WILD BEE CONSERVATION IN POLLINATOR-INDEPENDENT CROP SYSTEMS

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Abstract

Wild bees are undergoing global declines due to multiple interacting stressors including habitat loss, pesticides, climate change, and interactions with managed and non-native species. These threats are especially prevalent in agricultural landscapes, where natural habitats are replaced with intensively managed monocultures and bees are exposed to agrochemicals and managed pollinators. Pollinator-independent crops - those not reliant on animal pollination for yield or quality - may still support wild bee communities. Chapter 1 presents a systematic review of wild bee conservation research in pollinator-independent crop systems. The review shows strong geographic and crop biases, with commonly studied factors influencing wild bees including ground vegetation management, pesticide use, and surrounding landscapes.

Chapter 2 explores how management practices influence wild bee communities in one such pollinator-independent crop, the wine grape (*Vitis vinifera*). Bee surveys across commercial vineyards showed that reduced between-row mowing consistently supported higher bee abundance and diversity. In contrast, practices like uniform cover cropping, organic production, and certified sustainable management had limited or sometimes negative impacts, suggesting the need for more targeted approaches and further research. Chapter 3 further examines how vineyard bee communities are impacted by local- and landscape-scale variables. Surrounding land-uses and soil factors within a 300m radius around vineyards were analyzed to determine their influence on bee abundance, diversity, and functional traits. Results reveal that wild bees were positively associated with a higher proportion of surrounding semi-natural habitats while sites with coarser soils supported more ground-nesting bees, highlighting the importance of considering both nesting and foraging resources for wild bee conservation and research in agroecosystems.

Chapter 4 investigates whether wild bees use floral resources provided by pollinator-independent crops by documenting foraging activity on wine grape flowers. Very few bees were observed using

grapevine pollen, though some species from Apidae, Andrenidae and Halictidae were recorded. This suggests that wine grapes alone provide minimal floral resources for bees, emphasizing the importance of non-crop vegetation for sustaining bee populations in vineyard landscapes. Together, this thesis provides new insights into bee conservation within pollinator-independent crop systems and highlights practical strategies and research gaps for enhancing wild bee communities in agroecosystems.

Dedication

Dedicated to my mentor, supervisor, role model, and dear friend, Dr. Sheila Colla. This work would not have been possible without your unwavering guidance, support, and inspiration. Your legacy lives on through all of us - past and present students of the Colla Conservation Science Lab - and through everyone fortunate enough to have known you.

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This PhD has been, at different times, a challenge, a lifeline, a source of insanity, and ultimately, one of my greatest accomplishments. I feel incredibly grateful for the privilege of dedicating my time and energy to a topic I care about so deeply and believe in wholeheartedly. The little girl who spent her childhood chasing bugs with a dollar-store net would be thrilled to know she's still at it, just with a much more expensive one. I've learned so much from the world of bees - about the intricate interconnections within our ecosystems and the inseparable relationship between humans and the natural world. Small actions, even planting a single flower, can make a difference. Perhaps saving the bees is, at its core, an act of resilience and hope.

I am deeply grateful for people like my supervisor, Dr. Sheila Colla, who dedicated their lives to the conservation of wild bees - a commitment that was often thankless, yet profoundly meaningful. I am especially grateful to Sheila for providing me with an academic experience grounded in kindness, compassion, support, and grace. I have never felt more encouraged or uplifted in my work, research, goals, and aspirations than I have in the Colla Lab. I wish every graduate student could experience academia in this way. Over the course of my degree, Sheila supported me through a global pandemic, a sabbatical in Italy, personal losses, and, most heartbreakingly, during her own courageous battle with mesothelioma. Somehow, even amidst all this, she would still find time to send a 2:00 a.m. email reply. Sheila was not only an exceptional academic mentor but also a dear friend. I will always cherish the memories of our lab retreats, hikes, socially distanced hangouts, backyard gatherings, and time spent with her family in Italy. Sheila changed my life in countless ways, and I am eternally grateful to have known her during such a formative period in mine. She remains an inspiration to young scientists everywhere and will be deeply missed.

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I would also like to express my deep gratitude to the grape growers, vineyard managers, and wineries who supported my research and made much of this data collection possible. I learned a great deal from each of you about vineyard management and truly appreciate the time you took out of your busy schedules to allow me to sample bees on your properties. Thank you to 20 Bees Winery, Dim Wine Co., Featherstone Estate Winery and Vineyard, Frogpond Farm Organic Winery, Laundry Vineyards, Henry of Pelham Family Estate Winery, Hernder Estate Wines, Hidden Bench Estate Winery, Hughes Vineyards, K.J. Watson Vineyards, Malivoire Wine Company, On Seven Estate Winery, Pearl Morissette Winery, Pillitteri Estates Winery, Queenston Mile Vineyard, Reif Estate Winery, Saunders Family Vineyard, Southbrook Vineyards, Stratus Vineyards, Strewn Winery, Sue-Ann Staff Estate Winery, Tawse Winery, Molek Vineyards, and Vieni Estates.

Outside of the research world, I want to extend a big thank you to my sister and close friends who always cheered me on and patiently feigned interest in bees just to appease me. And to my parents - words

cannot fully express my gratitude, but I'll try. Thank you for never judging my pursuit of research, something unfamiliar to all of us. Thank you for supporting me through moments of overwhelm. And thank you for the daily inspiration in the form of asking, "So, when are you going to get a job?" I am incredibly grateful for your love and support throughout all these years of schooling,

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Preface

Growing concern has mounted over global evidence of pollinator declines including unexplained losses of honey bee colonies, reductions in wild bee species richness, and range contractions across taxa. With no single cause, pollinator declines have been attributed to multiple, interacting threats, including habitat loss, pesticide exposure, climate change, and negative interactions with non-native and managed pollinator species such as the spread of pests and disease. To halt these declines, and ideally reverse them, it is essential to manage landscapes in ways that reduce pollinator exposure to these threats and mitigate negative impacts. Agriculture represents one of the largest human land uses and the way that these lands are managed carries profound implications for pollinator conservation. Increasing interest in sustainable food systems underscores the need for research on how agricultural practices influence pollinators.

This thesis focuses on a specific subset of agricultural systems that has received little attention in the context of pollinator conservation: pollinator-independent crops. These crops do not require or substantially benefit from animal pollination, relying instead on self-fertilization or abiotic factors like wind. Unlike pollinator-dependent crops, their management may be undertaken with limited consideration of pollinators. However, the lack of dependence does not necessarily imply a lack of pollinators in and around these crop lands. Pollinators may still visit crop flowers for food (ex. pollen), forage on weedy or non-crop plants within these systems, or nest in adjacent habitats. As such, pollinator-independent crops can provide important opportunities for conservation, and their managers may be motivated to adopt pollinator-friendly practices as part of broader sustainability goals.

This thesis is organized into four chapters on the topic of wild bee conservation in pollinator-independent crop systems. **Chapter 1** presents a systematic review of the current state of knowledge on wild bee conservation in pollinator-independent crops, synthesizing available evidence, identifying knowledge gaps, and highlighting promising interventions. **Chapter 2** presents a case study in wine grapes, a pollinator-independent crop system in the Niagara Region of Ontario, Canada. Here, I examine

wild bee responses to common vineyard management practices with the goal of providing growers with evidence-based recommendations. **Chapter 3** builds on this work by investigating which spatial scales most strongly influence wild bee communities in vineyards. By comparing wild bee responses to vineyard management, surrounding land-uses, and soil characteristics, this chapter aims to highlight the factors which shape bee communities, taking into account functional traits such as nesting requirements and foraging ranges. **Chapter 4** examines whether wild bees utilize wine grape pollen as a foraging resource by documenting foraging behavior during grapevine bloom. This chapter evaluates the nutritional opportunities and risks vineyards present for bees, filling a key knowledge gap in the conservation of bees within this pollinator-independent crop.

Together, these chapters address critical questions about how pollinator-independent agricultural systems can be managed to better support wild bees. By generating new ecological insights and practical recommendations, this work aims to inform sustainable agriculture policy and practice in Canada and beyond.

Chapter 1: Introduction - A review of bee conservation in pollinator-independent crop systems[1]

Abstract

Wild bees are facing global declines due to interacting threats such as habitat loss, pesticide exposure, pests and pathogens, and climate change - many of which are intensified in agricultural landscapes. While extensive research has focused on promoting pollinators in crops that benefit from animal pollination, less is known about wild bee conservation in pollinator-independent crops. This is despite their prevalence for global food production and the likelihood that bees are still exposed to various threats in these systems. This systematic review analyzed 34 peer-reviewed studies examining the effects of local and landscape variables on wild bee abundance and diversity in pollinator-independent crop systems. Most studies were conducted in Europe and North America, with grapes, wheat, and olives being the most frequently studied crops. Several major pollinator-independent crops (e.g., maize, rice, sugarcane, barley) were understudied or unstudied. Across studies, common variables examined included landscape composition, pesticide/fertilizer use, and ground management practices. Results showed that increased within-field floral and vegetation resources, reduced pesticide inputs, and greater amounts of semi-natural habitat in the surrounding landscape often had positive effects on wild bee communities. However, there was high variability in methodologies and sampling intensity across studies, making broad conclusions challenging. This review highlights key knowledge gaps in crop types and geographies and underscores the potential of pollinator-independent crop systems to support wild bees. Expanding research in these systems can strengthen conservation efforts in agricultural landscapes beyond traditional pollination services.

[1] Briann Dorin was responsible for research design and conceptualization, data collection, analysis, and writing. Sheila Colla provided supervision and feedback throughout the project.

Introduction

Wild bees play a vital role in pollinating both wild flora and agricultural crops, yet growing evidence indicates that wild bee species are declining on a global scale (Zattara and Aizen, 2021). With more than 20, 500 species worldwide, the consequences of these declines are challenging to predict and will likely differ by region. In general, they pose risks such as reduced food stability and crop yields, cultural and aesthetic losses, and detrimental effects on wild plants and broader ecosystems (Dicks et al., 2021). The primary threats to bees include pesticide exposure, habitat loss, climate change, and the spread of pests and pathogens from managed and non-native species (Goulson et al., 2015; Dicks et al., 2021; Lima et al., 2022). Many of these pressures are particularly prevalent in agricultural areas, where bees are exposed to a variety of pesticides including insecticides, fungicides, and herbicides, face extensive land-use changes that reduce habitat availability, and may encounter non-native species such as non-native managed bees introduced for crop pollination (Zattara and Aizen, 2021). Moreover, these threats can interact with one another to intensify their effects - such as simultaneous exposure to multiple pesticides increasing their toxicity or pesticide exposure combined with nutritional stress weakening bees' immune response to pathogens (Goulson et al., 2015). This highlights the importance of addressing the threats facing bees in areas where threats are prevalent and co-occurring and, thus, where risks to bees may be heightened. Agricultural landscapes are one such environment where further research and targeted action are essential for bee conservation.

Significant research has been conducted to address bee conservation in agricultural landscapes (Kennedy et al., 2013). However, research on this topic varies widely in terms of the crop systems and geographies studied, as well as in the specific variables examined for their impacts on bees, including various local factors, which encompass various farm management practices within individual crop fields or margins, and broader landscape-level factors, which refer to features outside the crop field (reviewed below). Local farm management variables investigated may include tillage, mowing, intercropping, cover cropping, crop rotations, spray regimes, sustainability certifications, perimeter plantings, and hedgerows, among others (ex. Clausen et al., 2022). Landscape variables often encompass the proportion of natural or

semi-natural lands, developed lands, and other crop types within set distances from the crop field, or may focus on metrics such as landscape heterogeneity, habitat-patch size, or connectivity (ex. Vega et al., 2023). While studies have investigated these topics, it remains critical to conduct this research across a diversity of crop systems and geographic regions, given the substantial differences in bee communities, farm management options, climate, and land uses across regions and crop types (Kehinde et al., 2018; Kratschmer et al., 2019). For example, research has shown that the pesticide residues in pollen, a major threat facing bees, differs significantly in pollen collected from different crops (Pettis et al., 2013). Other research has shown that certain crops and semi-natural lands may be more important for bees than others (Rollin et al., 2019). Therefore, factors such as the practices farmers are willing to implement in specific crop types growing within a specific area are important to consider (Acchiardo Vallejo, 2017).

Due to the large number of studies on the topic of conserving or promoting pollinators or pollination in farmlands, several review papers have been published on this general topic. Two non-systematic reviews focused on the importance of weeds for bees (Bretagnolle and Gaba, 2015; Rollin et al., 2016) and one on the importance of floral resources within and around farmlands for bees (Nicholls and Altieri, 2013). Several studies have looked at the impact of various agricultural variables on crop pollination or crop pollinators including the impact of biologically diversified farms (Kremen and Miles, 2012), pollinator habitat provision (Venturini et al., 2017), and semi-natural habitats (Holland et al., 2017; Ricketts et al., 2008). Kovács-Hostyánszk et al., (2017) critically assessed the effects of several ecological intensification practices (ex. intercropping) on pollinators and crop pollination. In another more recent study, a meta-analysis was performed by Zamorano et al., (2020) to determine the impact of crop field margin floral enhancements (flower strips and hedgerows) on pollinator abundance or richness in crop fields as well as crop flower visitation and yield. More recently, Tschanz et al., (2024) reviewed 10 papers on the impacts of tillage on ground-nesting bees while Duque-Trujillo et al., (2023) reviewed 55 papers to determine the most prevailing agricultural elements that positively impact bee abundance or diversity in crop fields. Shackelford et al., (2013) performed a meta-analysis on 46 studies that compared pollinator and/or pest-predator responses to local and landscape complexity around crop fields. Lastly, Kennedy et

al., (2013) synthesized findings from primary research papers and unpublished data across 39 crops to assess the effects of local and landscape factors on bee richness and abundance in farmlands.

While these reviews are extensive, many focus on crop pollination, crop flower visitors, or pollinator-dependent cropping systems. In the Kennedy et al. (2013) review of 39 crops, none of the included data came from pollinator-independent crop systems. However, pollinator-independent crops may still offer significant opportunities to support and conserve bees within broader agricultural landscapes and should not be overlooked. In fact, the top four global food crops by total production are pollinator-independent (Klein et al., 2007). And while bees may not visit pollinator-independent crop flowers frequently (Dorin and Colla, 2024) these systems can still pose high risks to bees through pesticide exposure, such as spray drift onto surrounding flowers (Simon-Delso et al., 2017), as well as through habitat loss (Cane and Tepedino, 2001). Thus, it is still important to determine strategies to protect bees within pollinator-independent crop systems. It is also crucial to identify geographic regions where research on this topic is lacking, as findings may vary by country or region. For example, the Ricketts et al. (2008) meta-analysis on the relationship between semi-natural habitats and crop flower visitation found a stronger effect in tropical regions compared to temperate regions. And yet, many global regions may be largely lacking data. In a study on the research looking at the relationship between pesticide exposure and bees, most publications had come from the U.S. and Europe with many global regions having no or few studies on the topic (Abati et al., 2021). Another study reviewing neonicotinoids and their impacts on bees demonstrated similar results (Lundin et al., 2015). Therefore, the goals of this review are to: 1) highlight understudied pollinator-independent crops and geographies in terms of wild bee conservation, 2) identify the local and landscape variables investigated for their impacts on wild bees to determine underrepresented research areas, 3) compare the methodologies used across studies to identify common approaches and opportunities for improvement in future research, and 4) synthesize the current state of knowledge on successful local- and landscape-scale interventions for wild bee conservation in pollinator-independent crop systems.

Methods

Pollinator-independent crops were determined using Klein et al. (2007) which synthesized the pollinator dependence of the leading world crops for human consumption, in terms of global production (Mt), using information from the Food and Agriculture Organization of the United Nations (FAO). Commodity crops, which are groups of less commonly grown individual crops categorized by FAO under one commodity (ex “tropical fruits”), were not included in the analysis due to the focus on crop-specific research. In total, Klein et al., (2007) determined there are 57 leading single crops with an annual production > 4 million Mt. Of these crops, 39 have some benefit from animal pollination while 18 were considered pollinator-independent, showing no benefit from animal pollination (Table 1).

The search engine Web of Science was used to search for primary research papers on the topic of bee conservation in agricultural lands for the top global pollinator-independent crops (see Figure 1 for the PRISMA flow diagram (Page et al., 2021)). Specifically, studies looking at the responses of bee abundance and/or diversity to either on-farm management practices and/or surrounding landscape factors. Two primary searches were conducted, one with specific crop names and one with a general pollinator-independent crop search. Search terms and their Boolean operators were determined based on an exploratory analysis of relevant papers and using an iterative procedure that added, removed, and adjusted search terms to find a reasonable level of scope - one that would exclude a large number of highly irrelevant papers (primarily, those focused on other crops, pollination services, or other taxa) but would capture the broad nature of the research questions. Search terms are included in Appendix A for both searches. In general, both searches required the title to mention pollinators, animals or wildlife as well as at least one term related to sustainable agriculture, crop management, or landscape factors. The abstract then required the specific mention of bees (to exclude papers that focused on other taxa or that did not separate bees from pollinators or other insects) and any of the 18 pollinator-independent crop names (crop-specific search) or any combination of terms that would capture pollinator-independent crops more generally (general pollinator-independent crop search). The latter search included the term cereals due to the high number of papers that describe cereals rather than specific crop names for some of the target

pollinator-independent crops (ex. wheat, barley). The search was limited to research articles, English language documents, and those published in the last 20 years.

From these two initial searches, titles and abstracts were screened to exclude studies that did not sample wild bees or did not assess local or landscape parameters in at least one of the target crops. Studies were retained at this stage if their relevance was unclear. In this initial scan, papers were excluded primarily for the following reasons: studies only investigating honey bees, managed bees or only one or two species or those that only sampled floral resources. Many papers were also excluded due to being pollination studies, breeding experiments, occurring in a non-pollinator-independent crop, or were occurring in a non-agricultural environment. Pesticide residue investigations were also excluded including in bee tissues, bee products (ex. pollen traps) or in flowers. Other reasons for exclusion included social science investigations, modelling-based studies, methods-based research (ex. comparing sampling techniques), or highly irrelevant papers (ex. bee-product medicinal properties, computer vision models for crop disease detection etc.). Studies were retained that looked at groups of bees such as an entire genus or a functional group (ex. Bombus, leaf-cutter bees, or cavity-nesting bees) which was often the result of the methods used to sample bees (ex. trap nests). Duplicate papers from both searches were removed. The remaining studies were then scanned across their full text to ensure they met the review criteria, which included confirming the crop(s) studied, response variables investigated (wild bee abundance and/or diversity), and the local and/or landscape variable(s) researched. Studies were primarily removed during this phase for two reasons – one being that they did not separate results of wild bees from other taxa groups (ex. pollinators) or the second reason being studies that sampled across multiple crop types which included at least one pollinator-dependent crop. This was often due to the study comparing various crop types (ex. mass flowering crops vs anemophilous crops, perennial vs annual crops, traditional crops vs bioenergy crops etc.) or simply due to sampling in multiple crops to investigate general agricultural land uses. Studies that primarily focused on methodological comparisons (e.g., pan traps vs. netting) or on the pollination of select plants across habitat types were also excluded as were studies that did not report bee abundance and/or diversity metrics (ex. those reporting only plant-pollinator networks, functional traits,

or community composition), as these measures were not consistently reported or analyzed across studies, making direct comparisons difficult. For studies that occurred in “cereals” they were included in the analysis if the methods clearly stated which cereal crops were studied and that they were all pollinator independent. Studies that specifically examined fallow land or crop rotations were also included, as these are common practices in several pollinator-independent cropping systems (Campbell et al., 2024). However, to maintain consistency and ensure the focus remained solely on pollinator-independent crops, papers were only retained on this topic when the focal crop(s) sampled were pollinator-independent. Additionally, two papers were removed due to their official publication date being beyond the target range.

From each study, the following variables were extracted, where possible: the year of publication, the location of the study (country/countries), the crop(s) sampled, the local and landscape variables examined, the bee sampling methods used, the temporal span of sampling within a season (~number of months) and across seasons (number of years), the abundance and species/taxon richness of bees recorded, and the significant results - the latter referring to results which were significant in at least one year and one location/country (as reported by each study, commonly $p<0.05$). Results regarding metrics reported beyond bee abundance and diversity (ex. richness, Shannon diversity index) were not included as these were the most commonly reported result across studies that could be easily compared and summarized consistently. Thus, results such as bee functional traits, community composition, temporal stability, beta or gamma diversity, subsets of the overall bee pool (ex. certain taxa), or plant-pollinator networks were not summarized. Only methods and results specific to bees were reported, excluding information regarding the sampling of other insects, plants, or other taxa. Furthermore, for studies that reported data both including and excluding honey bees, the results were reported without honey bees. However, several studies retained honey bees alongside other bee species or did not specify whether honey bees were excluded or not.

Results

In total, 34 peer-reviewed primary research papers on the topic of wild bee conservation in pollinator-independent crops have been published in the last 20 years (since 01-01-2005) (Table 2, Appendix B for list of references). The pollinator independent crops with the most research papers on the topic are grapes (N=14), wheat (N=11), and olives (N=5) (Figure 2A). Other crops studied include maize (N=2), chickpea (N=1), and rice (N=1). This leaves several pollinator-independent crops largely understudied on this topic, with the following crops having no papers that met the review criteria: garden pea, sugar cane, sugar beet, barley, sorghum, millet, oat, lettuce, rye, triticale, spinach, and date palm. However, both barley (N=2) and maize (N=1) were additionally sampled as a secondary crop in some papers - meaning that they were either additional fields sampled but in much fewer numbers or they were used to compare to the primary crop. Of all the papers sampled, regarding the primary crops studied, 44% of papers occurred in annual crop systems and 56% in perennial crop systems (Figure 2B).

The geographic distribution of this research spanned 4 continents, with the majority of studies taking place in Europe (69%) followed by North America (14%), Africa (11%) and Asia (6%) (Figure 3A). Of these regions, the country with the most research on this topic was Germany with 8 papers, followed by the United States with 5 papers, South Africa and Austria both with 4 papers, France, Italy, Greece and Spain each with 3, and India, Hungary, Belgium, the Philippines, Switzerland, and Romania each with one (Figure 3B). Multiple studies conducted their research in multiple countries and for these results each country sampled was counted as a tally of one to accurately represent the spatial distribution of research effort. The temporal distribution of this research showed a clear increase on the topic after 2017 (Figure 4). Only 21% of papers were published prior to 2018 (N=7) while 79% were published in 2018 onwards (N=27) with the largest publication year occurring in 2018, specifically, producing 8 papers in that year alone.

