating vineyards, even those that were deemed 'conventional', may artificially represent sites with higher levels of sustainability due to the growers' willingness to participate in this study. It is also important to note that approximately half of the organic sites were also SWO-certified. In the analysis, however, the 'highest' certification level was utilized to isolate the effects of the certified sustainable designation on bee communities. Future research should investigate the extent to which vineyard management practices change when undertaking sustainability certifications (Moscovici and Reed, 2018) as well as the temporal response time between certifications and their impacts on wild bee communities (Griffin et al., 2017).

Floral richness and vegetation height were also lower in certified sustainable vineyards. Anecdotally, one certified sustainable grower described their practice of mowing between rows before spraying pesticides to minimize exposure of bees to these sprays. This site continuously had low between-row vegetation height, floral abundance, and floral richness, as well as bee abundance and diversity. This highlights the importance of future research investigating how to balance protecting bees from pesticide exposure versus providing floral resources in agricultural lands (Raine and Rundlöf, 2024). Furthermore, both the bee communities and the floral communities differed significantly between vineyard management types. Thus, certain bee species or taxonomic groups may be associated with specific floral resources, spray regimes, or other factors that differ with management type, not measured here. It is possible that regional beta and gamma diversity may actually benefit from having vineyards under varying management regimes throughout the landscape (Socolar et al., 2016).

The consistent and strong temporal variation in vineyard bee abundance and diversity seen in this study is consistent with the literature, as bee communities are known to vary over a growing season and between years (Turley et al., 2022). This highlights the importance of sampling bees sufficiently over the growing season when investigating crop management impacts on wild bees, especially for crops that have particularly long growing seasons, such as grapes. Sampling intensity, however, must be balanced with grower schedules as a lack of time is an often-limiting factor in grower participation in research (Delate et al., 2017). Lastly, models of bee abundance and species diversity (richness and Shannon diversity index) explained only 32%–52% of the variability in the bee response variables. Thus, there are still factors outside of those measured in this study that are influencing vineyard bees, which could include climate, specific pesticide uses, soil characteristics, or landscape contexts. However, this range of R^2 is consistent with other studies looking at pollinator or arthropod responses to vineyard management (Zielonka et al., 2024; Biella et al., 2025). There was also a high degree of model uncertainty for each of the models, with 4–8 models having a delta AICc <2. This is likely, in part, due to the correlations between the vegetation and floral variables included in the models. While these variables had low enough VIFs to include in modeling procedures, they likely explained similar variability in the bee response variables. Overall, further research is needed to understand how vineyard management can most effectively support diverse and abundant bee communities, including how sustainable practices such as certification programs, mowing frequency, alternate row management, and cover cropping shape floral and vegetation characteristics and ultimately influence wild bee communities.

Conclusion

The results of this study suggest that reducing mowing frequency should be prioritized to support wild bee communities in vineyards. Allowing between-row vegetation to grow taller, potentially by mowing every second row to manage costs, may support more abundant and diverse bees. The results also reinforce existing evidence that vegetation cover, particularly when it includes floral resources, is beneficial for wild bees. However, while cover cropping is often promoted to increase both vegetation cover and flowers in vineyards, this study indicates that current cover cropping practices do not enhance overall bee abundance or diversity. Bee-specific cover crops may be necessary to better support the diversity of wild bees. Additionally, these findings suggest that more research is needed on organic and sustainable certifications for wild bee conservation, including how these certification programs can be adapted to better

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support pollinators, how outcomes differ across spatial scales, and longer-term studies to detect impacts at the community level.

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Data availability statement. Select anonymized data that support the findings of this study are available from the corresponding author, B.D., upon reasonable request.

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Author contribution. B.D. and S.C. formulated the research questions and study design. B.D. collected the data, analyzed the data, and wrote the manuscript. S.C. provided funding and resources as well as manuscript edits and feedback.

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