Across studies, where many papers investigated multiple local and/or landscape variables and each variable was counted as a tally of one per study, the most commonly examined variable was the composition of the surrounding landscape (N = 22) (Figure 5). This includes research papers that looked

at different land types and land uses around crop fields at varying radii or distances such as the proportion of land that is natural or semi-natural (which was the most commonly investigated landscape composition variable) as well as various crop types, non-crop land and developed land, or other land uses relevant to various regions and research contexts (ex. woody habitat for above-ground nesting bees) (Table 2). The second most commonly studied variable was the use of pesticides and/or fertilizers within crop fields (N=15). This category primarily consisted of studies comparing organic to conventional crop management but also included studies on integrated pest and pollinator management (IPPM) or studies looking at specific pesticide and/or fertilizer uses such as different types or application frequencies. The third most commonly studied variable was ground management (N=14) which included investigations into the non-crop vegetation occurring within the crop fields themselves and the various practices that impact this vegetation. This research often looked at either intercropping, within-field cover cropping or floral plantings, or herbicide and mechanical vegetation removal practices (ex. tillage, mowing). These studies often quantified ground cover and vegetation resources through measurements of vegetation percent cover, vegetation height, and/or floral resources such as the abundance and diversity of flowers. The fourth most commonly studied variable was the surrounding landscape structure (N=9) which included aspects of landscape configuration such as habitat patch size, shape, and the distance to specific elements (ex. natural or woody elements). Other variables that were less commonly investigated include four studies on various aspects of soils, slope and/or elevation, two studies on flowering field margins or flowering fields neighbouring crop fields, two studies on crop rotations and/or fallow land management, and one study that specifically looked at vineyard orientation and terracing.

A variety of bee sampling methods were used across studies. For studies that employed multiple methods, each method was counted separately as one instance, consistent with how results were tallied. The most common methods used were pan trapping (N=17) and netting (N=16) (Figure 6A). One study additionally used an aspirator alongside netting, which was grouped in with netting for this review. Five studies also used visual observations of bees, either for all bees or for select groups that are easier to identify on the wing (ex. bumble bees). Four studies used sampling methods specific to bee nesting

behaviours or overwintering including three studies using trap nests to sample cavity-nesting bees and one study using emergence cages (with pan traps inside) to sample overwintering bees. Other less commonly used methods include window-intercept traps (N=2), yellow sticky traps (N=2), and blue vane traps (N=3). Most studies sampled bees for 3 months within a growing season (N=11) and the majority of papers sampled bees for a minimum of two months, with only one study sampling bees for just one month (Figure 6B). However, most studies (N=19) only sampled bees for one year/growing season, with twelve studies sampling for two years, two studies for three years, and one study for four years (Figure 6C).

Across studies, where reported, the number of bees collected ranged from 51 - 8710 bees, though it is important to note that some studies retained honey bees in these numbers and the sampling intensity varied drastically across studies (Table 2). Bee species or taxon richness, where reported, ranged from 6-340 species/taxa. Most of these studies identified bees to species level or morphospecies, where uncertain, with only one paper identifying all bees to genus level only. It is also important to note, however, that some of these studies only looked at specific groups of bees. For example, the paper with 6 species investigated leaf-cutter bees only. Across studies, several local and landscape variables showed a positive impact on bee abundance and/or diversity (ex. species or genus richness, Shannon diversity index) in at least one year and/or country investigated. Several studies showed a positive impact of greater local vegetation or floral resources within and along crop fields - either naturally occurring or as a result of practices such as planting flowering fields or margins, reduced tillage, intercropping, or planting floral strips or cover cropping (N = 16). Several studies showed a positive impact of reduced pesticide or fertilizer usage (N=2), IPPM (N=1) or organic management (N=7). Several landscape factors showed positive impacts on bees including the amount of forests, woody or shrubby habitat (N=4), natural or semi-natural habitat (SNH) (N=4), or non-crop habitat, uncultivated fields, or less crop area (N=3). Landscape level fallow (N=2), landscape diversity or complexity (N=2), slope (N=1), artificial entities (N=1), and a specific bee-habitat metric (N=1) also positively impacted bees. Landscape configuration metrics were also important including the distance to woody habitats or SNH (N=2), smaller crop field sizes (N=1), or the mean shape index for habitat patches (N=1). Overall, several variables were shown to

consistently positively impact bees - especially practices that enhance local floral and vegetation resources, that reduce pesticide exposure and toxicity, and that enhance the amount of natural and semi-natural lands in the surrounding landscape.

Discussion

This systematic review highlights several areas where further research is needed to fully understand the potential for wild bee conservation in pollinator-independent crops. Notably, several crops had no research on this topic that met the inclusion criteria, including garden pea, sugar cane, sugar beet, barley, sorghum, millet, oat, lettuce, rye, triticale, spinach, and date palm. Interestingly, the majority of research was concentrated in just three crops: grapes, wheat, and olives, which together accounted for 30 of the 34 studies reviewed. The reasons for this disproportionate focus are unclear, though it may relate to factors such as the farm-gate value of these crops, the regions where they are primarily grown and the corresponding support for pollinator-related research, the nature of crop management and available bee-beneficial practices, or the level of interest from producers or industry in pollinator conservation. Another factor that may have contributed to this crop-bias is the requirement that papers be published in English, which likely excluded research conducted in countries or regions where English is not the primary language and where studies are published in other languages. Still, the findings underscore the need to expand this research to other major pollinator-independent crops such as maize, sugarcane, and rice, for which little published research currently exists. This is particularly important given that these crops, alongside wheat, made up approximately half of global primary crop production in 2023 (FAO, 2023).

Some crops, such as maize, may have been more widely studied if the inclusion criteria had not been as strict regarding studies that sampled both pollinator-independent and pollinator-dependent crops. Several studies were excluded because they sampled within common crop rotations such as maize-soybean systems, where data from soybean, a pollinator-dependent crop, excluded the study from the analysis. Similarly, papers that examined broader agricultural landscapes containing a mix of crop types were also excluded, though they may still offer valuable insights into bee conservation in pollinator-independent systems, particularly in relation to landscape composition and configuration. It is also

possible that the search terms used in this review did not fully capture all regionally specific crop management practices or landscape characteristics, potentially leading to an underrepresentation of research on certain crops or regions. Lastly, the comprehensive review by Klein et al. (2007) was used to determine which pollinator-independent crops to include in the analysis. However, this paper is now somewhat dated and may not reflect important variation in pollinator dependence among newer cultivars or findings from more recent research (Siopa et al., 2024). Consequently, some of the crops in this review may no longer be considered strictly pollinator-independent. In addition, crops that require animal pollination only for breeding purposes, such as potatoes (Klein et al., 2007) were excluded. Future research on this topic may consider including crops with low pollinator dependence, where even limited benefits from pollinators may justify conservation efforts.

There was also a clear geographic skew in the research on this topic, with most studies originating from Europe or the United States, likely in part due to the English-language requirement of the search criteria used. However, this may also be partly due to the focus of this review on individual pollinator-independent crops, which limits the inclusion of smallholder mixed or subsistence farms - farming systems more common in regions outside North America and Europe (Scheader et al., 2018). Moreover, many European countries have placed strong political emphasis on pollinator conservation, with several national and regional pollinator protection policies in place (Underwood et al., 2017). These policies often encourage pollinator conservation in agricultural landscapes and help address key research gaps on this topic. Finally, most studies on this topic were published after 2017, aligning with the growing emphasis on pollinator conservation research and policy over the past decade (Underwood et al., 2017; Abati et al., 2021).

There was also considerable variation in the methodologies used across studies. While most papers employed pan traps and/or netting, commonly used methods for sampling wild bees in a variety of contexts, other methods, such as trap nests or emergence traps sampled only a subset of the wild bee community (Klaus et al., 2024). Additionally, passive sampling methods like blue vane traps may be preferred in certain agricultural research contexts, as they can be left in fields for longer periods and may

cause fewer disruptions to farming activities (Acharya et al., 2022). Some methods, such as visual observations, generally lack the taxonomic resolution required to identify bees to the species level and, therefore, may not be sufficient to fully assess impacts on bee diversity. However, in the included studies, visual observations were often used to supplement other sampling techniques. It is also worth noting that approximately half of the studies included in this review sampled additional insect taxa beyond bees (data not included). These included other pollinators (e.g., butterflies, syrphid flies), as well as pests and pest-predators. Some of these studies used less bee-targeted methods, such as yellow sticky traps, which are more appropriate for sampling broader arthropod communities. Others used additional techniques not detailed here to sample non-bee taxa, such as pitfall traps. Emerging sampling technologies like environmental DNA (eDNA) may further expand future research capabilities (Kestel et al., 2022).

A high level of variability in the temporal aspects of bee sampling was found, particularly in terms of sampling across years. Most studies sampled bees for three or more months within a growing season, which is important given that bee communities can vary substantially over time (Turley et al., 2022). However, the frequency of sampling within those months was not assessed, and some studies sampled bees only a few times during that period. Furthermore, most studies sampled bees for only one year, which presents a challenge as bee communities can also vary significantly between years (Turley et al., 2022). Moreover, several multi-year studies sampled different sites or fields in different years and had large differences in the number of sites sampled each year (Magagnoli et al., 2024). This limits the ability to assess the temporal stability of relationships over time. In many cases, however, this was due to the nature of crop rotations, so even when the same farm was sampled across years, the exact field location shifted to follow the same crop type (Magagnoli et al., 2024; Holzschuh et al., 2010; Hüber et al., 2022). Overall, future research on this topic should increase sampling intensity, potentially through the use of more passive methods like blue vane traps or eDNA, and increase sampling frequency both within and across years. This will help capture intra- and inter-annual variation and improve understanding of the long-term effects of land management practices and land-uses on wild bees.

The most commonly analyzed local and landscape variables across studies were surrounding landscape composition, pesticide and/or fertilizer use, and ground management. This is unsurprising, given the significant increase in research on the impacts of pesticides on bees over the past several years (Abati et al., 2021) and the well-established importance of floral resources and semi-natural habitats within and around farmlands for bees (Nicholls and Altieri, 2013; Holland et al., 2017). These findings are consistent with those of Duque-Trujillo et al. (2023), who found in their review that proximity to natural habitats, grassland management, floral resources, and organic farming were the most prevalent factors positively affecting pollinators in crop fields. Similarly, in this review of pollinator-independent crop fields, several studies that examined organic farming, the amount of or proximity to semi-natural habitats, and local floral resources (enhanced through various practices) reported positive impacts on bee abundance and/or diversity. These tools may, therefore, offer broad conservation benefits to wild bees, regardless of the crop type or production system. However, multiple studies also reported no significant effects of these variables, and each case warrants individual consideration to interpret the results. In general, farm management practices such as flower strips, cover cropping, intercropping, reduced tillage, organic farming, and lowered pesticide use were associated with positive effects on bee abundance and diversity. At the landscape level, semi-natural habitats, forested and shrubby areas, and greater landscape heterogeneity were also beneficial. Finally, this review demonstrates that pollinator-independent crop fields and landscapes can support highly abundant and diverse bee communities, as reflected in the reported bee abundances and species richness across studies. This further highlights the importance of implementing pollinator conservation actions in these systems, even in the absence of direct economic incentives related to crop yield (Siopa et al., 2024).

Conclusion

This review demonstrates that wild bee conservation research in pollinator-independent crops is limited in scope, both taxonomically and geographically. Most studies focused on just three crops: grapes, wheat, and olives, and were concentrated in Europe and North America. This leaves significant knowledge gaps for major global crops such as maize, rice, sugarcane, and barley, as well as for regions

like South America, Asia, and Africa. Across studies, variables most commonly associated with positive impacts on wild bees included local vegetation enhancements (e.g., planting floral resources, reduced tillage), reduced pesticide use, and higher amounts of semi-natural lands in the surrounding landscapes. However, variability in sampling methods and intensity limits the comparability of results and highlights the need for more standardized methodologies with multi-year studies to capture temporal variability in bee communities and relationships. These studies also demonstrate that pollinator-independent crop systems can support abundant and diverse wild bee communities, reinforcing their value in broader conservation efforts. Overall, this review suggests that targeted local and landscape interventions can benefit bees even in non-pollination-dependent systems, but expanding and harmonizing research across crops, regions, and methods is necessary to inform policy and action.

References

Abati, R., Sampaio, A. R., Maciel, R. M. A., Colombo, F. C., Libardoni, G., Battisti, L., ... & Potrich, M. (2021). Bees and pesticides: the research impact and scientometrics relations. *Environmental Science and Pollution Research*, *28*(25), 32282-32298.

Acharya, R. S., Burke, J. M., Leslie, T., Loftin, K., & Joshi, N. K. (2022). Wild bees respond differently to sampling traps with vanes of different colors and light reflectivity in a livestock pasture ecosystem. *Scientific Reports*, *12*(1), 9783.

Acchiardo Vallejo, C. (2017). Preventing a Risk/Risk Trade-off: An Analysis of the Measures Necessary to Increase US Pollinator Numbers. *Pace Environmental Law Review*, 34(2), 489.

Bretagnolle, V., & Gaba, S. (2015). Weeds for bees? A review. *Agronomy for Sustainable Development*, *35*(3), 891-909.

Campbell, J. W., Rand, T. A., West, N. M., Morphew, A., Allen, B. L., Jabro, J. D., & Dangi, S. R. (2024). Pollinators and Other Beneficial Insects Within Two Brassicaceous Oilseeds and a Cover Crop Mix Under Evaluation as Fallow Surrogates for Dryland Production Systems of the Northern Great Plains. *Journal of the Kansas Entomological Society*, *96*(3), 78-92.

Cane, J. H., & Tepedino, V. J. (2001). Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conservation Ecology*, *5*(1).

Clausen, M. A., Elle, E., & Smukler, S. M. (2022). Evaluating hedgerows for wild bee conservation in intensively managed agricultural landscapes. *Agriculture, Ecosystems & Environment*, 326, 107814.

Dicks, L. V., Breeze, T. D., Ngo, H. T., Senapathi, D., An, J., Aizen, M. A., ... & Potts, S. G. (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature ecology & evolution*, *5*(10), 1453-1461.

Dorin, B., & Colla, S. (2024). Observations of wild bees foraging on wine grape (Vitis vinifera L.) flowers–first records and future research directions. *The Journal of the Entomological Society of Ontario*, *155*.

Duque-Trujillo, D., Hincapié, C. A., Osorio, M., & Zartha-Sossa, J. W. (2023). Strategies for the attraction and conservation of natural pollinators in agroecosystems: a systematic review. *International Journal of Environmental Science and Technology*, *20*(4), 4499-4512.

FAO - Food and Agriculture Organization of the United Nations. (2023). World Food and Agriculture – Statistical Yearbook 2023. Rome, Italy. https://doi.org/10.4060/cc8166en

Goulson, D., Nicholls, E., Botías, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957.

Holland, J. M., Douma, J. C., Crowley, L., James, L., Kor, L., Stevenson, D. R., & Smith, B. M. (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agronomy for Sustainable Development*, *37*(4), 1-23.

Holzschuh, A., Steffan-Dewenter, I., & Tscharntke, T. (2010). How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids?. *Journal of Animal Ecology*, *79*(2), 491-500.

Hüber, C., Zettl, F., Hartung, J., & Müller-Lindenlauf, M. (2022). The impact of maize-bean intercropping on insect biodiversity. *Basic and Applied Ecology*, *61*, 1-9.

Kehinde, T., von Wehrden, H., Samways, M., Klein, A. M., & Brittain, C. (2018). Organic farming promotes bee abundance in vineyards in Italy but not in South Africa. *Journal of insect conservation*, *22*(1), 61-67.

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., ... & Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology letters*, *16*(5), 584-599.

Kestel, J. H., Field, D. L., Bateman, P. W., White, N. E., Allentoft, M. E., Hopkins, A. J., ... & Nevill, P. (2022). Applications of environmental DNA (eDNA) in agricultural systems: Current uses, limitations and future prospects. *Science of the Total Environment*, *847*, 157556.

Klaus, F., Ayasse, M., Classen, A., Dauber, J., Diekötter, T., Everaars, J., ... & Pistorius, J. (2024). Improving wild bee monitoring, sampling methods, and conservation. *Basic and Applied Ecology*, *75*, 2-11.

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the royal society B: biological sciences*, *274*(1608), 303-313.

Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A. J., Settele, J., Kremen, C., & Dicks, L. V. (2017). Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecology Letters*, *20*(5), 673-689.

Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guzmán, G., Goméz, J. A., ... & Winter, S. (2019). Response of wild bee diversity, abundance, and functional traits to vineyard inter-row management intensity and landscape diversity across Europe. *Ecology and Evolution*, *9*(7), 4103-4115.

Kremen, C., & Miles, A. (2012). Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecology and society*, *17*(4).

Lima, M. A. P., Cutler, G. C., Mazzeo, G., & Hrncir, M. (2022). The decline of wild bees: Causes and consequences. *Frontiers in Ecology and Evolution*, *10*, 1027169.

Lundin, O., Rundlöf, M., Smith, H. G., Fries, I., & Bommarco, R. (2015). Neonicotinoid insecticides and their impacts on bees: a systematic review of research approaches and identification of knowledge gaps. *PLoS one*, *10*(8), e0136928.

Magagnoli, S., Bosi, S., Negri, L., Dinelli, G., Burgio, G., & Masetti, A. (2024). Flowering areas enhance insect pollinators and biological control agents in wheat intensive agro-ecosystems. *Insect Conservation and Diversity*, *17*(5), 884-893.

Nicholls, C. I., & Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable development*, *33*(2), 257-274.

Page, M. J., McKenzie, J. E., Bossuyt, P. M., Boutron, I., Hoffmann, T. C., Mulrow, C. D., ... & Moher, D. (2021). The PRISMA 2020 statement: an updated guideline for reporting systematic reviews. *BMJ*, 372, n71. https://doi.org/10.1136/bmj.n71

Pettis, J. S., Lichtenberg, E. M., Andree, M., Stitzinger, J., & Rose, R. (2013). Crop pollination exposes honey bees to pesticides which alters their susceptibility to the gut pathogen Nosema ceranae. *PloS one*, *8*(7), e70182.

Ricketts, T. H., Regetz, J., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., Bogdanski, A., ... & Viana, B. F. (2008). Landscape effects on crop pollination services: are there general patterns?. *Ecology letters*, *11*(5), 499-515.

Rollin, O., Benelli, G., Benvenuti, S., Decourtye, A., Wratten, S. D., Canale, A., & Desneux, N. (2016). Weed-insect pollinator networks as bio-indicators of ecological sustainability in agriculture. A review. *Agronomy for sustainable development*, *36*(1), 1-22.

Rollin, O., Pérez-Méndez, N., Bretagnolle, V., & Henry, M. (2019). Preserving habitat quality at local and landscape scales increases wild bee diversity in intensive farming systems. *Agriculture, Ecosystems & Environment*, *275*, 73-80.

Schrader, J., Franzén, M., Sattler, C., Ferderer, P., & Westphal, C. (2018). Woody habitats promote pollinators and complexity of plant–pollinator interactions in homegardens located in rice terraces of the Philippine Cordilleras. *Paddy and Water Environment*, *16*, 253-263.

Shackelford, G., Steward, P. R., Benton, T. G., Kunin, W. E., Potts, S. G., Biesmeijer, J. C., & Sait, S. M. (2013). Comparison of pollinators and natural enemies: a meta-analysis of landscape and local effects on abundance and richness in crops. *Biological Reviews*, *88*(4), 1002-1021.

Simon-Delso, N., San Martin, G., Bruneau, E., Delcourt, C., & Hautier, L. (2017). The challenges of predicting pesticide exposure of honey bees at landscape level. *Scientific Reports*, *7*(1), 1-10.

Siopa, C., Carvalheiro, L. G., Castro, H., Loureiro, J., & Castro, S. (2024). Animal-pollinated crops and cultivars—A quantitative assessment of pollinator dependence values and evaluation of methodological approaches. *Journal of Applied Ecology*, *61*(6), 1279-1288.

Tschanz, P., Walter, A., Keller, T., & Albrecht, M. (2024). A review of soil tillage impacts on ground-nesting wild bees–mechanisms, implications, and future research perspectives. *Agriculture, Ecosystems & Environment*, *375*, 109224.

Turley, N. E., Biddinger, D. J., Joshi, N. K. and López-Uribe, M. M. (2022). Six years of wild bee monitoring shows changes in biodiversity within and across years and declines in abundance. Ecology and Evolution, 12(8), e9190.

Underwood, E., Darwin, G., & Gerritsen, E. (2017). Pollinator initiatives in EU Member States: Success factors and gaps. *Report for European Commission under contract for provision of technical support related to Target*, *2*.

Vega, S., Vázquez-Rivera, H., Normandin, É., Fournier, V., & Lessard, J. P. (2023). Large remaining forest habitat patches help preserve wild bee diversity in cultivated blueberry bush. *Diversity*, 15(3), 405.

Venturini, E. M., Drummond, F. A., Hoshide, A. K., Dibble, A. C., & Stack, L. B. (2017). Pollination reservoirs for wild bee habitat enhancement in cropping systems: a review. *Agroecology and Sustainable Food Systems*, *41*(2), 101-142.

Zamorano, J., Bartomeus, I., Grez, A. A., & Garibaldi, L. A. (2020). Field margin floral enhancements increase pollinator diversity at the field edge but show no consistent spillover into the crop field: a meta-analysis. *Insect Conservation and Diversity*, *13*(6), 519-531.

Zattara, E. E., & Aizen, M. A. (2021). Worldwide occurrence records suggest a global decline in bee species richness. *One Earth*, *4*(1), 114-123.

Tables

Table 1: List of the 18 single crops with no yield benefit/increase from animal pollination from Klein et al., (2007) and the number of primary research papers found on the topic of wild bee conservation per crop through a Web of Science systematic literature search. Primary crop refers to the main crop investigated or sampled in a study, while secondary crops are those that were either sampled at fewer sites or included primarily for comparison with the primary crop.

Scientific name(s)	Common name(s)	Number of papers - primary crop	Number of papers - secondary crop
Cicer arietinum	Chickpea, gram, garbanzo bean	1	0
Pisum sativum, P. arvense	Garden pea, field pea	0	0
Vitis vinifera	Table grape, vine grape	14	0
Olea europaea	Olive	5	0
Saccharum officinarum	Sugar cane	0	0
Zea mais	Maize, green corn, sweet corn	2	1
*Triticum spp. (*mainly *T. aestivum, T. durum, T. spelta)*	Wheat	11	0
*Oryza ssp. (*mainly *O. sativa)*	Rice, paddy	1	0
Beta vulgaris	Sugar beet	0	0
Hordeum disticum, also included *Hordeum vulgare*	Barley	0	2
Sorghum guineense, S. vulgare, S. dura	Sorghum	0	0
Echinocloa frumentacea, Eleusine coracana, Eragrostis abyssinica, Panicum miliaceum, Paspalum scrobiculatum, Pennisetum glaucum, Setaria italica	Millet	0	0
Avena spp., mainly Avena sativa	Oat	0	0
Lactuca sativa	Lettuce	0	0
Secale cereale	Rye	0	0
Triticale sp.	Triticale	0	0
Spinacia olearacea	Spinach	0	0

Phoenix dactylifera	Date palm	0	0

Table 2: Overview of each paper in the literature review including the year of publication, the crops and countries studied, local and landscape variables investigated, and main results. The primary crop is the main crop studied (majority of sites), while secondary crops were either less sampled (N=2) or included for comparison (N=1). Bee abundance and richness values exclude honey bees, where possible. Richness is based on the finest taxonomic resolution used (typically species or morphospecies). Missing values indicate data not clearly reported. Results reflect significant positive effects on bee abundance and/or diversity (e.g., richness, Shannon index) in at least one year or location. Significance follows the authors' criteria, usually $p < 0.05$. Missing values in the results column indicate no significant effect on abundance or diversity. SNH = Semi-natural habitat or elements, IPPM = Integrated Pest and Pollinator Management.

Article information		Methods					Results			
Authors	Year	Primary crop	Secondary crop	Country(s)	Local variables tested	Landscape variables tested	No. bees	Bee richness	Positive local variables	Positive landscape variables
Boetzl et al.	2022	Wheat		Germany	Flowering fields		51	21	Recently resown flowering fields	
Shankar & Mukhtar	2024	Chickpea		India	Bio-insecticides (IPPM)			6	Bio-insecticides	
Meagher Jr et al.	2020	Maize		United States	Intercrop cover crops		863	17		
Adhikari et al.	2019	Wheat		United States	Ground management, organic	Composition	8710	109		
Carrié et al.	2018	Wheat	Barley	France		Composition, slope	2494	77		Slope
Kovács-Hostyánszki et al.	2011	Wheat	Barley	Hungary	Fertilizer and insecticide use	Composition	4884	105	Decreased fertilizer and pesticide use	
Magagnoli et al.	2024	Wheat		Italy	Flowering margins		1432	81	Flowering margins	
Holzschuh et al.	2010	Wheat		Germany	Organic	Composition, configuration		7	Organic management	Non-crop habitat, fallow strips
Happe et al.	2018	Wheat		Germany	Organic	Configuration	1915	81	Organic management	Smaller fields/scall-scale agriculture
Amy et al.	2018	Wheat		Belgium	Intercrop flower strips		601	43		
Campbell et al.	2024	Wheat		United States	Fallow/crop rotation		399	42	Cover cropping fallow	
Holzschuh et al.	2007	Wheat		Germany	Organic	Composition	1507	37	Organic management	
Bryan et al.	2021	Wheat		United States	Fallow/crop rotation		5898	106	Cover cropping fallow	
Hűber et al.	2022	Maize		Germany	Intercropping, organic		98	11	Intercropping	
Hass et al.	2018	Rice		Philippines		Composition	494	31		Agroforests
Stavrianakis et al.	2024	Olive		Greece	Ground management		2194	85	Reduced tillage	

Martínez-Núñez et al.	2020	Olive		Spain	Ground management, organic	Composition, configuration		15	Organic management, extensive ground management	Intermediate landscape complexity
Karamaouna et al.	2019	Olive		Greece	Ground management				Sown flowers	
Pascual	2021	Olive		Spain		Composition	3255	27		Scrubland, mean shape index, less olive groves
Tscheulin et al.	2011	Olive		Greece		Composition	3673	340		Bee habitat area
Brittain et al.	2010	Grapes	Maize	Italy	Insecticide use and drift	Composition	3233	61	Reduced insecticide use	Uncultivated fields
Blaise et al.	2022	Grapes		France	Ground management		766		Between-row vegetation cover and flowers	
Bosco et al.	2023	Grapes		Switzerland	Ground management	Composition, configuration	450	43		
Kehinde & Samways	2012	Grapes		South Africa	Organic	Composition, configuration	1910	25		Natural sites
Kehinde et al.	2018	Grapes		South Africa, Italy	Organic	Composition	1482	25	Organic management, flower density	
Kehinde & Samways	2014	Grapes		South Africa	Organic	Composition, configuration, slope		31		
Wersebeckmann et al.	2023	Grapes		Germany	Field orientation/terracing, soil texture	Composition, configuration	3385	115	Smaller soil particles, local shrubs	Vineyard fallows, vineyard cover, SNH
Kratschmer et al.	2018	Grapes		Austria	Ground management	Composition, configuration, slope	493	84	Alternate-row tillage, flower cover	Artificial entities, distance to SNH
Kratschmer et al.	2019	Grapes		Spain, France, Austria, Romania	Ground management	Composition	719	113	Floral resources and vegetation cover	Landscape diversity
Uzman et al.	2020	Grapes		Germany	Organic	Composition, configuration		15	Organic management	SNH, proximity to woody habitat
Kratschmer et al.	2021	Grapes		Austria, South Africa	Organic, ground management	Composition	3202	122	Inter-row vegetation cover, floral functional diversity	Woody habitat
Kaczmarek et al.	2024	Grapes		Germany	Organic, pesticide use	Composition	2015	85	Organic management, vegetation cover	
Rasran et al.	2018	Grapes		Austria	Ground management	Composition		41	Floral abundance, plant diversity	
Wilson et al.	2018	Grapes		United States	Ground management	Composition	420	17	Cover cropping	

Figures

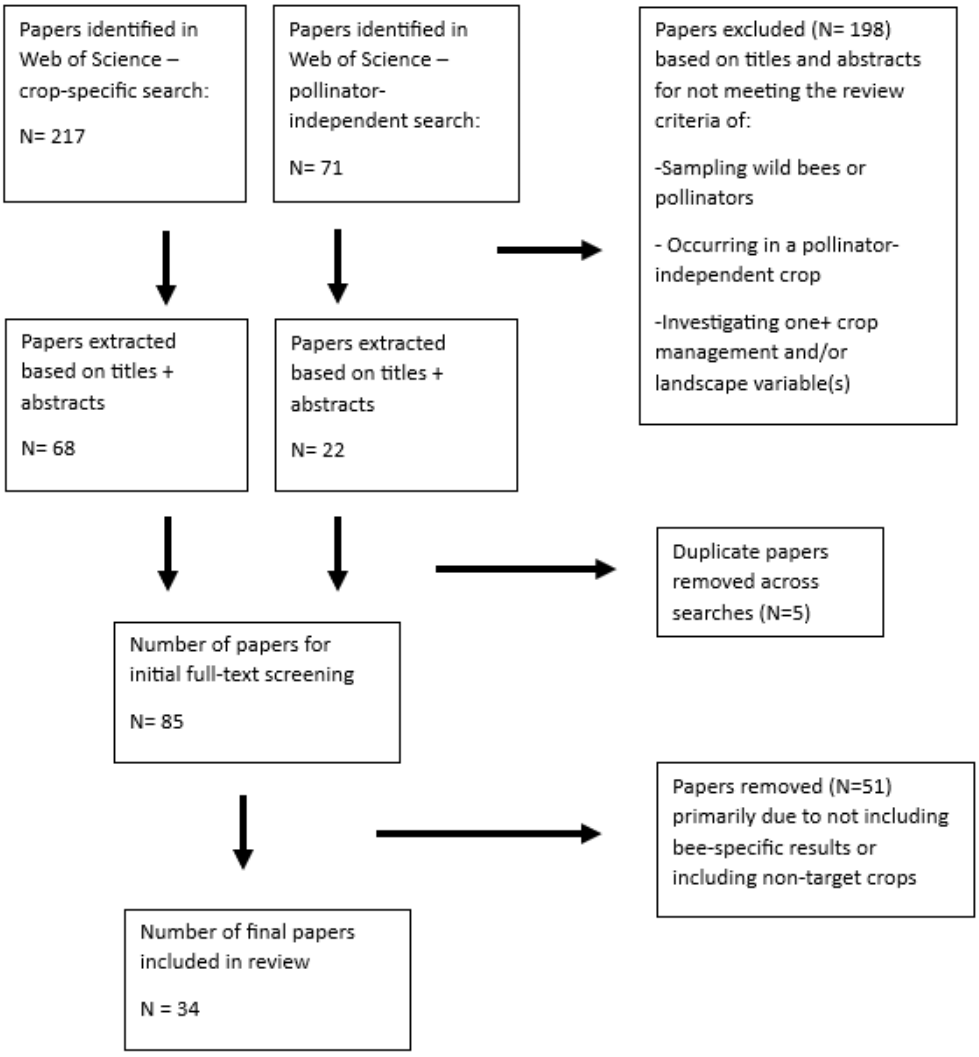

Figure 1: PRISMA flow diagram for the Web of Science search process showing the number of papers identified, screened, excluded, and retained for a systematic review on wild bee conservation in pollinator-independent crop systems. Includes details on where papers were removed, how many underwent full-text review, and the final number of studies included in the analysis. Search criteria were limited to primary research papers published in English between January 1, 2005, and December 31, 2024.

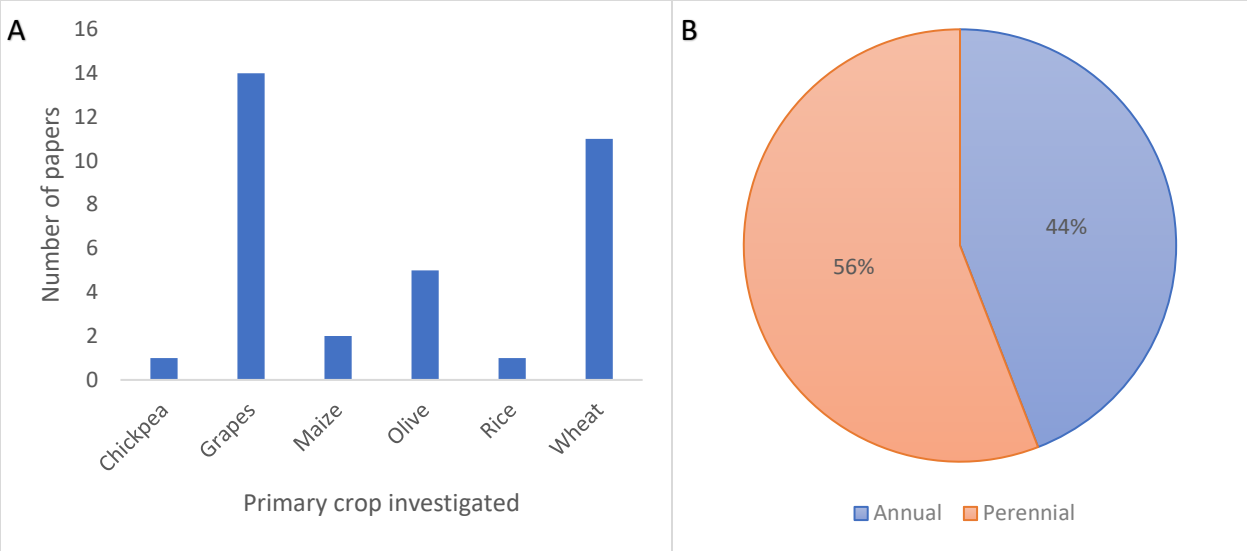

Figure 2: Primary crops investigated across studies on wild bee conservation in pollinator-independent agriculture. (A) Number of papers that investigated each crop as the primary crop. (B) Proportion of studies where the primary crop was an annual vs. perennial crop.

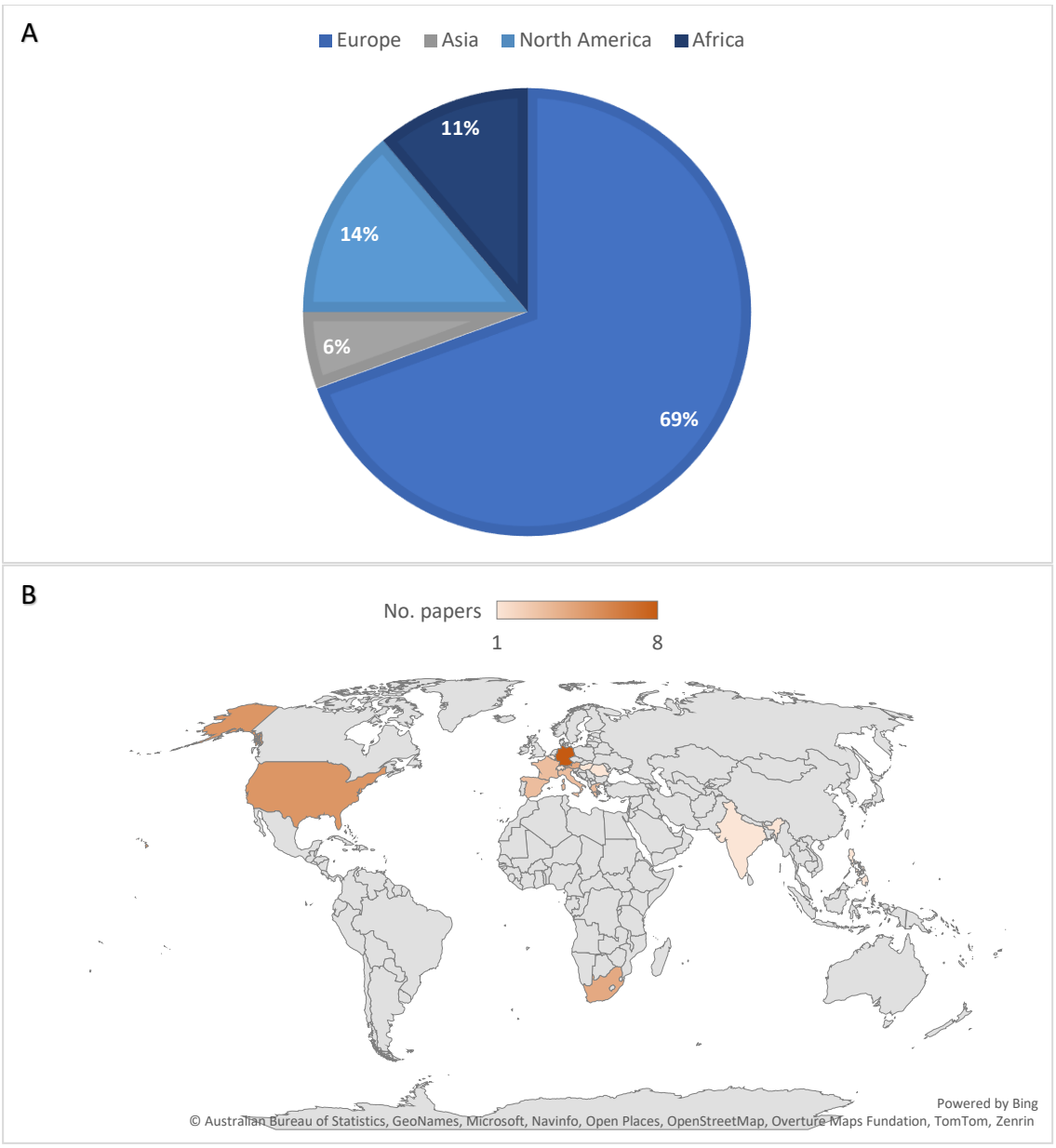

Figure 3: Geographic distribution of studies included in the literature review on wild bee conservation in pollinator-independent crop systems. (A) Proportion of studies conducted across different continents. (B) World map showing the number of studies per country. Studies conducted in multiple countries were counted once per country to accurately represent the spatial distribution of research effort. The map was created using Microsoft Excel (Microsoft Corporation, 2022).

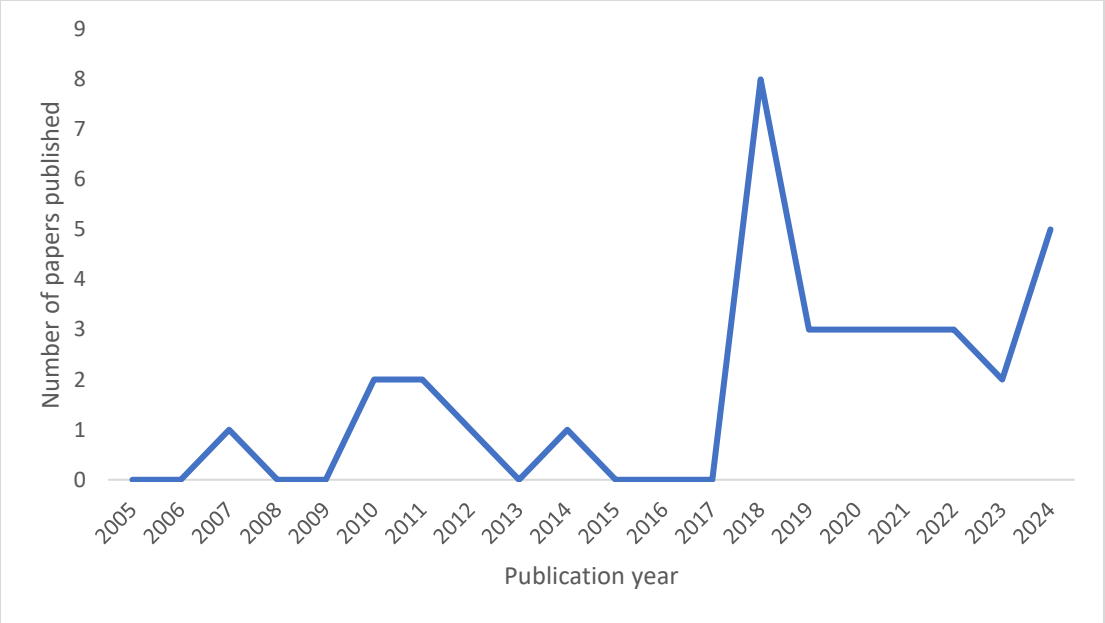

Figure 4: Annual number of publications retrieved from a systematic literature review in Web of Science on wild bee conservation in pollinator-independent crop systems over the past 20 years.

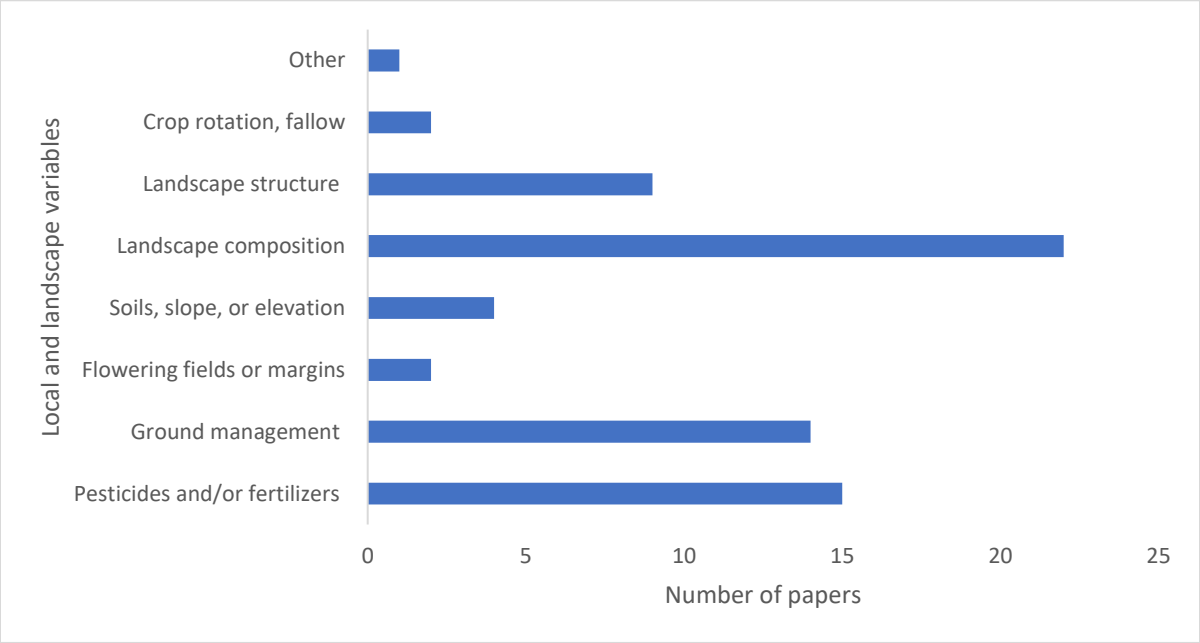

Figure 5: Number of papers investigating the impacts of local and landscape variables on wild bees in pollinator-independent crop systems. Studies examining multiple variables contributed one count per variable to highlight the level of investigation for each variable. 'Other' encompasses factors such as field orientation and terracing. 'Landscape structure' includes metrics of patch size, configuration, and spatial

arrangement while 'landscape composition' pertains to the proportion of land types (ex. semi-natural habitat, SNH) surrounding sites. 'Ground management' refers to in-field practices like cover cropping, intercropping, spontaneous ground vegetation, and flower strips, distinct from cover crops or plantings in crop rotation fallows or outside of crop fields in margins or neighbouring areas. 'Pesticides and/or fertilizers' includes studies on organic management, IPM/IPPM, and specific fertilizer and pesticide uses including different types and application frequencies.

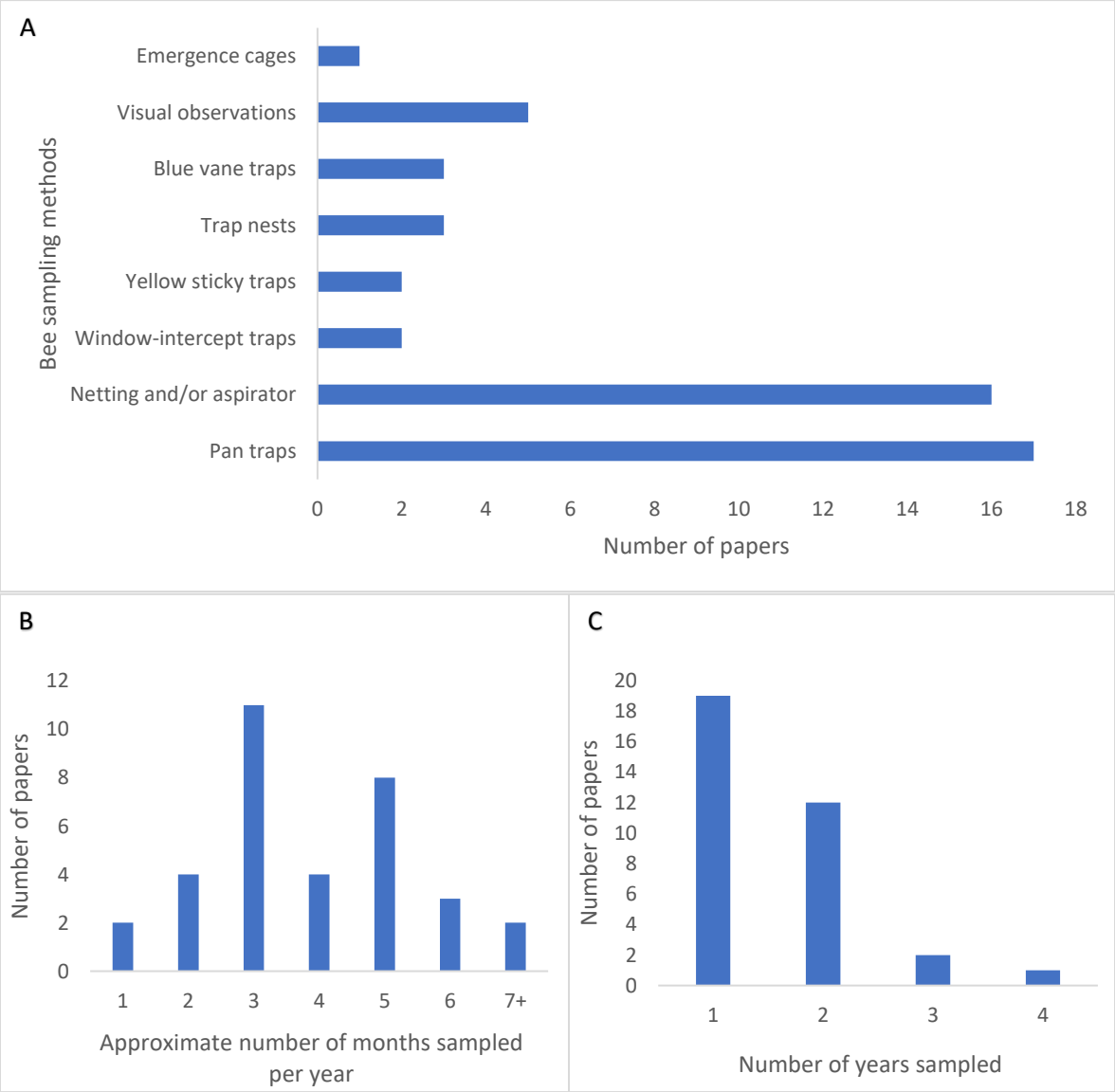

Figure 6: Summary of bee sampling methods across studies on wild bee conservation in pollinator-independent crop systems. (A) Bee sampling methods used, total counts exceed n = 34 as studies

employing multiple methods were counted in each category. (B) Approximate number of months sampled per year, reflects the maximum range of months sampled across sites, years, or locations, without accounting for sampling frequency or intensity within those months. (C) Number of sampling years per study, includes studies that sampled multiple years even if sampling was conducted in different fields or locations each year.

Chapter 2: Are broad sustainability practices sufficient to support wild bees? A case study in cool-climate vineyards[2]

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 two 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 no significant effects on bee abundance or 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.

[2] Briann Dorin was responsible for research design and conceptualization, data collection, analysis, and writing. Sheila Colla provided supervision and feedback throughout the project.

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 (Mallinger et al., 2017). These threats will persist as global agricultural production intensifies and expands (Lanz et al., 2018) prompting continued research into how to protect and conserve pollinators within farmlands (Bretagnolle and Gaba, 2015; Kovács-Hostyánszki et al., 2017; Kremen and Miles, 2012; Nicholls and Altieri, 2013; Zamorano et al., 2020). 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 grown 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 organic production, integrated pest management, cover cropping, reduced mowing, and low- or no-till soil management (Griffiths-Lee et al., 2022b). 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 et al., 2024) while others have shown limited effects (Brittain et al., 2010; Kehinde and Samways 2012; Biella et al., 2025). Studies on the impact of between-row vegetation compared to between-row tillage on wild bees show varying results (Kratschmer et al., 2018; Kratschmer et al., 2019; Popescu et al., 2019; Blaise et al., 2022; Rocher et al., 2024); while the floral cover in the between-row spaces generally has positive impacts on bee abundance and diversity (Wilson et al., 2018; Blaise et al., 2022; Griffiths-Lee et al., 2022a). 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 nutrient, 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.

Furthermore, in studies that collected data across multiple countries, the bee communities and responses to vineyard management differed between geographic locations (Kratschmer et al., 2019; Kehinde et al., 2018). 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 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 (Hutchinson et al., 2022; McCravy, 2018; Schindler

et al., 2013; Russo et al., 2015). 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, the effects of: (1) cover cropping and the extent of between-row vegetation and floral cover; (2) the mowing frequency 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 vineyards that plant flowering cover crops between rows would provide greater floral resources for bees, leading to higher wild bee abundance and diversity. Similarly, vineyards that mow less frequently would allow more forb species to flower, increasing both flower and bee abundance and diversity. In contrast, alternate-row management practices, such as alternating tillage, mowing, or seeding, were predicted to reduce the total vegetation and floral resources available, negatively impacting bees. It was also hypothesized that conventional pesticide use, including herbicides, would negatively affect both bees and floral resources lending to higher bee and flower abundance and diversity in organic vineyards compared to conventional vineyards. Certified sustainable vineyards, which were predicted to be more likely to implement practices such as cover cropping and integrated pest management (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 favouring certain taxa over others driven by differences between species in factors such as their floral preferences, nesting sites, and active periods.

Methods

See Supplemental methods for more details and information regarding methods used.

Site selection

Grapes are the 3rd 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, n.d.). 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 certification program (SWO, n.d.)[3]. This program requires that vineyard management considers factors such as biodiversity, water use, and soil health and recommends practices such as cover cropping and integrated pest management (IPM). Sites that were managed organically and were also certified sustainable (i.e. growers that had both certifications) were categorized as organic for this study to investigate the sustainability certification in isolation and due to the often-stricter environmental regulations for organic certifications (Seufert et al., 2017). In Year 1, 20 sites were sampled: ten organic, five conventional and five certified sustainable. In Year 2, 24 sites were sampled, eight organic, eight conventional, and eight certified sustainable (Supplemental Table 1). Thus, some sites were sampled for only one year (Figure 1). Sites covered the various grape growing sub-appellations of the region (VQA, n.d.) and were at minimum 600 m apart to sample independent bee communities (Gathmann and Tscharntke, 2002; Knight et al., 2005; Zurbuchen et al., 2010).

Bee and vegetation surveys

Bee and vegetation sampling occurred every four weeks from May through August in 2021 and 2022 (Schindler et al., 2013). Bees were sampled using both pan traps and aerial netting. A 400 m^2 area was marked out in the centre of each vineyard block spanning two neighbouring between-row spaces (Kratschmer et al., 2018). Aerial netting was performed for 30 minutes in the morning and afternoon using collecting jars with ethyl acetate (BioQuip 1121 Series Collecting Jars). Twenty-four pan traps of 3.25 oz (96 mL) of yellow, blue, or white paint (New Horizons bee bowls, Maryland) were placed underneath the central vine row spaced ~3 m apart with alternating colours before 9:00 am and collected after 5:00 pm.

[3] Sites were identified by contacting grape growers through existing networks and by searching relevant industry websites, including Grape Growers Ontario, Sustainable Winegrowing Ontario, and the Organic Council of Ontario. Email inquiries were sent to individual growers and wineries to assess their interest in participating and to arrange site visits. These visits allowed us to select research sites and vineyard blocks that aligned with our study design, ensuring coverage of diverse management practices, surrounding landscapes, and sub-appellations.

On the same days of bee sampling, vineyard floral resources and vegetation characteristics were also recorded. A 1 m² quadrat was semi-randomly placed eight times along the 400 m² sampling area. Flower species and their abundances were documented for all open flowers inside the quadrat (Carvell et al., 2004; Baldock et al., 2019). 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 while vegetation height was recorded by measuring the tallest pieces of vegetation. The mean of vegetation and floral data were calculated per site and sampling round. 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, Supplemental 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 (Packer et al., 2007; see Appendix C for the list of published keys 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* sub-genus Dialictus, *Hylaeus affinis/modesutus/illinoinesis*, *Sphecodes atlantis/cressonii*, and one distinct morphospecies of *Sphecodes* sp. All results and discussion at the "species" level here forth include these sub-genus level identifications unless otherwise specified. A subset of identifications, per species, were 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, 2014) and excluded honey bees (Kratschmer et al., 2018). 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. 2014), "lmerTest" (Kuznetsova et al., 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 repeated measures and unmeasured site-level variation (Supplemental Table 3). All numeric explanatory variables were scaled and centred and one variable, floral abundance, was log(x+1) transformed (Zuur et al., 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 using the package "performance" (Lüdecke et al., 2021) and the packages "gstat" (Gräler et al., 2016) and "sp" (Bivand et al., 2013) for spatial variograms of model residuals (Harrison et al., 2018; Zuur and Ieno, 2016).

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). 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 modelled as above. First, models were run with genus-level bee richness and Shannon diversity index. Secondly, the abundance of *Lasioglossum* (*Dialictus*) bees, which were highly abundant and not identified to species level, were modelled separately. Lastly, models were also run separately for total bee abundance by pan trap and net collections to account for potential differences between sampling methods (Supplemental Table 3).

GLMMs were also used to test how floral and vegetation metrics varied by management type and a correlation matrix was used to examine relationships among these variables (averaged over time). Cover crop use and alternate row management were compared across vineyard management types using ANOVA and Fisher's Exact tests. Lastly, to examine how vineyard management influenced bee community composition, bee species abundances per site were averaged over years and Hellinger transformations were applied (Zuur et al., 2007). Non-metric multidimensional scaling (NMDS) using the "vegan" package (Oksanen et al. 2022) were run on this 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 significantly correlated with the NMDS were determined using the *envfit* function. To further examine how bee communities varied among management types, negative binomial Generalized Linear Models (GLMs) were run using the "MASS" package (Venables & Ripley, 2002) for select genera. Models were run separately for each year on the total abundance of the most widespread and abundant genera across sites (Supplemental Table 4), with management type included as the fixed effect. Lastly, NMDS analyses were performed on Hellinger-transformed floral species data to assess floral community differences by management types, adding floral and vegetation variables as well as individual flower species that were significantly correlated with the NMDS axes.

Results

After removing honey bees, 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 all 26 sites, Agapostemon, Andrena, Augochlorella, Bombus, and Halictus collected in 25 sites, Ceratina in 23 sites and Hylaeus in 21 sites (Supplemental Table 4).

Modelling of bee responses to vineyard management practices and temporal variables displayed a strong influence of both month and year on bee abundance and 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 model. In general, bee abundance and diversity were highest in midsummer months (June and July), lowest in May, and higher in 2021 than 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; Figure 2A) as did bee species richness (estimate = 0.076, Z = 2.03, p = 0.043; Figure 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; Figure 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 (Figure 2D). Genus-level results were generally similar to species-level but with less significance (Supplemental Table 5). Interestingly, bee genus richness was most impacted by floral richness, rather than vegetation height, 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, Supplemental 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) (Figure 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) (Figure 3B) as well as between vegetation height and Shannon diversity index (estimate = 0.15, Z = 3.48, p = 0.0005) (Figure 3C) and Shannon genus diversity index (estimate = 0.11, Z = 2.28, p = 0.023). Bee species richness was negatively associated with sustainable management in mid-summer (estimate = -0.23, Z = 2.04, p = 0.042) however, post-hoc comparisons were not significant (Figure 3D). Models specifically examining *Lasioglossum* (Dialictus) abundance revealed a negative relationship with floral abundance (estimate = -0.17, Z = 2.06, p = 0.040; Supplemental 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 bee abundance collected 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 (estimate = -0.38, Z = 1.86, p = 0.0630) (Supplemental Table 8). In mid-summer, similar relationships existed with vegetation height and floral richness while a nearly 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).

The bee community composition differed significantly between vineyard management categories (Permutational Multivariate Analysis of Variance F=2.18, R^2=0.16, p=0.003; Figure 4). Certified sustainable sites were associated with *Lasioglossum (Dialictus), Andrena commoda*, and *Agapostemon virescens* while 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 (Figure 4). Comparisons of the abundance of select genera between management types further highlighted some of these differences (Supplemental Table 9). In at least one year of the study, Bombus and Hylaeus had lower abundance in sustainable sites while Lasioglossum were more abundant in sustainable sites compared to organic sites. Ceratina were more abundant in conventional sites compared to sustainable sites, Andrena were more abundant in organic compared to conventional and sustainable sites, and Augochlorella were more abundant in organic compared to sustainable sites.

Comparison of the local vegetation characteristics and floral resources across vineyard management categories (Supplemental Table 10) revealed that certified sustainable vineyards had the lowest floral richness (estimate = -0.70, $p = 0.02$; Figure 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 (Figure 5B). Furthermore, aggregated floral and vegetation data across months and years showed that several of these variables were significantly correlated with one another ($p<0.05$) (Supplemental Figure 1). Vegetation height, vegetation cover, floral abundance, and floral richness were all positively correlated with one another while the vegetation height ratio (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 (Supplemental Figure 2A) or in the use of alternate row management (Supplemental Figure 2B). Lastly, grouping of sites by their flower species and abundances

showed that the floral community composition differed significantly between vineyard management categories, with organic vineyards being most dissimilar to conventional and certified sustainable vineyards (PERMANOVA $F=1.81$, $R^2=0.14$, $p=0.005$; Figure 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 (*Taraxacum officinale*) while high floral abundance sites were associated with prostrate knotweed (*Polygonum aviculare*).

Discussion

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 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). Of the vineyard management practices investigated in this study, the most consistently impactful variable on bee abundance and diversity was between-row vegetation height, which was used as a proxy for mowing frequency but is also influenced by factors such as the plant community composition, tillage practices, soils and nutrients, and light and water availability (den Hollander et al., 2007). These results are 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 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 that the floral community composition would differ with vegetation height, as taller vegetation would allow more forbs to reach flowering. 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 Shannon diversity index and vegetation cover had a positive relationship with bee abundance during mid-summer months. The positive influence of vegetation cover 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 (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 towards 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 nearly significant in the bee genus richness model and was also significantly associated with the NMDS of sites by bee community composition. Furthermore, floral richness had opposing relationships with bee abundance based on the collection methods used - having a positive relationship with netted bees and a negative relationship with pan trap collected bees. The negative relationship with pan trapped bees may be explained by the taxonomic bias of pan trap collections towards certain bees, such as Halictidae, which may not require as diverse of floral resources (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). Still, these results together suggest that vineyard floral diversity may be more strongly associated with certain bees rather than with overall bee abundance or diversity metrics.

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 in the study sites which were predominantly clover species (*Trifolium* sp.) – with white clover (*Trifolium repens*) being the 4th 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 (Supplemental Table 4), may be unable or unlikely to utilize the clover cover crops. In contrast, Wilson et al., (2017) 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. 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 and thus reflected 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). The 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.

There was a limited impact of organic vineyard management on bee abundance or diversity - with only a slightly higher Shannon species diversity index in organic vineyards when compared to sustainable vineyards. 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 (Campani et al., 2025; OMAFRA, 2021). 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 maybe an important consideration for pollinator conservation in farmlands. Ostandie et al. (2021) also found that insecticide use intensity, both organic or 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 non-organic vineyards. This increased frequency of sprays had a stronger negative effect on arthropod diversity than considerations 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 three 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.

Interestingly, a negative impact of vineyard sustainability certification was seen on bee Shannon species diversity when comparing organic and certified sustainable vineyards. Bee species richness in mid-summer was also negatively impacted by sustainable management, but post-hoc testing of estimated marginal means was not significant. 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 2–219 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 un-mowed 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 et al., 2021).

Overall, 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 harbour 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, n.d.) 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 which were deemed "conventional", may artificially represent sites with higher levels of sustainability due to the growers willing participation 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 in 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 lowest 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 associating 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).

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

References

Abad, F. J., Marín, D., Imbert, B., Virto, I., Garbisu, C. and Santesteban, L. G. (2023). Under-vine cover crops: Impact on physical and biological soil proprieties in an irrigated Mediterranean vineyard. *Scientia Horticulturae*, *311*, 111797.

Agriculture and Agri-Food Canada. (2021). Statistical Overview of the Canadian Fruit Industry 2020. Prepared by Horticulture Section Crops and Horticulture Division Agriculture and Agri-Food Canada. https://agriculture.canada.ca/sites/default/files/documents/2021-08/fruit_report_2020-eng.pdf

Antoine, C. M. and Forrest, J. R. (2021). Nesting habitat of ground-nesting bees: a review. *Ecological Entomology*, *46*(2), 143-159.

Ascher, J. S. and Pickering, J. (2022). Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). http://www.discoverlife.org/mp/20q?guide =Apoidea_species [accessed May 2024].

Audet, T., Romero, N. and Richards, M. (2021). Negative effects of early spring mowing on a bee community: a case study in the Niagara Region. *The Journal of the Entomological Society of Ontario*, *152*, 39-55.

Baldock, K. C., Goddard, M. A., Hicks, D. M., Kunin, W. E., Mitschunas, N., Morse, H., ... and Memmott, J. (2019). A systems approach reveals urban pollinator hotspots and conservation opportunities. *Nature ecology and evolution*, *3*(3), 363-373.

Bartoń, K. (2024). MuMIn: Multi-Model Inference. R package version 1.48.4, https://CRAN.R-project.org/package =MuMIn

Bates, D., Maechler, M., Bolker, B. and Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. Journal of Statistical Software, 67(1), 1-48. doi:10.18637/jss.v067.i01.

Biella, P., Ramazzotti, F., Parolo, G., Galimberti, A., Labra, M., and Brambilla, M. (2025). Vineyard footprint on pollinators is mediated by flower vegetation, organic farming, seasonal and weather factors, a case study from North Italy. *Agriculture, Ecosystems and Environment*, *378*, 109297.

Bivand, R., Pebesma, E. and Gomez-Rubio, V. (2013). Applied spatial data analysis with R, Second edition. Springer, NY

Blaise, C., Mazzia, C., Bischoff, A., Millon, A., Ponel, P. and Blight, O. (2022). Vegetation increases abundances of ground and canopy arthropods in Mediterranean vineyards. *Scientific reports*, *12*(1), 3680.

Bolker, B. M. (2015). Chapter 13: Linear and generalized linear mixed models. *Ecological Statistics:Contemporary Theory and Application*, Fox. G.A., Negrete-Yankelevich, S. and Sosa, V. J. eds. Oxford University Press. pp 309-333.

Bretagnolle, V. and Gaba, S. (2015). Weeds for bees? A review. *Agronomy for Sustainable Development*, *35*(3), 891-909.

Brittain, C., Bommarco, R., Vighi, M., Settele, J. and Potts, S. G. (2010). Organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biological Conservation*, *143*(8), 1860-1867.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. and Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378-400. doi: 10.32614/RJ-2017-066.

Campani, T., Manieri, G., Caliani, I., Di Noi, A. and Casini, S. (2025). Apis mellifera as a Model Species to Evaluate Toxicological Effects of Fungicides Used in Vineyard Agroecosystems. *Journal of Xenobiotics*, *15*(1), 18.

Carvell, C., Meek, W. R., Pywell, R. F. and Nowakowski, M. (2004). The response of foraging bumblebees to successional change in newly created arable field margins. *Biological Conservation*, *118*(3), 327-339.

Daane, K. M., Vincent, C., Isaacs, R. and Ioriatti, C. (2018). Entomological opportunities and challenges for sustainable viticulture in a global market. *Annual review of entomology*, *63*, 193-214.

de Bello, F., Carmona, C. P., Dias, A. T. C., Götzenberger, L., Moretti, M. and Berg, M. P. (2021). Community Metrics. In: *Handbook of Trait-Based Ecology: From Theory to R Tools*. Cambridge University Press:75-104.

Delate, K., Canali, S., Turnbull, R., Tan, R. and Colombo, L. (2017). Participatory organic research in the USA and Italy: Across a continuum of farmer–researcher partnerships. *Renewable Agriculture and Food Systems*, *32*(4), 331-348.

den Hollander, N. G., Bastiaans, L. and Kropff, M. J. (2007). Clover as a cover crop for weed suppression in an intercropping design: I. Characteristics of several clover species. *European Journal of Agronomy*, *26*(2), 92-103.

Dicks, L. V., Baude, M., Roberts, S. P., Phillips, J., Green, M. and Carvell, C. (2015). How much flower-rich habitat is enough for wild pollinators? Answering a key policy question with incomplete knowledge. *Ecological Entomology*, *40*, 22-35.

Dorin, B. and Colla, S. (2024). Observations of wild bees foraging on wine grape (*Vitis vinifera* L.) flowers–first records and future research directions. *The Journal of the Entomological Society of Ontario*, *155*.

Fitch, G., Glaum, P., Simao, M. C., Vaidya, C., Matthijs, J., Iuliano, B. and Perfecto, I. (2019). Changes in adult sex ratio in wild bee communities are linked to urbanization. *Scientific Reports*, *9*(1), 3767.

Fox, J. and Weisberg, S. (2019). An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. <https://www.john-fox.ca/Companion/>.

Gathmann, A. and Tscharntke, T. (2002). Foraging ranges of solitary bees. *Journal of animal ecology*, *71*(5), 757-764.

Goulson, D., Nicholls, E., Botías, C. and Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, *347*(6229), 1255957.

Gräler, B., Pebesma, E. and Heuvelink, G. (2016). Spatio-Temporal Interpolation using gstat. The R Journal 8(1), 204-218.

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589-596.

Griffin, S. R., Bruninga-Socolar, B., Kerr, M. A., Gibbs, J. and Winfree, R. (2017). Wild bee community change over a 26-year chronosequence of restored tallgrass prairie. *Restoration Ecology*, *25*(4), 650-660.

Griffiths-Lee, J., Davenport, B., Foster, B., Nicholls, E. and Goulson, D. (2022a). Sown wildflowers between vines increase beneficial insect abundance and richness in a British vineyard. *Agricultural and Forest Entomology*.

Griffiths-Lee, J., Goulson, D. and Nicholls, E. (2022b). Grape expectations: A survey of British vineyard land management practices from an environmental perspective. *Journal of Agriculture and Sustainability*, *15*.

Guerra, B. and Steenwerth, K. (2012). Influence of floor management technique on grapevine growth, disease pressure, and juice and wine composition: A review. *American Journal of Enology and Viticulture*, *63*(2), 149-164.

Harris, C. and Ratnieks, F. L. (2022). Clover in agriculture: combined benefits for bees, environment, and farmer. *Journal of Insect Conservation*, *26*(3), 339-357.

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. ... and Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, *6*, e4794.

Hartig, F. (2024). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.7, https://CRAN.R-project.org/package =DHARMa.

Hutchinson, L. A., Oliver, T. H., Breeze, T. D., O'Connor, R. S., Potts, S. G., Roberts, S. P. and Garratt, M. P. (2022). Inventorying and monitoring crop pollinating bees: Evaluating the effectiveness of common sampling methods. *Insect Conservation and Diversity*, *15*(3), 299-311.

Jorge, F. C., Nehring, R., Osteen, C., Wechsler, S., Martin, A. and Vialou, A. (2014). Pesticide Use in U.S. Agriculture: 21 Selected Crops, 1960-2008, EIB-124, U.S. Department of Agriculture, Economic Research Service.

Kaczmarek, M., Entling, M. H. and Hoffmann, C. (2024). Wild Bee Conservation in Viticulture: Effects of Semi-Natural Habitats, Organic Management, and Fungicide Reduction. *Ecology and Evolution*, *14*(10), e70378.

Kehinde, T. and Samways, M. J. (2012). Endemic pollinator response to organic vs. conventional farming and landscape context in the Cape Floristic Region biodiversity hotspot. *Agriculture, ecosystems and environment*, *146*(1), 162-167.

Kehinde, T., von Wehrden, H., Samways, M., Klein, A. M. and Brittain, C. (2018). Organic farming promotes bee abundance in vineyards in Italy but not in South Africa. *Journal of insect conservation*, *22*(1), 61-67.

Kline, O. and Joshi, N. K. (2020). Mitigating the effects of habitat loss on solitary bees in agricultural ecosystems. *Agriculture*, *10*(4), 115.

Knight, M. E., Martin, A. P., Bishop, S., Osborne, J. L., Hale, R. J., Sanderson, R. A. and Goulson, D. (2005). An interspecific comparison of foraging range and nest density of four bumblebee (Bombus) species. *Molecular Ecology*, *14*(6), 1811-1820.

Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A. J., Settele, J., Kremen, C. and Dicks, L. V. (2017). Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecology Letters*, *20*(5), 673-689.

Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guernion, M., Burel, F. ... and Winter, S. (2018). Tillage intensity or landscape features: What matters most for wild bee diversity in vineyards?. *Agriculture, Ecosystems and Environment*, *266*, 142-152.

Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guzmán, G., Goméz, J. A. ... and Winter, S. (2019). Response of wild bee diversity, abundance, and functional traits to vineyard inter-row management intensity and landscape diversity across Europe. *Ecology and Evolution*, *9*(7), 4103-4115.

Kratschmer, S., Pachinger, B., Gaigher, R., Pryke, J. S., van Schalkwyk, J., Samways, M. J. ... and Winter, S. (2021). Enhancing flowering plant functional richness improves wild bee diversity in vineyard inter-rows in different floral kingdoms. *Ecology and Evolution*, *11*(12), 7927-7945.

Kremen, C. and Miles, A. (2012). Ecosystem services in biologically diversified versus conventional farming systems: benefits, externalities, and trade-offs. *Ecology and society*, *17*(4).

Kuznetsova, A., Brockhoff, P. B. and Christensen, R. H. B. (2017). "lmerTest Package: Tests in Linear Mixed Effects Models." Journal of Statistical Software, *82*(13), 1-26. doi:10.18637/jss.v082.i13.

Lanz, B., Dietz, S. and Swanson, T. (2018). The expansion of modern agriculture and global biodiversity decline: an integrated assessment. *Ecological Economics*, *144*, 260-277.

Lenth, R. (2024). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.10.6, <https://CRAN.R-project.org/package =emmeans>.

Lüdecke, D., Ben-Shachar, M. S., Patil, I., Waggoner, P. and Makowski, D. (2021). performance: An R package for assessment, comparison and testing of statistical models. *Journal of Open Source Software*, *6*(60). https://easystats.github.io/performance/

MacKell, S., Elsayed, H. and Colla, S. (2023). Assessing the impacts of urban beehives on wild bees using individual, community, and population-level metrics. *Urban Ecosystems*, *26*(5), 1209-1223.

Mallinger, R. E., Gaines-Day, H. R. and Gratton, C. (2017). Do managed bees have negative effects on wild bees?: A systematic review of the literature. *PloS one*, *12*(12), e0189268.

McCravy, K. W. (2018). A review of sampling and monitoring methods for beneficial arthropods in agroecosystems. *Insects*, *9*(4), 170.

Moscovici, D. and Reed, A. (2018). Comparing wine sustainability certifications around the world: History, status and opportunity. *Journal of Wine Research*, *29*(1), 1-25.

Nelson, W., Evans, L., Donovan, B. and Howlett, B. (2023). Lasioglossum bees–the forgotten pollinators. *Journal of Apicultural Research*, *62*(1), 39-46.

Newcomb, L. (1989). Newcomb's Wildflower Guide. Little, Brown and Company, Boston, Massachusetts, United States.

Nicholls, C. I. and Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable development*, *33*(2), 257-274.

OIV (International Organisation of Vine and Wine Intergovernmental Organisation). (2019). "2019 Statistical Report on World Vitiviniculture". Retrieved from: https://www.oiv.int/public/medias/6782/oiv-2019-statistical-report-on-world-vitiviniculture.pdf

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P. … and Weedon, J. (2024). Vegan: Community Ecology Package. R package version 2.6-8, <https://CRAN.R-project.org/package =vegan>.

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). (2009). "Weed Gallery". Ontario Crop IPM. http://www.omafra.gov.on.ca/IPM/english/weeds-herbicides/gallery/index.html

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). (2021). Publication 360C Crop Protection Guide for Grapes 2021. https://www.publications.gov.on.ca/store/20170501121/Free_Download_Files/300691.pdf

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). (2023a). Weed identification guide for Ontario crops. Retrieved from: https://www.ontario.ca/document/weed-identification-guide-ontario-crops

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). (2023b). Cover Crops. Retrieved from: https://omafra.gov.on.ca/english/crops/facts/cover_crops01/covercrops.htm

Onuferko, T. M., Kutby, R. and Richards, M. H. (2015). A list of bee species (Hymenoptera: Apoidea) recorded from three municipalities in the Niagara region of Ontario, including a new record of Lasioglossum furunculum Gibbs (Halictidae) in Canada. *The Journal of the Entomological Society of Ontario*, *146*.

Ostandie, N., Giffard, B., Bonnard, O., Joubard, B., Richart-Cervera, S., Thiéry, D., and Rusch, A. (2021). Multi-community effects of organic and conventional farming practices in vineyards. *Scientific reports*, *11*(1), 11979.

Packer, L., Genaro, J. A. and Sheffield, C. S. (2007). The bee genera of eastern Canada. *Canadian Journal of Arthropod Identification*, *3*(3), 1-32.

Popescu, D., Comsa, M., Hoble, A., Bunea, C. I., Gaman, T., Tamas, A. S. ... and Winter, S. (2019). Biodiversity and ecosystem service in Transylvania–new approach to a sustainable vineyards. *Journal of Environmental Protection and Ecology*, *20*(4), 1870-1879.

Portman, Z. M., Bruninga-Socolar, B., & Cariveau, D. P. (2020). The state of bee monitoring in the United States: A call to refocus away from bowl traps and towards more effective methods. *Annals of the Entomological Society of America*, *113*(5), 337-342.

Raine, N. E. and Rundlöf, M. (2024). Pesticide exposure and effects on non-Apis bees. *Annual review of entomology*, *69*(1), 551-576.

Requier, F., and Leonhardt, S. D. (2020). Beyond flowers: including non-floral resources in bee conservation schemes. *Journal of Insect Conservation*, *24*(1), 5-16.

Rocher, L., Melloul, E., Blight, O. and Bischoff, A. (2024). Effects of sown and spontaneous inter-row vegetation on weeds and beneficial arthropods in vineyards. *Basic and Applied Ecology*, *81*, 17-24.

Rosenheim, J. A., Cass, B. N., Kahl, H. and Steinmann, K. P. (2020). Variation in pesticide use across crops in California agriculture: Economic and ecological drivers. *Science of The Total Environment*, *733*, 138683.

Russo, L., Park, M., Gibbs, J. and Danforth, B. (2015). The challenge of accurately documenting bee species richness in agroecosystems: bee diversity in eastern apple orchards. *Ecology and Evolution*, *5*(17), 3531-3540.

Schindler, M., Diestelhorst, O., Haertel, S., Saure, C., Schanowski, A. and Schwenninger, H. R. (2013). Monitoring agricultural ecosystems by using wild bees as environmental indicators. *BioRisk*, *8*(1), 53-71.

Seufert, V., Ramankutty, N., & Mayerhofer, T. (2017). What is this thing called organic?–How organic farming is codified in regulations. *Food Policy*, *68*, 10-20.

Sharifi, M., Salimi, K., Rosa, D. and Hart, M. (2024). Screening Cover Crops for Utilization in Irrigated Vineyards: A Greenhouse Study on Species' Nitrogen Uptake and Carbon Sequestration Potential. *Plants*, *13*(14), 1959.

Socolar, J. B., Gilroy, J. J., Kunin, W. E. and Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation?. *Trends in ecology & evolution*, *31*(1), 67-80.

SWO (Sustainable Winegrowing Ontario). (n.d.). "Sustainable Winegrowing Ontario certified" Retrieved from: https://sustainablewinegrowingontario.ca

Turley, N. E., Biddinger, D. J., Joshi, N. K. and López-Uribe, M. M. (2022). Six years of wild bee monitoring shows changes in biodiversity within and across years and declines in abundance. *Ecology and Evolution*, *12*(8), e9190.

Vanbergen, A. J. and The Insect Pollinators Initiative. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and the Environment*, *11*(5), 251–259.

Venables, W. N. and Ripley, B. D. (2002). Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

VQA (Vintners Quality Alliance) (n.d.). The Niagara Peninsula Appellation Overview. https://www.vqaontario.ca/Appellations/Niagara-Peninsula/

Wickham, H. (2016). ggplot2: Elegant Graphics for Data Analysis. Springer-Verlag New York. ISBN 978-3-319-24277-4.

Wilson, H., Wong, J. S., Thorp, R. W., Miles, A. F., Daane, K. M. and Altieri, M. A. (2018). Summer flowering cover crops support wild bees in vineyards. *Environmental Entomology*, *47*(1), 63-69.

Zamorano, J., Bartomeus, I., Grez, A. A. and Garibaldi, L. A. (2020). Field margin floral enhancements increase pollinator diversity at the field edge but show no consistent spillover into the crop field: a meta-analysis. *Insect Conservation and Diversity*, *13*(6), 519-531.

Zattara, E. E., & Aizen, M. A. (2021). Worldwide occurrence records suggest a global decline in bee species richness. *One Earth*, *4*(1), 114-123.

Zielonka, N. B., Shutt, J. D., Butler, S. J. and Dicks, L. V. (2024). Management practices, and not surrounding habitats, drive bird and arthropod biodiversity within vineyards. *Agriculture, Ecosystems and Environment*, *367*, 108982.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. and Dorn, S. (2010). Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, *143*(3), 669-676.

Zuur, A. F., Ieno, E. N. and Smith, G. M. (2007). *Analysing ecological data* (Vol. 680). New York: Springer.

Zuur, A. F., Ieno, E. N. and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution*, *1*(1), 3-14.

Zuur, A. F. and Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*(6), 636-645.

Tables

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

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

*Government of Canada (2024). Station Results - Historical Data. https://climate.weather.gc.ca/historical_data/search_historic_data_e.html

Table 2: Generalized Linear Mixed Model (GLMM) summaries for each bee response variable with 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 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).

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				

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. 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).

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				

Figures

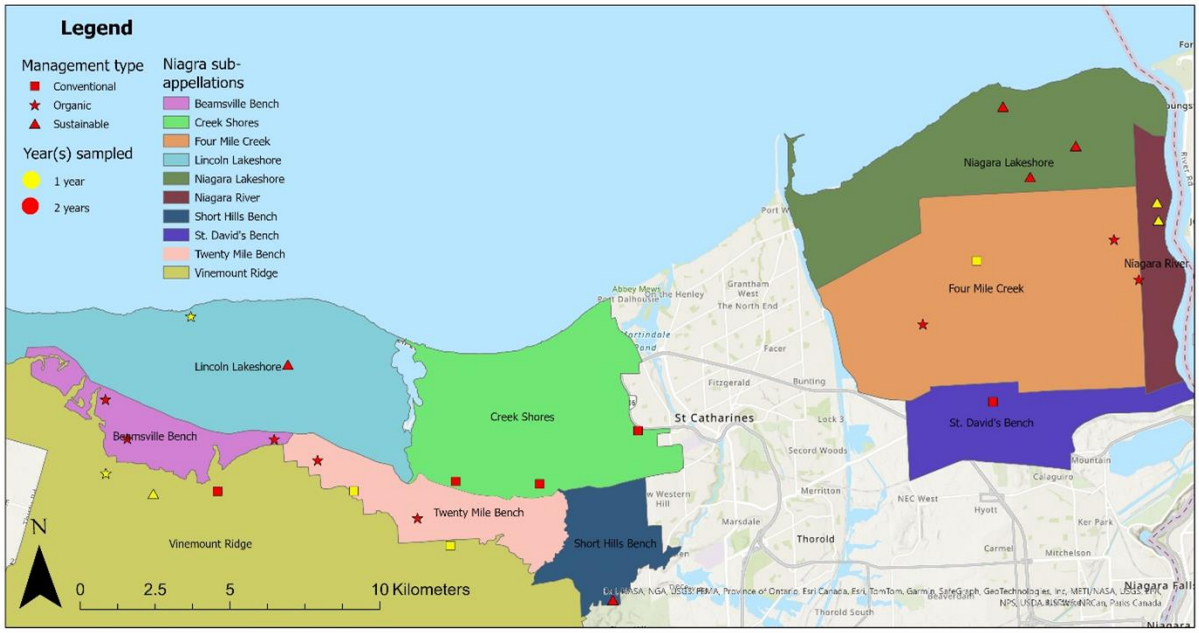

Figure 1: Vineyard sites for bee sampling across the Niagara Region, ON created in ArcMap Pro 3.0.2 (Esri, Redlands, CA) with the World Topographic and World Hillshade basemaps. Sites were overlaid on the VQA map of sub-appellations for wine growing (Brock University Maps, Data & GIS. Niagara Sub-Appellations.2016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

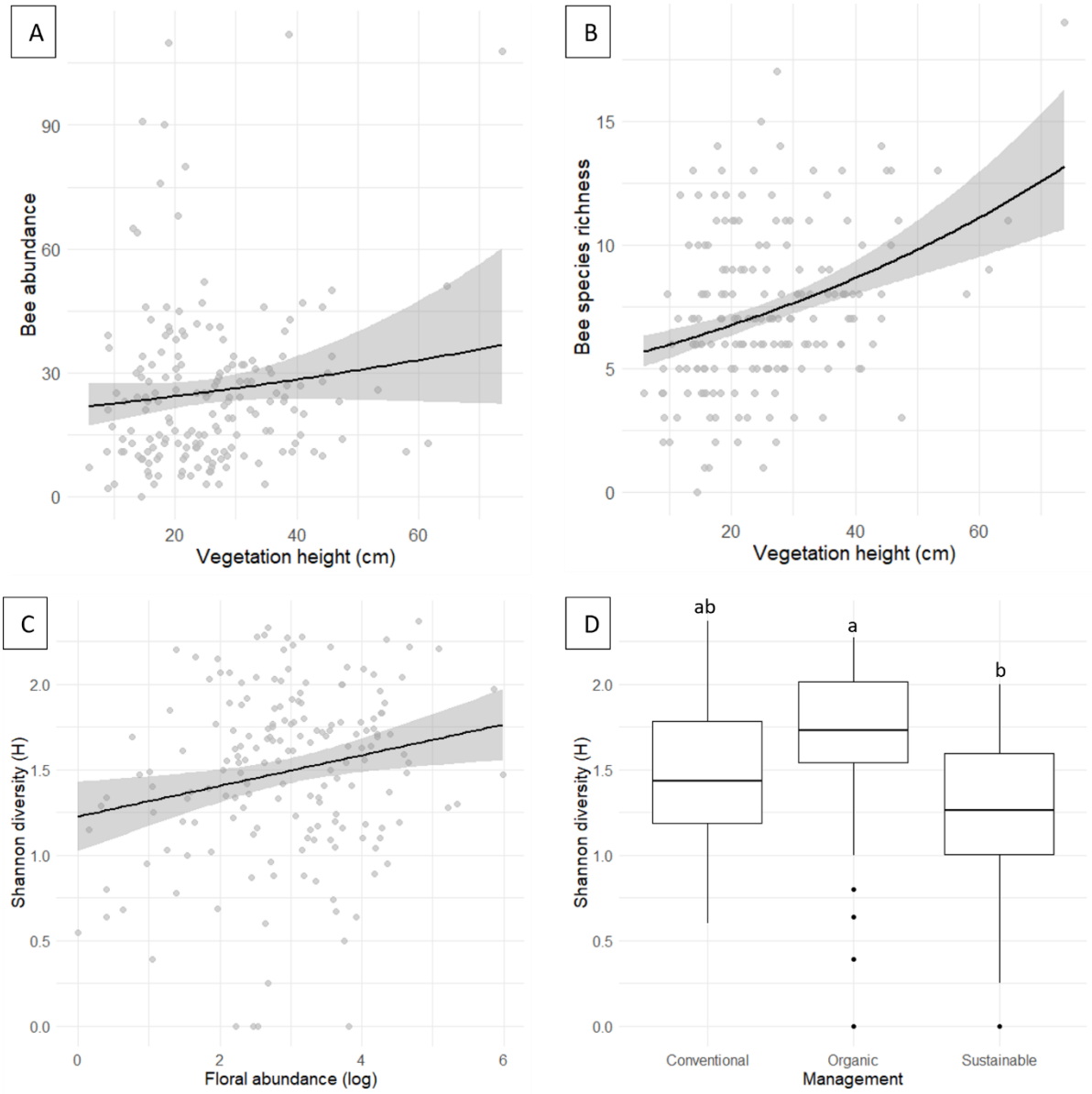

Figure 2: Significant ($p<0.05$) vineyard management predictors from the Generalized Linear Mixed Models (GLMM) of bee response variables: bee abundance (A), bee species richness (B), and Shannon diversity index (C, D). Final GLMMs were averaged from the top models using delta AICc <2. Graphs show the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

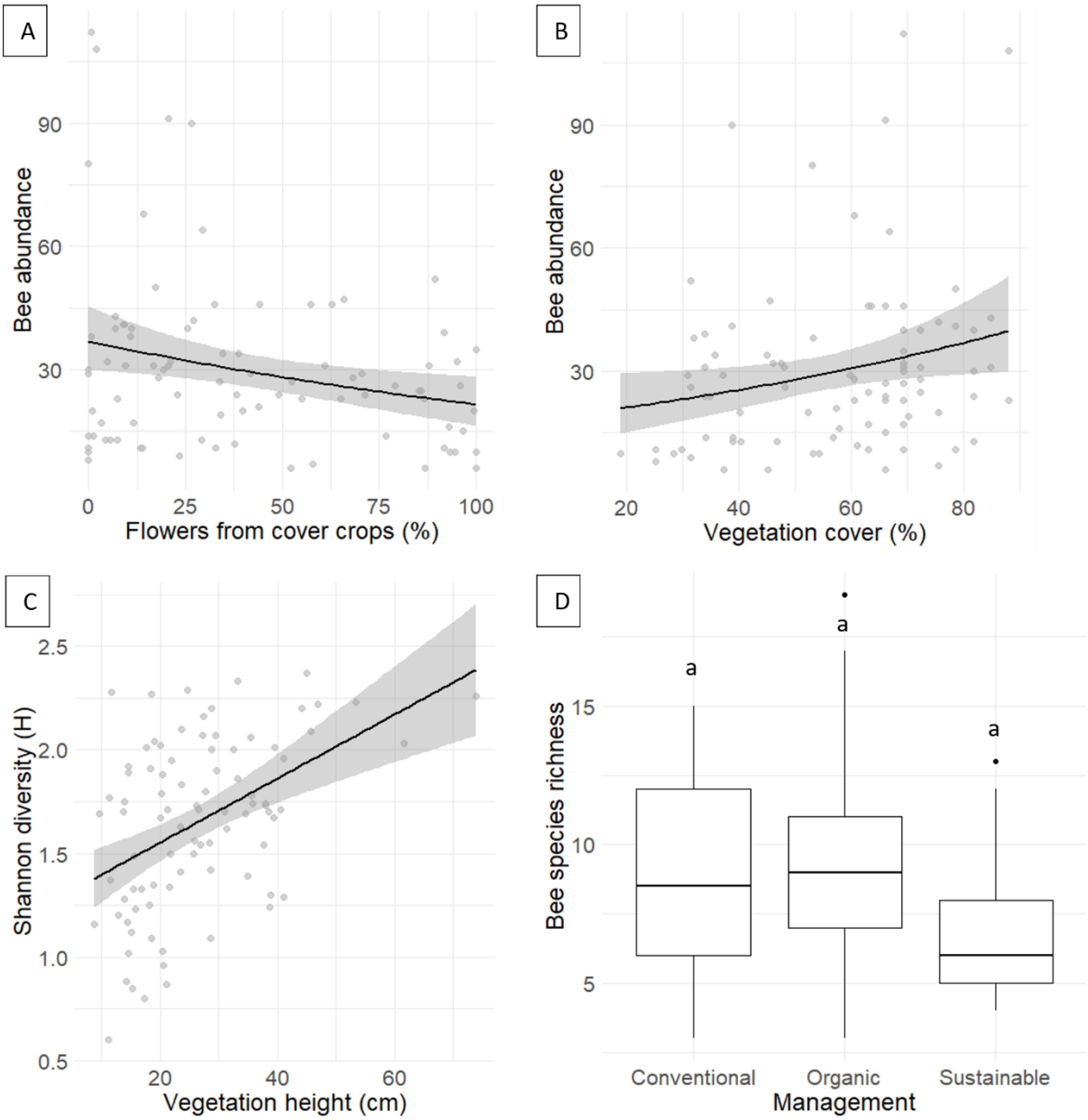

Figure 3: Newly significant ($p<0.05$) vineyard management predictors from the Generalized Linear Mixed Models (GLMM) for bee response variables from mid-summer months only (June and July) for bee abundance (A, B), Shannon Diversity of bee species (C) and bee species richness (D). Final GLMMs were averaged 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 ($p<0.05$).

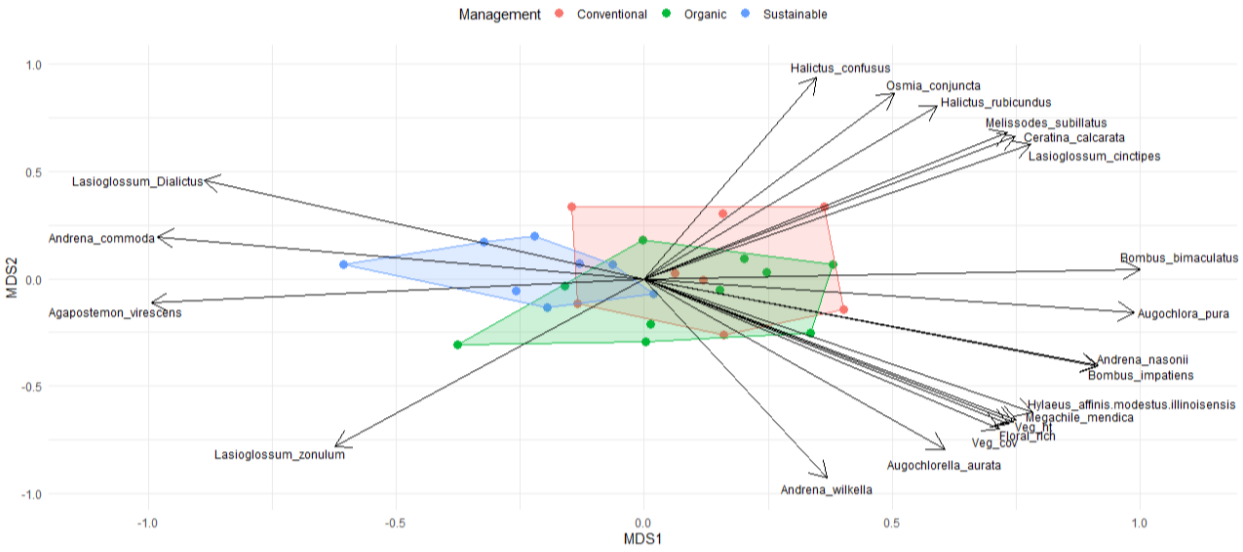

Figure 4: Non-metric multidimensional scaling (NMDS) of bee community composition data aggregated per site across months and years (n=26) using Bray-Curtis dissimiliarity of Hellinger-transformed abundance data (stress=0.20). Convex hulls represent different vineyard management categories (Permutational 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).

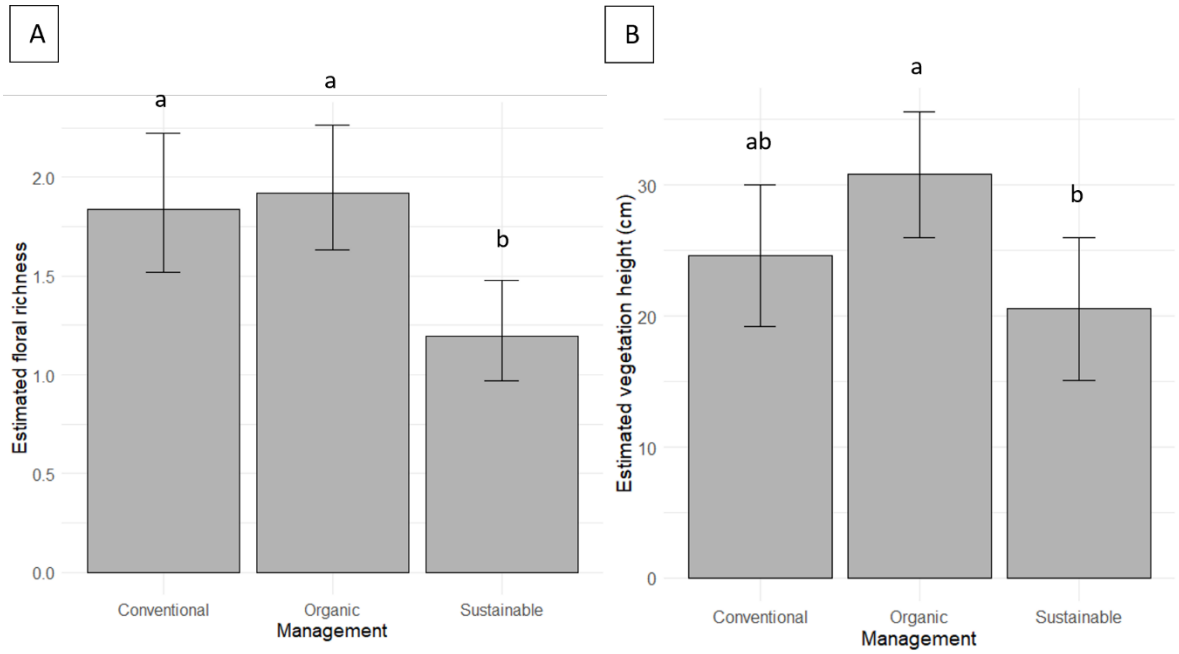

Figure 5: Comparison of floral richness (A) and vegetation height (B) in vineyards under different management types. Graphs show the estimated marginal means from (General) Linear Mixed Models of each response variable with month, year, and vineyard management as fixed effects and site as a random effect.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

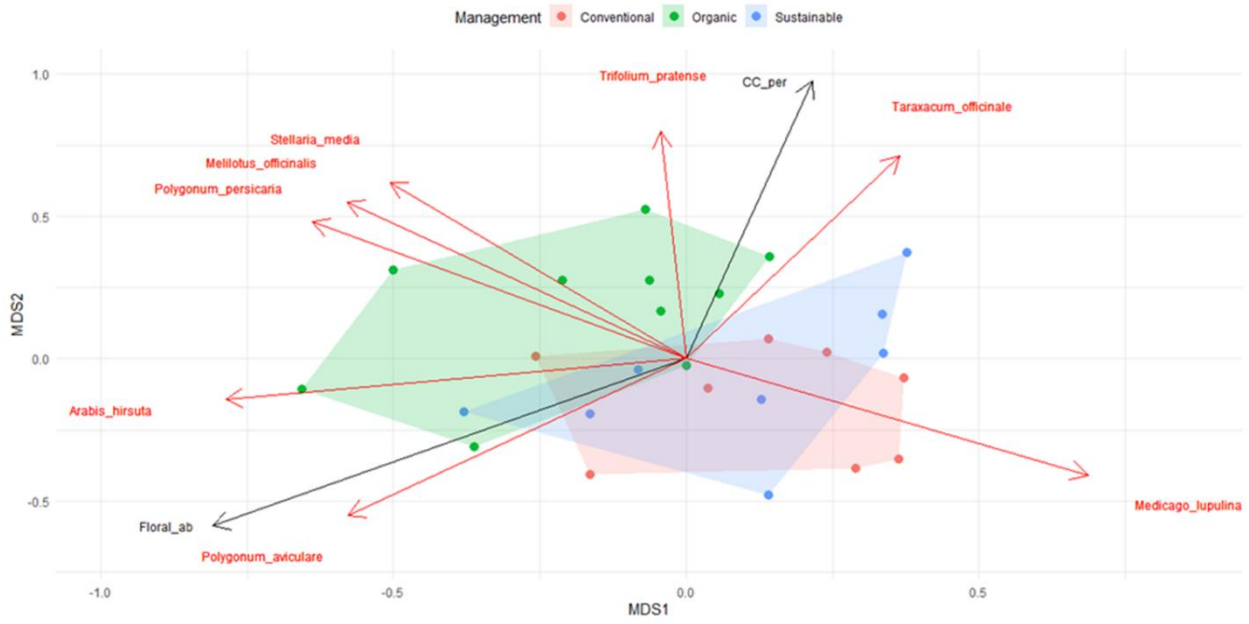

Figure 6: Non-metric multidimensional scaling (NMDS) of flower community composition data aggregated per site (n=26) using Bray-Curtis dissimiliarity of Hellinger-transformed abundance data (stress=0.25). Convex hulls represent vineyard management categories (PERMANOVA $F=1.81$, $R^2=0.14$, $p=0.005$). 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*).

Chapter 3: Multi-scale drivers of wild bee communities in vineyard agroecosystems[4]

Abstract

Conservation measures to protect and conserve pollinators, such as wild bees, in agricultural lands require an understanding of the scale at which interventions are most impactful. This includes determining whether bee communities are more influenced by local on-farm resources or surrounding landscape factors as most bees are central place foragers. This study assessed how wild bees were influenced by vineyard management, local floral and vegetation resources, surrounding land-uses and surrounding soils in 26 vineyards across the Niagara Region in Canada. Bees, along with vineyard flowers and vegetation, were sampled over two growing seasons from vineyards under differing management regimes. The soil texture, slope, and landscape composition were extracted from publicly available data within a 300m radius around each vineyard site. The results demonstrate that both local and landscape factors largely influence vineyard bee communities. The height of vegetation between vine rows positively influenced bee abundance and diversity, while certified sustainable vineyard management showed slightly negative associations with bee diversity compared to organic and conventional sites. The amount of semi-natural land around sites had a positive impact on bee abundance and diversity and larger soil textures positively influenced bee abundance, particularly for below-ground nesting bees. These results indicate that both farm management practices and broader land-use planning tools are crucial for bee conservation in agricultural landscapes, with soil factors being an important and often overlooked consideration, particularly in relation to nest site availability.

Introduction

Wild bees play an important role in social and ecological systems as pollinators of a wide range of wild and cultivated plants (Matias et al., 2017; Klein et al., 2018). However, studies documenting

[4] Briann Dorin was responsible for research design and conceptualization, data collection, analysis, and writing. Sheila Colla provided supervision and feedback throughout the project.

declines in wild bees identified multiple threats including land-use intensification, climate change, and the spread of non-native species and diseases (Vanbergen and The Insect Pollinators Initiative, 2013; Zattara and Aizen, 2021). To effectively protect and conserve wild bees, research is needed to identify the land-management practices that support diverse and abundant bee communities (Dicks et al., 2021), especially in agricultural landscapes where threats to bees such as pesticide exposure and habitat loss may be intensified.

Examination of land management practices should include the scale at which actions are most impactful such as local (e.g., farm management) or landscape (e.g., land use planning) level interventions (Patricio-Roberto & Campos, 2014). Several farm management practises have been shown to influence wild bees across various crop systems. These include planting floral resources within and around farmlands - as central place foragers, most bees require resources such as pollen and nectar within the foraging range from their nest sites (Antoine and Forrest, 2021; Nicholls and Altieri, 2013; Zamorano et al., 2020). Other studied factors include organic farming, reduced agrochemical inputs, and farm-level diversification such as intercropping (Kovács-Hostyánszki et al., 2017; Walker et al., 2025). Features important at the landscape-scale include the proximity to and amount of surrounding natural and semi-natural lands (Carré et al., 2009; Le Féon et al., 2010), proportion of urban land cover (Carré et al., 2009), percentage and types of agricultural lands (Carré et al., 2009; Martins et al., 2018), and structural considerations such as distance, connectivity, and habitat patch size (Rahimi et al., 2022). Landscape-level research may also include determination of nest site availability for different bee taxa such as bare soil, sloping ground, and nesting cavities (Potts et al., 2005) as bee species responses may differ based on functional traits (Basu et al., 2016; Carré et al., 2009; Williams et al., 2010). Landscape-factors may also serve to buffer the impacts of local-factors such as intensive farm management and pesticide exposure (Kennedy et al., 2013; Park et al., 2015). Further research is needed to understand how wild bees respond to local and landscape-level factors across different crop types, as these relationships are likely context-dependent (Kratschmer et al., 2019; Kehinde et al., 2018).

Grapes are one of the largest cultivated fruit crops in terms of global acreage, grown on all inhabited continents in environments that range from temperate to tropical and desert-like (Daane et al., 2018; Marcelino et al., 2024). Vineyards are considered a highly intensive agricultural system though management practices can vary substantially across regions and grape growers ranging from high input to organic, biodynamic, and sustainable management (Daane et al., 2018; Popescu et al., 2019). While wine grapes (*Vitis vinifera* L.) do not require animal pollination, vineyards can still provide habitat for wild bees and may also exist in agricultural landscapes with other pollinator-dependent crops such as orchard fruits (Dorin and Colla, 2024). Both local and landscape factors have been shown to influence wild bee communities in vineyards, though their relative importance varies across studies. For example, Popescu et al., (2019) found that the local management practice of between-row tillage influenced vineyard bees more than the surrounding landscape diversity while Wersebeckmann et al., (2023) found that nest site availability in the surrounding landscape, such as semi-natural habitats and soil texture, had greater impacts on bees than local resources. Other studies have shown that local management practices, such as enhancing between-row vegetation and flower cover, can positively impact bee abundance and diversity (Kratschmer et al., 2018; Wilson et al., 2018; Popescu et al., 2019) while others have shown that surrounding landscapes, particularly the amount of and proximity to semi-natural habitats, positively influences bee abundance and diversity (Kratschmer et al., 2018; Uzman et al., 2020). However, landscape effects are sometimes secondary to local management and can interact with local conditions to impact bees - such as a higher landscape diversity compensating for the negative effect of low floral resources in vineyards for certain bees (e.g., abundance of eusocial bees) (Kratschmer et al., 2019).

The variability in results across studies highlights the importance of examining these relationships across diverse geographies and contexts (Kehinde et al., 2018). Few studies have been conducted in cool-climate grape growing regions and none in Canada, despite grapes being the third largest fruit crop by total acreage (AAFC, 2021). Within Canada, the Niagara Region in Ontario is the largest grape producing region (VQA, n.d). This region lies within the Carolinian Zone, a relatively highly biodiverse area that consists of both woodland and tall grass prairie ecosystems (Richards et al., 2011) supporting some of the

highest bee diversity in Canada (Sheffield et al., 2014). The region also has high levels of urbanization and intensive agriculture systems (Niagara Region, 2024) with predominant crop types of fruits, tree nuts, oilseed, and grains (Niagara Region, n.d.).

This study examines how vineyard management, landscape, and soil factors impact the bee communities in Niagara, ON vineyards to inform bee conservation efforts. Specifically, the influence of between-row vegetation and floral resources, vineyard management certifications, surrounding land uses, and soil types on wild bee abundance and diversity. The prediction was that vineyards with greater vegetation and floral cover between vine rows would support higher abundances and diversity of bees by providing enhanced forage resources. It was also predicted that organic and certified sustainable vineyards (SWO, n.d.) would have more abundant and diverse bee communities than conventional vineyards due to reductions in pesticide use and increased uptake of practises such as cover cropping that can provide floral resources. On the landscape scale, it was predicted that vineyards surrounded with a greater amount of semi-natural lands would provide enhanced nesting and foraging habitat for bees and would support a higher diversity and abundance of wild bees. It was also predicted that the soils in the surrounding landscape would affect bees by impacting both the surrounding vegetation as well as soil nest site availability. Lastly, it was predicted that bees would respond differentially to local and landscape variables due to differences in functional traits such as foraging ranges, diet, sociality, and nest site requirements.

Methods

Sites, bees and local vegetation sampling

Commercial wine grape blocks of any variety were selected across the Niagara Region, Ontario. Sites were managed conventionally, organically, or certified sustainably per the Sustainable Winegrowing Ontario (SWO) certification program (SWO, n.d.)[5]. This program certifies vineyards that use practices

[5] Site visits, grower-provided maps, and satellite imagery were used to confirm that selected sites encompassed a range of surrounding landscape compositions and soil types across the Niagara Region. At sites adjacent to semi-

that benefit the environment like cover cropping and integrated pest management (IPM). However, some sites were both organic and SWO certified - in which case, these sites were categorized as organic for this study to reflect stricter standards (Seufert et al., 2017). In 2021, 20 sites were sampled: ten organic, five conventional and five certified sustainable. In 2022, 24 sites were sampled: eight organic, eight conventional, and eight certified sustainable (Figure 1). Vineyard blocks were selected in collaboration with grape growers to cover a variety of landscape compositions, soils, and to keep a minimum distance of 600 m between sites to sample independent bee communities (Zurbuchen et al., 2010). At each site, a 400 m^2 area was marked out in the centre of the block spanning three neighbouring vine rows, or two between-row spaces, adjusting the length to the different row spacing (i.e. widths) across sites. Data were collected monthly May through August, with each site sampled four times over a growing season. Site sampling dates per month were based on grower availability and weather forecasts.

Bees were sampled using both pan traps and aerial netting on precipitation-free days. Netting was performed for 30 minutes in the morning and afternoon, for 15 minutes per neighbouring between-row space. Twenty-four 3.25 oz (96 mL) plastic pan traps (New Horizons bee bowls, Maryland) were placed every ~3m under the central vine row alternating colours of yellow, blue, and white filled with soapy water with unscented dish soap. If the under-vine area consisted of tall vegetation, then traps were raised to the height of the vegetation using dark green commercial garden stakes. Pan traps were placed prior to 9:00 am and collected after 5:00 pm while all netting occurred between these hours.

Vineyard floral and vegetation characteristics were sampled on the same day as bees using a 1 m^2 quadrat placed semi-randomly on the ground eight times along the same sampling area, with four quadrats per row. Half the quadrats were placed in the centre of the between-row space while the other half were placed towards the vine rows to capture all available floral resources. Flower species and abundances were documented for all open flowers inside the quadrat (excluding grasses, rushes and sedges) using the Newcomb's Wildflower Guide (Newcomb, 1989) and the Ontario Ministry of Agriculture, Food, and

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natural habitats, research blocks were selected at varying distances from these habitats to capture differences in potential bee foraging ranges.

Rural Affairs (OMAFRA) resources (OMAFRA, 2009; 2023). Vegetation cover (%) was visually estimated using a modified DAFOR scale of Dominant >76%, Abundant 51–75%, Frequent 26–50%, Occasional 11–25%, and Rare <10% (Kratschmer et al., 2018). Vegetation height (cm) was measured by dividing each quadrat into four equal sections and measuring the tallest piece of vegetation in each section. The mean vegetation height, floral abundance, floral richness, and vegetation cover were calculated per site and sampling round (month), the latter using the median value of the DAFOR scale.

Bee identification and functional traits

Bees were identified using a dissecting microscope and several identification guides (Packer et al., 2007, see Appendix D for the list of published guides used) and Discover Life (Ascher and Pickering, 2022). Due to difficulty in accurate species identifications, the following groups of bees were not identified to the species-level: *Lasioglossum* sub-genus *Dialictus*, *Hylaeus affinis/modesutus/illinoiensis*, *Sphecodes atlantis/cressonii*, and one morphospecies of *Sphecodes* sp. Unless otherwise noted, all species-level results and discussion incorporate these subgenus and species-group identifications. Bee identifications were verified for a subset of specimens by other graduate students in York University's Centre for Bee Ecology, Evolution and Conservation. Total bee abundance, species and genus richness, and species- and genus-level Shannon diversity indices were calculated from all bees collected per site per year while the mean of floral and vegetation data were calculated across months.

Bee functional traits

Functional traits were determined for collected bees, taken primarily from existing literature (see Appendix D for the resources used to determine functional traits). Traits included: diet, sociality, native versus exotic, and nesting habitat type (Antoine and Forrest, 2021). Nesting habitat requirements for cuckoo bees were taken from the typical nesting behaviour of their common host species (Antoine and Forrest, 2021). Majority (98%) of bees collected were polylectic and thus, diet was removed from further analyses. Body size, which is associated with foraging ranges (Greenleaf et al., 2007), was taken primarily from MacKell et al., (2023) using tegular-distance or measured following their methods. The

number of rare bees per site was also calculated, defined as species that represented less than 1% of all collected bees across sites and years. The number of males was also calculated as sex ratios have been shown to be impacted by land uses (Fitch et al., 2019). To estimate functional trait information for bees not identified to species level, the average or most common functional trait was taken from the species group (de Bello et al., 2021). For *Lasioglossum* (*Dialictus*) bees and *Sphecodes* sp., the average or most common functional traits were taken across the list of species found in the Niagara Region per Onuferko et al., (2015).

Landscape composition and soils

The surrounding landscape composition around each vineyard site was extracted from the Agriculture and Agri-Food Canada (AAFC) Annual Crop Inventory geo-spatial data at a spatial resolution of 30m (AAFC, 2023a; 2023b). The central GPS coordinate for each site was taken from Google Maps Satellite Imagery (Imagery@2021,2022 CNES/Airbus, Maxar Technologies, U.S. Geological Survey, USDA/FPAC/GEO, Map data @2021, 2022). Site coordinates were then mapped in ArcGIS Pro 3.0.2 (ESRI 2022, Redlands CA; Environmental Systems Research Institute) using the NAD1983 UTM 17N projected coordinate system. A circular buffer around each site centre with a radius of 300m was created to account for the expected majority of realized bee foraging ranges (Zurbuchen et al., 2010; Kendall et al., 2022). The "Tabulate Area" tool was used to calculate the total area of each land-type from the crop inventory data. The total area associated with different landscape categories per site was then summed using various levels of refinement, with the broadest categories being water, semi-natural land, agricultural land, and impervious surfaces (Supplemental Table 1). These data were then converted into the percentage of the total landscape per site.

Soil data were taken from the OMAFRA Soil Survey Complex generalized soil map (OMAFRA, 2015). Variables extracted were soil texture and slope due to their potential importance for ground-nesting bees (Antoine and Forrest, 2021). The OMAFRA soil survey data were acquired from various sources over a range of scales with a minimum accuracy of 200 m across the Niagara Region (OMAFRA, 2015;

2019). Like landscape composition data, the soil data were also extracted with a 300m radius circular buffer around each site. The soil map data (polygon data) were first converted to a raster file for each target soil attribute (texture and slope) using the Polygon to Raster tool by maximum area, using the first portion of the soil complex, where applicable. For soil texture (A horizon), the total area of each class (ex. silt loam, clay loam) was calculated using the Tabulate Area tool. Organic content was manually excluded, as it was not recorded for most sites. Soils were then grouped by particle size into coarse, medium, and fine categories which were quantitatively ranked (Kingston and Presant, 1989; FAO, n.d.). The proportion of each category by area was calculated, with manual adjustments for any unmapped or undifferentiated cells. An overall texture score was then calculated by multiplying the rank of each category by its proportion and summing the results - where higher values indicate coarser soil texture. For slope, data were extracted from the mapped median slopes (%) which were taken from classes ranging from level (0.2%) to very steep slopes (125%). Missing data were first removed from the raster file using the Set Null tool and then the Zonal Statistics tool was used to calculate the mean slope within site buffers.

Statistical analyses

All analyses were performed in R v.4.4.2 (R Core Team, 2014) without honey bees (*Apis mellifera* L.) as surrounding hive information was not known and the goal was to focus on wild bee conservation. To determine which local, landscape, and soil variables most impacted bee abundance, species and genus richness, and species- and genus-level Shannon diversity Index - Generalized Linear Models (GLM) were run selecting the best model(s) per the Akaike Information Criterion (AIC) using the packages "MASS" (Venables and Ripley, 2002), "performance" (Lüdecke et al., 2021), "glmmTMB" (Brooks et al., 2017), and "MuMIn" (Bartoń, 2024) following Zuur and Ieno (2016). Because some sites were only sampled for one year (8 sites), and bee communities can vary substantially across years (Turley et al., 2022), models were run for each year separately. Landscape and soil data per site were kept constant across years as they were not expected to change significantly between years, whereas bee data

were summed annually and local vegetation and floral data were averaged across months per year (Kratschmer et al., 2019). A Spearman's correlation matrix was run using "corrplot" (Wei and Simko, 2024) and "Hmisc" (Harrell, 2025) on the local floral and vegetation variables, averaged across years for sites sampled in multiple years, to determine the least correlated variables to include in model selection (Supplemental Figure 1). For landscape data, similarly, a Spearman's correlation matrix was run with all categories across levels of refinement to select the least correlated variables (Supplemental Figure 2). A linear model was then run on the selected variables to test for multicollinearity with the package "car" (Fox and Weisberg, 2019) and variables with the highest VIF were removed until all variables had a VIF under 3 (Zuur et al., 2010). The final global model consisted of the landscape variables of semi-natural lands (primarily broadleaf forests, also includes shrubs and wetlands), vineyards (accounts for block size as well as neighbouring vineyards), annual crops (primarily soybean, corn, and wheat), and impervious surfaces (primarily built-up land such as buildings and roads, includes greenhouses, rocks/rubble, and mines). Soil variables of slope and soil texture were also included. The local variables were the between-row vegetation height and floral abundance as well as the vineyard management type (sustainable, conventional, or organic). Supplemental Table 2 discusses the hypotheses and predictions associated with each fixed effect included in the global model. Kruskal-Wallis tests were run to determine if the local, landscape or soil variables differed significantly between vineyard management types. Before running models, all numeric explanatory variables were z-score standardized (Harrison et al., 2018).

Models were fitted with Gaussian family and an identity link for Shannon diversity index, Poisson family or Conway-Maxell-Poisson (CMP) with a log link for bee richness, and Negative Binomial with a log link for bee abundance. Furthermore, due to *Lasioglossum* (*Dialictus*) bees being highly abundant (38% of all bees) and not identified to species level, the abundance of this group of bees was also modelled using a Negative Binomial 2 family with log link. Global models were first assessed for model fit and diagnostics using the package "DHARMa" (Hartig, 2024). Model selection was based on the second order Akaike Information Criterion (AICc) using the function *dredge* from the MuMIn package which ranks all possible models. Model averaging was then performed when multiple top models

had delta AICc<2 using the "conditional model" which calculates the average predictor coefficients only from models where that predictor is included (Kratschmer et al., 2018). To get final model R^2 values for averaged models, a GLM was run with all fixed effects included in the final averaged model, significant or not. Due to an inability to calculate an R^2 for CMP models, a comparable R^2 value was calculated from a Poisson-log model fit with the same fixed effects. When vineyard management was significant in final averaged models, the "emmeans" package (Lenth, 2024) was used to obtain back-transformed estimated marginal means (EMMs) and to perform Tukey's post-hoc tests.

To see how bee community composition differed between sites, the abundance of each species per site was Hellinger-transformed for each year (Zuur et al., 2007). Non-metric multidimensional scaling (NMDS) was performed for each year using the "vegan" package (Oksanen et al. 2024) with Bray-Curtis distances and 2-dimensional solutions - applying 95% confidence ellipses around vineyard management categories. A permutational multivariate analysis of variance (PERMANOVA) was performed to see if bee communities differed significantly between management categories. Bee functional traits were calculated per site and year using community weighted means (CWM). The *envfit* function was used to test correlations between bee functional traits as well as all local, soil, and landscape variables with the NMDS ordination using 999 random permutations (Kratschmer et al., 2018). Significant ($p<0.05$) variables were then added to the NMDS plot for visualization. This analysis was performed with and without *Lasioglossum* (*Dialictus*) bees to account for the lack of identification to species-level for this group. The functional trait of bee nesting behaviour was largely associated with the NMDS and additional GLMs with the abundance of above- and below-ground nesting bees were run using a Negative Binomial model with a log link.

Results

In total, 4,490 bees from 27 genera and 95 species or species groups were collected across both years (excluding honey bees), with 2,510 bees collected in 2021 and 1,980 bees in 2022. Of all collected bees, most (92%) were native, female (89%), and polylectic (98%). Bee abundance per site in 2021

ranged from 47-333 bees with a median of 108 and in 2022 ranged from 34-150 bees with a median of 75. Bee species richness per site ranged from 9-33 species with a median of 20 in 2021 and 9-28 species with a median of 17 in 2022. Most bees were below ground nesters (88%) and social (66%) while 33% were solitary and 1% cuckoo (Supplemental Table 3). The most common bee species or species groups collected over both years were *Lasioglossum* (*Dialictus*) (Robertson) (38% of bees), *Agapostemon virescens* (Fabricius) (9.3% of bees), *Augochlorella aurata* (Smith) (7.5%), *Halictus confusus* Smith (6.9% of bees), and *Bombus impatiens* Cresson (5%).

Modeling of bee abundance demonstrated that soils, landscape composition, and vineyard management all influenced the abundance of bees in vineyards (Table 1). In 2021, slope had a negative relationship with bee abundance (estimate= -0.21, Z= 2.06, p= 0.04; Figure 2A). Also in 2021, soil texture had a positive relationship with bee abundance (estimate= 0.24, Z= 2.41, p= 0.02; Figure 2B) while in 2022 this was marginally insignificant (estimate= 0.15, Z= 1.86, p= 0.06). In 2022, the percentage of semi-natural lands had a positive relationship with bee abundance (estimate= 0.16, Z= 2.24, p= 0.03; Figure 2C) as did vineyard vegetation height (estimate= 0.17, Z= 2.31, p= 0.02; Figure 2D) while vineyard floral abundance had a marginally insignificant positive association (estimate= 0.14, Z= 1.88, p=0.06).

Bee species richness was influenced mostly by landscape composition and vineyard management (Table 1). In 2021, species richness had a positive relationship with the percentage of semi-natural lands (estimate= 0.13, Z= 2.48, p= 0.01; Figure 3A) while in 2022 this was marginally insignificant (estimate= 0.091, Z= 1.75, p= 0.08). In 2021, vineyard management type also influenced species richness, with a negative impact of both organic (estimate= -0.33, Z= 2.25, p= 0.02) and sustainable management (estimate= -0.35, Z= 2.15, p= 0.03) compared to conventional management (Figure 3B). Lastly, species richness had a positive relationship with vegetation height in both years (2021 estimate= 0.17, Z= 2.76, p= 0.006; 2022 estimate= 0.17, Z= 3.47, p= 0.0005; Figure 3C). Genus richness models exhibited similar relationships to those of species richness, but with greater model uncertainty (number of top models) and lower explanatory power (R^2). Genus richness models showed a significant ($p<0.05$) positive association

with the percentage of semi-natural lands in both years, a negative association with certified sustainable management in both years, and a positive relationship with vegetation height in 2022 (Supplemental Table 4).

Taking evenness into account, the Shannon species diversity index (H) was influenced mostly by soils and vineyard management (Table 1). Shannon diversity was negatively associated with soil texture in 2021 (estimate= -0.24, Z= 3.13, p= 0.002; Figure 4A) and positively with vegetation height in both years (2021 estimate= 0.24, Z= 3.6, p= 0.0003; 2022 estimate= 0.27, Z= 3.06, p= 0.002; Figure 4B). Additionally, certified sustainable management had a marginally insignificant negative association with H in 2022 (estimate= -0.30, Z= 1.68, p= 0.09). Genus-level Shannon diversity (H′) results mirrored those at the species level, with similar model uncertainty and comparable explanatory power (Supplemental Table 4). In 2021, like species H, genus H' was significantly negatively associated with soil texture and positively associated with vegetation height. In 2022, genus H' was significantly negatively associated with sustainable management and had a nearly significant positive relationship with vegetation height (estimate= 0.15, Z= 1.89, p= 0.06).

Multivariate analyses (NMDS) revealed differences in bee communities and functional traits among sites with landscape, soil, and vineyard management variables associated with these patterns (Figures 5 and 6). Bee community composition differed significantly between vineyard management types in both 2021 (PERMANOVA: F= 1.78, p= 0.009; Figure 5) and 2022 (F= 1.92, p= 0.007; Figure 6). These patterns remained when *Lasioglossum* (*Dialictus*) were excluded from analyses, although the difference in 2022 was marginally non-significant (p= 0.06; Supplemental Figures 3 and 4). Sustainable sites were associated with ground-nesting bees while aboveground-nesting bees were associated with organic and conventional sites. Sustainable sites were also associated with social bees in 2022 when all bees were included, but with solitary bees in both years when *Lasioglossum* (*Dialictus*) were excluded - a group of primarily social bees in Niagara, ON. In analyses with all bees, floral richness (both years) and vegetation height (2022) were associated with organic and conventional sites. This was further supported when comparing the local vegetation, soil, and landscape characteristics between vineyard types which

demonstrated that vineyard vegetation height and floral richness differed significantly between categories (Supplemental Table 5). Vegetation height was tallest in organic vineyards (median 29.4 cm) when compared to sustainable (median 19.6 cm) vineyards while conventional vineyards didn't differ from either category (median 22.5 cm). Furthermore, floral richness was marginally higher in both conventional (median 1.99) and organic (median 1.8) vineyards compared to sustainable vineyards (median 1.39).

NMDS associations among bee functional traits and environmental variables (local, landscape, and soil) revealed several relationships. Ground nesting bees were positively associated with soil texture in both years. In 2022, underground nesting bees were also associated with woody crops and agricultural lands - which had similar vectors due to most agricultural land around the vineyard sites being either orchards or vineyards (Supplemental Figure 2). Aboveground-nesting bees were associated with slope in 2022 and male bees were associated with floral richness in 2021. Additionally, in 2022, bee body size and solitary bees were associated with both floral richness and vegetation height - variables that showed similar vectors due to their high correlation (Supplemental Figure 1). Excluding *Lasioglossum* (*Dialictus*) affected the ordination of sites and altered some of the observed associations with environmental variables, though underground-nesting bees were still associated with soil texture in both years. Modeling of the abundance of *Lasioglossum* (*Dialictus*) bees provided further insights into their influence on community composition (Supplemental Table 4). In 2021, their abundance was positively associated with soil texture (estimate= 0.41, Z= 3.20, p= 0.001) and negatively associated with vegetation height (estimate= –0.40, Z= 3.07, p= 0.002). In contrast, the 2022 model of *Lasioglossum* (*Dialictus*) abundance had a lower explanatory power (R^2 = 0.31) and no variables were significant in the final model, although vegetation height showed a nearly significant negative association (estimate= –0.29, Z= 1.94, p= 0.05). Modelling of the abundance of belowground and aboveground nesting bees separately further revealed the influence of soil texture on underground nesting bees (Supplemental Table 6). A positive relationship was seen in 2021 (estimate= 0.31, Z= 3.02, p= 0.003) while in 2022 this was marginally insignificant (estimate= 0.17, Z= 1.85, p= 0.06). In 2022, surrounding semi-natural lands also had a positive impact on

underground nesting bees (estimate= 0.18, Z= 2.14, p= 0.03) while vegetation height had a nearly significant positive relationship (estimate= 0.15, Z= 1.93, p= 0.05). Vegetation height also had a positive impact on aboveground nesting bees in 2022 (estimate= 0.40, Z= 2.88, p= 0.004) though this was marginally insignificant in 2021 (estimate= 0.22, Z= 1.88, p= 0.06). Soil texture, interestingly, had a negative impact on aboveground nesting bees in 2021 (estimate= -0.40, Z= 2.90, p= 0.004) though this was not significant in 2022 (estimate= -0.27, Z= 1.67, p= 0.09). Additionally, in 2022, aboveground nesting bees were positively associated with impervious surfaces (estimate= 0.35, Z= 2.68, p= 0.007) and negatively with surrounding vineyard cover (estimate= -0.36, Z= 2.33, p= 0.02). Overall, bee community composition differed significantly among sites associated with several bee functional traits and influenced by various local, landscape, and soil variables.

Discussion

Our results demonstrate that vineyard management, surrounding land-uses, and soil factors all played an important role in shaping bee communities in Canadian vineyards. This is consistent with the hypothesis that vineyard bees were shaped by both local- and landscape-scale variables. Multiple vineyard management factors impacted bee abundance and diversity, indicating that local variables largely influence vineyard bee communities. Previous studies have found that vineyard management had a larger impact on vineyard arthropods than did surrounding landscape factors (Kratschmer et al. 2019; Zielonka et al. 2024). In this study, the variable that most consistently impacted both bee abundance and diversity was between-row vegetation height - which positively influenced bee abundance, species and genus richness, and Shannon species and genus diversity in at least one year. The positive impact of vegetation height on vineyard bee diversity is consistent with the findings of Biella et al. (2025) and Zielonka et al. (2024) - the latter finding a positive impact of a vegetation cover metric based on both vegetation cover and height. These results indicate that practices that enable taller vegetation between rows will benefit wild bees, such as reduced mowing frequencies. Interestingly, the opposite pattern was seen for *Lasioglossum* (*Dialictus*) bees as their abundance was negatively associated with vegetation

height. This indicates that not all bees benefit from taller vegetation, or alternatively, this could be related to the methodology used and the impacts of pan trap visibility in tall-vegetation vineyards. As smaller bees, like Halictids, tend to be collected primarily in pan traps, vineyards with tall vegetation growing between rows may have less visible pan traps and were less likely to attract and collect bees (McCravy, 2018). It is important to note that the negative association between *Lasioglossum* (*Dialictus*) abundance and vegetation height could also be influencing the positive association between vegetation height and bee species richness and Shannon species diversity because this subgenus of bees was not identified to species level. This likely resulted in an underestimation of species richness and evenness in sites where this subgenus was highly abundant. However, Bosco et al. (2023) found that the various species within the genus of *Lasioglossum* demonstrated similar responses to local and landscape variables when considering their presence or absence in vineyards. Thus, it is possible that majority of collected *Lasioglossum* (*Dialictus*) bees responded similarly to vegetation height in this study. Furthermore, the results at the genus level also displayed a positive association with vegetation height demonstrating the importance of this vegetation characteristic for higher-level bee diversity.

The other vineyard management factor that was shown to impact vineyard bees in this study was the vineyard management type. Certified sustainable management had a negative association with species and genus richness and genus-level Shannon diversity in at least one year. This is opposite to the prediction that these vineyards would have higher bee abundance and diversity than conventional vineyards due to program requirements such as integrated pest management and cover cropping. Zielonka et al. (2024) also found no benefit of the Sustainable Wines of Great Britain 'SWGB' scheme on the abundance or diversity of arthropods in UK vineyards. Furthermore, in this study, organic vineyard management did not enhance bee abundance or diversity as expected. In fact, a negative association with species richness in 2021 was seen contrary to the prediction that reduced synthetic pesticide use would benefit bees. These results are consistent with previous studies showing limited or no benefits of organic management on vineyard arthropods including bees (Kehinde and Samways, 2012; Ostandie et al., 2021). One possible reason for this could be that these programs require more time to see an impact. The SWO

certification is an evolving program with several sites being newly accredited during this study. Furthermore, while organic vineyards in this study were managed organically for 3+ years, research has shown that pesticides and their byproducts can accumulate and persist in soils for several years or even decades depending on the products used (Komárek et al., 2010; Patinha et al., 2018). Detrimental effects of pesticide use on broader bee community metrics are often difficult to detect, even though laboratory and field experiments have demonstrated lethal and sublethal impacts of various pesticides on individual species (Raine and Rundlöf, 2024; Guzman et al., 2024). Exposure levels and responses also can vary across bee taxa, which can further conceal patterns when examining overall abundance and diversity metrics. Using species occupancy models linked with land-use data across the United States, Guzman et al. (2024) found that neonicotinoid and pyrethroid use had stronger negative effects on Andrenidae and Apidae compared to Halictidae and Megachilidae. Furthermore, this study assessed organic and sustainable management only at the local scale and bee responses may be more strongly influenced by landscape-scale exposure to these practices (Ostandie et al. 2021). Future research should explore the temporal and spatial scale of sustainability certifications and their impacts on wild bees.

While this research demonstrated the impact of multiple vineyard management practices on wild bees, landscape-scale variables were also found to largely shape vineyard bee abundance and diversity. This is consistent with other studies that have shown that surrounding landscape composition (including artificial areas, uncultivated land, semi-natural elements, and woody structures) influences vineyard pollinators including bees (Kehinde et al., 2018; Kratschmer et al., 2018; Kratschmer et al., 2021; Ostandie et al., 2021). In this study, the percentage of semi-natural lands was the most impactful surrounding land-use variable for both bee abundance and diversity. The percentage of semi-natural lands had a positive impact on bee abundance and species and genus richness in at least one year. For this study, this land type consisted primarily of forested land with small areas of wetlands and shrublands as well. These results highlight the importance of protecting treed habitat in vineyard-dominated landscapes and reinforces the importance of forest patches in agricultural lands (Rahimi et al., 2022). These results oppose those of other studies that found limited or no impact of landscape factors on vineyard bees

including the landscape composition heterogeneity or the proportion of natural, semi-natural, or uncultivated land (Brittain et al., 2010; Kehinde and Samways, 2012; Wilson et al., 2018; Popescu et al., 2019). The types of uncultivated and semi-natural lands in these studies varied from being predominantly gardens and fallow fields to different types of riparian, woodland, shrubland, and/or grassland habitat. The importance of this variability is noted by Brittain et al., (2010) where authors discuss that the quality of habitat for bees may be more important than simply the proportion of natural or semi-natural habitats around vineyards. Another reason that other studies may have found limited influence of landscape factors on vineyard bees may be due to the larger radii utilised when quantifying landscape composition around vineyard sites. These studies used buffers ranging from 500-1000m compared to the 300m radius used in this study. These larger buffers may represent foraging ranges that are uncommon for most bees - where the typical median realized foraging range is ~110m for solitary species and ~448m for primitively eusocial species (Kendall et al., 2022). Another important consideration is the amount of semi-natural land surrounding sites, as a certain threshold may be necessary before positive impacts on bees become detectable. In this study, the proportion of semi-natural land within 300 meters of vineyards ranged from 0% to 28%. Further research is needed to determine the structural requirements of semi-natural habitats that support wild bees, including patch size, configuration, and proximity to agricultural fields. Such information can guide land-use planning and policy aimed at protecting and restoring semi-natural habitats in agricultural landscapes.

While the percentage of semi-natural lands was significantly associated with bee abundance and diversity, no other land-use variables were significant in any of the bee response models. The percentage of annual crops, vineyards, and impervious surfaces were retained in at least one of the top models of bee abundance or diversity, though none of these relationships were significant or consistent across years, indicating limited influence on wild bee abundance or diversity in Niagara vineyards. This was surprising, as different crops are known to support different bee taxa and influence the regional bee community within the landscape (Martins et al., 2018). The crop types within the surrounding landscapes of previous studies have ranged from being almost entirely vineyards (Wilson et al., 2018) to having a variety of other

crops such as orchards and annual crops (Kehinde et al., 2018). In this study, most surrounding crop types were orchards and vineyards, as indicated by the high correlation between the percentage of agricultural land and the percentage of woody crops (Spearman's r=0.72). The lack of a detectable impact of vineyard cover in the surrounding landscape also suggests that field sizes in Niagara may fall within the typical foraging ranges of many wild bee species. Field size may be an important consideration when interpreting the role of surrounding landscape composition and can vary substantially across regions (Popescu et al., 2019; Kratschmer et al., 2021).

Lastly, this study found an impact of landscape soils on bee abundance and Shannon diversity. Soil texture had a positive impact on bee abundance in both years and a negative impact on Shannon species-level and genus-level diversity in 2021. A negative relationship between slope and bee abundance was also found in 2021. The positive relationship between soil texture and bee abundance opposes the results of Ostandie et al. (2021) who found no impact of soil texture on pollinator abundance. These results also oppose those of Wersebeckmann et al., (2023) who found lower bee abundance and species richness in vineyards with larger soil particle sizes, though in their study, sites with larger particles had high amounts of large gravel particles (minimum 40% gravel) while soils in this study ranged from silty clay to very fine sandy loam soils. Many ground-nesting bees prefer higher sand content which likely explains the positive relationship with bee abundance and soil texture (Antoine and Forrest, 2021). However, differences in soil texture may also impact plant communities within and around vineyards which could also impact bee communities (Renne et al., 2019). Similarly, the negative impact of slope on bee abundance in 2021 may be associated primarily with the topography of the Niagara Region. Higher slopes were associated with sites along the Niagara Escarpment - a 177m north-facing cliff formation that encompasses various grape growing sub-appellations (VQA, n.d.). It is possible that the impact of slope on bee abundance is associated with differences in environmental and plant characteristics associated with the Niagara Escarpment rather than with slope itself, though slope is also known to impact below-ground nest site selection as it can impact nest drainage, solar radiation and temperature (Antoine and Forrest, 2021). In general, more research is needed on bee nesting behaviour in agricultural lands and the

landscape variables important for nest site selection. This can help inform sustainable agricultural policies and programs to consider not only floral resource provision for pollinators but also nesting habitat management (Sardiñas and Kremen, 2014).

Bee community composition analyses and associations with functional traits and environmental variables provided further insights into the above relationships, especially regarding bee nesting behaviour. Surprisingly, while this study found a positive influence of semi-natural habitats on both bee abundance and diversity, there was no association of semi-natural habitats with the ordination of sites by bee community composition in either year. However, when above- and below-ground nesting bees were modelled separately, semi-natural land cover had a positive effect on both groups in one year of the study and was retained in the final models for both nesting groups in both years. Most of the semi-natural habitats around the vineyard sites in this study were treed habitat, which was predicted to provide the necessary nesting sites for above-ground nesting bees particularly (Rahimi et al., 2022). Wersebeckmann et al. (2023) found that above-ground nesting bees were associated with semi-natural habitat at 150m radius around vineyard sites, Uzman et al., (2020) found that the proportion of semi-natural habitat within a 1km radius around vineyard sites enhanced cavity nesting bee abundance and diversity, and Kaczmarek et al. (2024) found a positive influence of semi-natural habitat at 500m around vineyard sites on aboveground nesting bee abundance and richness. In this study, aboveground nesting bees in the NMDS were associated with higher slopes while in the GLMs, soil texture had a negative association with their abundance. These relationships are likely due to differences in environmental variables and/or plant communities along the soil texture and slope gradients of the Niagara Region and related to the Niagara Escarpment (Auditor General of Ontario, 2022). It may be that sites along the Niagara Escarpment, where soil texture is smaller and slopes are larger, consisted of larger tracts of continuous and connected forested land - an important factor regrading forest patches in agricultural lands for bees and a factor unaccounted for in the broad consideration of the percentage of semi-natural lands (Rahimi et al., 2022).

Similar to the findings of Kaczmarek et al. (2024), most of the bees collected in this study were below-ground nesting. Below-ground nesting bees were consistently associated with soil texture in the

community composition ordinations as well as in modelling of underground nesting bee abundance. This indicates that soil texture is largely influential on nest site availability for these bees and should be considered when planning bee conservation research and actions. Wersebeckmann et al. (2023) similarly found a strong association between soil texture and the richness and abundance of ground-nesting bees. More research is needed to determine where below-ground nesting bees are nesting in vineyard-dominated lands and the implications for exposure to pesticides through their accumulation in soils. Anecdotally, underground bee nests were observed under vine-rows while collecting data for this study.

Associations between environmental variables and functional traits other than nesting were observed, but were less consistent, often being observed during only one year of the study. In ordinations with all bees, associations were seen between floral richness and larger bodied bees, solitary bees, and male bees. While floral richness was not included in the GLMs due to collinearity with other variables, these results indicate that certain bee taxa are positively influenced by a diversity of flowers in vineyards. This is consistent with other studies that have found that floral-rich cover crops and between-row plantings positively impact pollinator diversity (Wilson et al., 2018; Griffiths-Lee et al., 2023). Kratschmer et al. (2021) directly demonstrated that certain bee functional traits (e.g., tongue length, lecty) were associated with various flower traits (ex. morphology, colour) in vineyards. These results highlight the importance of planting a variety of flower types, ideally ranging in floral traits such as size, shape, colour, and phenology, in vineyards to support a variety of bee taxa. In ordinations that excluded *Lasioglossum* (*Dialictus*), associations were seen between larger bodied bees and agricultural lands as well as social and native bees with developed lands. In the GLMs of bee nesting traits, aboveground nesting bee abundance in 2022 was negatively associated with vineyard cover and positively associated with impervious surfaces. Sites surrounded with higher percentages of agricultural lands and vineyards likely impact bees differentially based on their foraging ranges and nesting site availability within these cropped landscapes (Kendall et al., 2022; Lau et al., 2023). Larger bees may be able to nest further away from vineyards but still utilize flowers blooming within vineyards when needed. Furthermore, the positive association between social, native, and aboveground nesting bees and developed land in the broader

landscape aligns with findings that bee functional diversity is higher in suburban areas compared to urban or rural ones (Banaszak-Cibicka and Dylewski, 2021) possibly due to residential gardens providing more diverse and reliable floral resources (Samnegård et al., 2011). Kratschmer et al. (2018) found that bee abundance, species richness, and above-ground nesting bees increased with the proportion of artificial areas surrounding vineyard sites. They noted that bee diversity tends to peak when landscapes include up to 50% impervious surfaces. In this study, developed land ranged from 1–60%, reflecting the high levels of residential and suburban development surrounding many vineyard sites in the Niagara Region which has experienced rapid population growth (Niagara Region, 2024). Engaging non-farmer residents and landowners in agricultural pollinator conservation efforts may represent an underutilized opportunity for supporting pollinators in these landscapes.

Conclusion

Our findings underscore the need to consider not only on-farm management practices but also the broader context of surrounding land uses and soil characteristics when assessing factors that influence wild bee communities in agricultural landscapes. These elements should be incorporated into future research, conservation strategies, and policy development aimed at supporting pollinators in farmlands. At the local scale, these results suggest that taller between-row vegetation, likely due to reduced mowing frequencies, may be an underutilized strategy for supporting wild bees in perennial crop systems. At the landscape scale, this study highlights the importance of semi-natural habitats, particularly forested and treed areas, for conserving wild bees in vineyard-dominated landscapes. Land-use planning, conservation easements, and policy interventions should prioritize the protection and restoration of these habitat types. Soil characteristics also played a significant role in shaping vineyard bee communities, with coarser soil textures being positively associated with the abundance of ground-nesting bees. Overall, these results suggest that effective bee conservation in farmlands must account for nesting habitat requirements alongside forage resources. This includes moving beyond focusing solely on field-level interventions

towards coordinated, landscape-scale management that involves collaboration among growers and landowners.

References

AAFC [Agriculture and Agri-Food Canada]. (June, 2021). Statistical Overview of the Canadian Fruit Industry 2020. Prepared by Horticulture Section Crops and Horticulture Division Agriculture and Agri-Food Canada. Retrieved from: https://agriculture.canada.ca/sites/default/files/documents/2021-08/fruit_report_2020-eng.pdf

AAFC [Agriculture and Agri-Food Canada]. (June 27, 2023a). Annual Crop Inventory - Annual Crop Inventory, 2022. Accessed on August 24, 2023. Retrieved from: https://open.canada.ca/data/en/dataset/ba2645d5-4458-414d-b196-6303ac06c1c9/resource/9f1ed71f-1826-45b9-a583-b42b7f71b641

AAFC [Agriculture and Agri-Food Canada]. (June 27, 2023b). ISO 19131 Annual Crop Inventory – Data Product Specifications Revision: A. Retrieved from: https://agriculture.canada.ca/atlas/data_donnees/annualCropInventory/supportdocument_documentdesupport/en/ISO%2019131_AAFC_Annual_Crop_Inventory_Data_Product_Specifications.pdf

Antoine, C. M., & Forrest, J. R. (2021). Nesting habitat of ground-nesting bees: a review. *Ecological Entomology*, *46*(2), 143-159.

Ascher, J. S. and Pickering, J. (2022). Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Retrieved from: http://www.discoverlife.org/mp/20q?guide=Apoidea_species [accessed May 2024].

Auditor General of Ontario [Office of]. (2022). Conserving the Niagara Escarpment – 2022 Value-for-Money Audit. Retrieved from: https://www.auditor.on.ca/en/content/news/22_summaries/2022_summary_ENV_NiagaraEsc.pdf

Banaszak-Cibicka, W., & Dylewski, Ł. (2021). Species and functional diversity—A better understanding of the impact of urbanization on bee communities. *Science of the Total Environment*, *774*, 145729.

Bartoń, K. (2024). MuMIn: Multi-Model Inference. R package version 1.48.4, https://CRAN.R-project.org/package=MuMIn

Basu, P., Parui, A. K., Chatterjee, S., Dutta, A., Chakraborty, P., Roberts, S., & Smith, B. (2016). Scale dependent drivers of wild bee diversity in tropical heterogeneous agricultural landscapes. *Ecology and evolution*, *6*(19), 6983-6992.

Biella, P., Ramazzotti, F., Parolo, G., Galimberti, A., Labra, M., and Brambilla, M. (2025). Vineyard footprint on pollinators is mediated by flower vegetation, organic farming, seasonal and weather factors, a case study from North Italy. *Agriculture, Ecosystems and Environment*, *378*, 109297.

Bosco, L., Moser, V., Jones, M. M., Opedal, Ø., Ovaskainen, O., Sonja, G., ... & Jacot, A. (2023). Habitat area and local habitat conditions outweigh fragmentation effects on insect communities in vineyards. *Ecological Solutions and Evidence*, *4*(1), e12193.

Brittain, C., Bommarco, R., Vighi, M., Settele, J., & Potts, S. G. (2010). Organic farming in isolated landscapes does not benefit flower-visiting insects and pollination. *Biological Conservation*, *143*(8), 1860-1867.

Brooks, M. E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. and Bolker, B. M. (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378-400. doi: 10.32614/RJ-2017-066.

Carré, G., Roche, P., Chifflet, R., Morison, N., Bommarco, R., Harrison-Cripps, J., ... & Vaissière, B. E. (2009). Landscape context and habitat type as drivers of bee diversity in European annual crops. *Agriculture, Ecosystems & Environment*, *133*(1-2), 40-47.

Daane, K. M., Vincent, C., Isaacs, R. and Ioriatti, C. (2018). Entomological opportunities and challenges for sustainable viticulture in a global market. *Annual review of entomology*, *63*, 193-214.

de Bello, F., Carmona, C. P., Dias, A. T. C., Götzenberger, L., Moretti, M. and Berg, M. P. (2021). Community Metrics. In: *Handbook of Trait-Based Ecology: From Theory to R Tools*. Cambridge University Press:75-104.

Dicks, L. V., Breeze, T. D., Ngo, H. T., Senapathi, D., An, J., Aizen, M. A., ... & Potts, S. G. (2021). A global-scale expert assessment of drivers and risks associated with pollinator decline. *Nature ecology & evolution*, *5*(10), 1453-1461.

Dorin, B. and Colla, S. (2024). Observations of wild bees foraging on wine grape (*Vitis vinifera* L.) flowers–first records and future research directions. *The Journal of the Entomological Society of Ontario*, *155*.

FAO [Food and Agriculture Organization of the United Nations] (n.d.). 6. Soil Texture. Retrieved from: https://www.fao.org/fishery/static/FAO_Training/FAO_Training/General/x6706e/x6706e06.htm

Fitch, G., Glaum, P., Simao, M. C., Vaidya, C., Matthijs, J., Iuliano, B. and Perfecto, I. (2019). Changes in adult sex ratio in wild bee communities are linked to urbanization. *Scientific Reports*, *9*(1), 3767.

Fox, J. and Weisberg, S. (2019). An R Companion to Applied Regression, Third edition. Sage, Thousand Oaks CA. <https://www.john-fox.ca/Companion/>.

Greenleaf, S. S., Williams, N. M., Winfree, R., & Kremen, C. (2007). Bee foraging ranges and their relationship to body size. *Oecologia*, *153*(3), 589-596.

Griffiths-Lee, J., Davenport, B., Foster, B., Nicholls, E., & Goulson, D. (2023). Sown wildflowers between vines increase beneficial insect abundance and richness in a British vineyard. *Agricultural and Forest Entomology*, *25*(1), 139-151.

Guzman, L. M., Elle, E., Morandin, L. A., Cobb, N. S., Chesshire, P. R., McCabe, L. M., ... & M'Gonigle, L. K. (2024). Impact of pesticide use on wild bee distributions across the United States. *Nature Sustainability*, *7*(10), 1324-1334.

Harrell, Jr. F. (2025).Hmisc: Harrell Miscellaneous. R package version 5.2-2, <https://CRAN.R-project.org/package=Hmisc>.

Harrison, X. A., Donaldson, L., Correa-Cano, M. E., Evans, J., Fisher, D. N., Goodwin, C. E. ... and Inger, R. (2018). A brief introduction to mixed effects modelling and multi-model inference in ecology. *PeerJ*, *6*, e4794.

Hartig, F. (2024). DHARMa: Residual Diagnostics for Hierarchical (Multi-Level / Mixed) Regression Models. R package version 0.4.7, https://CRAN.R-project.org/package=DHARMa.

Kaczmarek, M., Entling, M. H., & Hoffmann, C. (2024). Wild Bee Conservation in Viticulture: Effects of Semi-Natural Habitats, Organic Management, and Fungicide Reduction. *Ecology and Evolution*, *14*(10), e70378.

Kehinde, T., & Samways, M. J. (2012). Endemic pollinator response to organic vs. conventional farming and landscape context in the Cape Floristic Region biodiversity hotspot. *Agriculture, ecosystems & environment*, *146*(1), 162-167.

Kehinde, T., von Wehrden, H., Samways, M., Klein, A. M., & Brittain, C. (2018). Organic farming promotes bee abundance in vineyards in Italy but not in South Africa. *Journal of insect conservation*, *22*(1), 61-67.

Kendall, L. K., Mola, J. M., Portman, Z. M., Cariveau, D. P., Smith, H. G., & Bartomeus, I. (2022). The potential and realized foraging movements of bees are differentially determined by body size and sociality. Ecology Entomological Society of America, *103*(11), 1-8.

Kennedy, C. M., Lonsdorf, E., Neel, M. C., Williams, N. M., Ricketts, T. H., Winfree, R., ... & Kremen, C. (2013). A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. *Ecology letters*, *16*(5), 584-599.

Kingston MS & Presant EW. 1989. The Soils of the Regional Municipality of Niagara. Vol. 2. Report 60 of the Ontario Institute of Pedology, Guelph, ON.

Klein, A. M., Boreux, V., Fornoff, F., Mupepele, A. C., & Pufal, G. (2018). Relevance of wild and managed bees for human well-being. *Current Opinion in Insect Science*, *26*, 82-88.

Komárek, M., Čadková, E., Chrastný, V., Bordas, F., & Bollinger, J. C. (2010). Contamination of vineyard soils with fungicides: a review of environmental and toxicological aspects. *Environment international*, *36*(1), 138-151.

Kovács-Hostyánszki, A., Espíndola, A., Vanbergen, A. J., Settele, J., Kremen, C., & Dicks, L. V. (2017). Ecological intensification to mitigate impacts of conventional intensive land use on pollinators and pollination. *Ecology Letters*, *20*(5), 673-689.

Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guernion, M., Burel, F., ... & Winter, S. (2018). Tillage intensity or landscape features: What matters most for wild bee diversity in vineyards?. *Agriculture, Ecosystems & Environment*, *266*, 142-152.

Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guzmán, G., Goméz, J. A., ... & Winter, S. (2019). Response of wild bee diversity, abundance, and functional traits to vineyard inter-row management intensity and landscape diversity across Europe. *Ecology and Evolution*, *9*(7), 4103-4115.

Kratschmer, S., Pachinger, B., Gaigher, R., Pryke, J. S., van Schalkwyk, J., Samways, M. J., ... & Winter, S. (2021). Enhancing flowering plant functional richness improves wild bee diversity in vineyard inter-rows in different floral kingdoms. *Ecology and Evolution*, *11*(12), 7927-7945.

Lau, P. W., Esquivel, I. L., Parys, K. A., Hung, K. L. J., & Chakrabarti, P. (2023). The nutritional landscape in agroecosystems: a review on how resources and management practices can shape pollinator health in agricultural environments. *Annals of the Entomological Society of America*, *116*(5), 261-275.

Le Féon, V., Schermann-Legionnet, A., Delettre, Y., Aviron, S., Billeter, R., Bugter, R., ... & Burel, F. (2010). Intensification of agriculture, landscape composition and wild bee communities: a large scale study in four European countries. *Agriculture, Ecosystems & Environment*, *137*(1-2), 143-150.

Lenth, R. (2024). emmeans: Estimated Marginal Means, aka Least-Squares Means. R package version 1.10.6, <https://CRAN.R-project.org/package=emmeans>.

Lüdecke et al., (2021). performance: An R Package for Assessment, Comparison and Testing of Statistical Models. Journal of Open Source Software, 6(60), 3139. https://doi.org/10.21105/joss.03139

MacKell, S., Elsayed, H. and Colla, S. (2023). Assessing the impacts of urban beehives on wild bees using individual, community, and population-level metrics. *Urban Ecosystems*, *26*(5), 1209-1223.

Marcelino, S. M., Gaspar, P. D., do Paço, A., Lima, T. M., Monteiro, A., Franco, J. C., ... & Lopes, C. M. (2024). Agricultural practices for biodiversity enhancement: Evidence and recommendations for the viticultural sector. *AgriEngineering*, *6*(2), 1175-1194.

Martins, K. T., Albert, C. H., Lechowicz, M. J., & Gonzalez, A. (2018). Complementary crops and landscape features sustain wild bee communities. *Ecological Applications*, *28*(4), 1093-1105.

Matias, D. M. S., Leventon, J., Rau, A. L., Borgemeister, C., & von Wehrden, H. (2017). A review of ecosystem service benefits from wild bees across social contexts. *Ambio*, *46*(4), 456-467.

McCravy, K. W. (2018). A review of sampling and monitoring methods for beneficial arthropods in agroecosystems. *Insects*, *9*(4), 170.

Newcomb, L. (1989). Newcomb's Wildflower Guide. Little, Brown and Company, Boston, Massachusetts, United States.

Niagara Region. (n.d.). Niagara Agriculture Profile. Retrieved from https://niagaracanada.com/wp-content/uploads/sites/7/2019/11/Niagara_Agriculture_Profile_web.pdf

Niagara Region. (2024). Niagara Official Plan – making our mark. May 2024 Consolidation. Retrieved from: https://www.niagararegion.ca/official-plan/pdf/2022-niagara-official-plan.pdf

Nicholls, C. I., & Altieri, M. A. (2013). Plant biodiversity enhances bees and other insect pollinators in agroecosystems. A review. *Agronomy for Sustainable development*, *33*(2), 257-274.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., O'Hara, R., Solymos, P. … and Weedon, J. (2024). Vegan: Community Ecology Package. R package version 2.6-8, <https://CRAN.R-project.org/package=vegan>.

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). (2009). "Weed Gallery". Ontario Crop IPM. Retrieved from: http://www.omafra.gov.on.ca/IPM/english/weeds-herbicides/gallery/index.html

OMAFRA [Ontario Ministry of Agriculture, Food and Rural Affairs] (2015). Soil Survey Complex Generalized soil map [computer file]. Retrieved from: https://geohub.lio.gov.on.ca/datasets/ontarioca11::soil-survey-complex/about

OMAFRA [Ontario Ministry of Agriculture, Food and Rural Affairs] (2019). Land Information Ontario Data Description Soil Survey Complex. Retrieved from: https://www.publicdocs.mnr.gov.on.ca/mirb/Soil%20Survey%20Complex%20-%20Data%20Description.pdf

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). (2023a). Weed identification guide for Ontario crops. Retrieved from: https://www.ontario.ca/document/weed-identification-guide-ontario-crops

Onuferko, T. M., Kutby, R., & Richards, M. H. (2015). A list of bee species (Hymenoptera: Apoidea) recorded from three municipalities in the Niagara region of Ontario, including a new record of *Lasioglossum furunculum* Gibbs (Halictidae) in Canada. *The Journal of the Entomological Society of Ontario*, *146*.

Ostandie, N., Giffard, B., Bonnard, O., Joubard, B., Richart-Cervera, S., Thiéry, D., & Rusch, A. (2021). Multi-community effects of organic and conventional farming practices in vineyards. *Scientific reports*, *11*(1), 11979.

Packer, L., Genaro, J. A. and Sheffield, C. S. (2007). The bee genera of eastern Canada. *Canadian Journal of Arthropod Identification*, *3*(3), 1-32.

Park, M. G., Blitzer, E. J., Gibbs, J., Losey, J. E., & Danforth, B. N. (2015). Negative effects of pesticides on wild bee communities can be buffered by landscape context. *Proceedings of the Royal Society B: Biological Sciences*, *282*(1809), 20150299.

Patinha, C., Duraes, N., Dias, A. C., Pato, P., Fonseca, R., Janeiro, A., ... & Cachada, A. (2018). Long-term application of the organic and inorganic pesticides in vineyards: Environmental record of past use. *Applied Geochemistry*, *88*, 226-238.

Patrício-Roberto, G. B., & Campos, M. J. (2014). Aspects of landscape and pollinators—what is important to bee conservation?. *Diversity*, *6*(1), 158-175.

Popescu, D., Comsa, M., Hoble, A., Bunea, C. I., Gaman, T., Tamas, A. S., ... & Winter, S. (2019). Biodiversity and ecosystem service in Transylvania–new approach to a sustainable vineyards. *Journal of Environmental Protection and Ecology*, *20*(4), 1870-1879.

Potts, S. G., Vulliamy, B., Roberts, S., O'Toole, C., Dafni, A., Ne'eman, G., & Willmer, P. (2005). Role of nesting resources in organising diverse bee communities in a Mediterranean landscape. *Ecological Entomology*, *30*(1), 78-85.

Rahimi, E., Barghjelveh, S., & Dong, P. (2022). Amount, distance-dependent and structural effects of forest patches on bees in agricultural landscapes. *Agriculture & Food Security*, *11*(1), 10.

Raine, N. E., & Rundlöf, M. (2024). Pesticide exposure and effects on non-Apis bees. *Annual review of entomology*, *69*(1), 551-576.

Renne, R. R., Bradford, J. B., Burke, I. C., & Lauenroth, W. K. (2019). Soil texture and precipitation seasonality influence plant community structure in North American temperate shrub steppe. *Ecology*, *100*(11), e02824.

Richards, M. H., Rutgers-Kelly, A., Gibbs, J., Vickruck, J. L., Rehan, S. M., & Sheffield, C. S. (2011). Bee diversity in naturalizing patches of Carolinian grasslands in southern Ontario, Canada. *The Canadian Entomologist*, *143*(3), 279-299.

Samnegård, U., Persson, A. S., & Smith, H. G. (2011). Gardens benefit bees and enhance pollination in intensively managed farmland. *Biological Conservation*, *144*(11), 2602-2606.

Sardiñas, H. S., & Kremen, C. (2014). Evaluating nesting microhabitat for ground-nesting bees using emergence traps. *Basic and Applied Ecology*, *15*(2), 161-168.

Seufert, V., Ramankutty, N., & Mayerhofer, T. (2017). What is this thing called organic?–How organic farming is codified in regulations. *Food Policy*, *68*, 10-20.

Sheffield, C. S., Frier, S. D., & Dumesh, S. (2014). The bees (Hymenoptera: Apoidea, Apiformes) of the Prairies Ecozone, with comparisons to other grasslands of Canada. *Arthropods of Canadian grasslands*, *4*, 427-467.

SWO (Sustainable Winegrowing Ontario). (n.d.). Sustainable Winegrowing Ontario certified. Retrieved from: https://sustainablewinegrowingontario.ca

Turley, N. E., Biddinger, D. J., Joshi, N. K. and López-Uribe, M. M. (2022). Six years of wild bee monitoring shows changes in biodiversity within and across years and declines in abundance. *Ecology and Evolution*, *12*(8), e9190.

Uzman, D., Reineke, A., Entling, M. H., & Leyer, I. (2020). Habitat area and connectivity support cavity-nesting bees in vineyards more than organic management. *Biological Conservation*, *242*, 108419.

Vanbergen, A. J. and The Insect Pollinators Initiative. (2013). Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and the Environment*, *11*(5), 251–259.

Venables, W. N. and Ripley, B. D. (2002). Modern Applied Statistics with S. Fourth Edition. Springer, New York. ISBN 0-387-95457-0

VQA (Vintners Quality Alliance) (n.d.). The Niagara Peninsula Appellation Overview. Retrieved from: https://www.vqaontario.ca/Appellations/Niagara-Peninsula/

Walker, E., Wooliver, R., Russo, L., & Jagadamma, S. (2025). The context-dependent benefits of organic farming on pollinator biodiversity: A meta-analysis. *Journal of Applied Ecology*, *62*(1), 41-52.

Wei, T. and Simko, V. (2024). R package 'corrplot': Visualization of a Correlation Matrix (Version 0.95). Available from https://github.com/taiyun/corrplot

Wersebeckmann, V., Warzecha, D., Entling, M. H., & Leyer, I. (2023). Contrasting effects of vineyard type, soil and landscape factors on ground-versus above-ground-nesting bees. *Journal of Applied Ecology*, *60*(4), 601-613.

Williams, N. M., Crone, E. E., T'ai, H. R., Minckley, R. L., Packer, L., & Potts, S. G. (2010). Ecological and life-history traits predict bee species responses to environmental disturbances. *Biological Conservation*, *143*(10), 2280-2291.

Wilson, H., Wong, J. S., Thorp, R. W., Miles, A. F., Daane, K. M., & Altieri, M. A. (2018). Summer flowering cover crops support wild bees in vineyards. *Environmental Entomology*, *47*(1), 63-69.

Zamorano, J., Bartomeus, I., Grez, A. A., & Garibaldi, L. A. (2020). Field margin floral enhancements increase pollinator diversity at the field edge but show no consistent spillover into the crop field: a meta-analysis. *Insect Conservation and Diversity*, *13*(6), 519-531.

Zattara, E. E., & Aizen, M. A. (2021). Worldwide occurrence records suggest a global decline in bee species richness. *One Earth*, *4*(1), 114-123.

Zielonka, N. B., Shutt, J. D., Butler, S. J. and Dicks, L. V. (2024). Management practices, and not surrounding habitats, drive bird and arthropod biodiversity within vineyards. *Agriculture, Ecosystems and Environment*, *367*, 108982.

Zurbuchen, A., Landert, L., Klaiber, J., Müller, A., Hein, S. and Dorn, S. (2010). Maximum foraging ranges in solitary bees: only few individuals have the capability to cover long foraging distances. *Biological Conservation*, *143*(3), 669-676.

Zuur, A. F., Ieno, E. N. and Smith, G. M. (2007). *Analysing ecological data* (Vol. 680). New York: Springer.

Zuur, A. F., Ieno, E. N. and Elphick, C. S. (2010). A protocol for data exploration to avoid common statistical problems. *Methods in ecology and evolution*, *1*(1), 3-14.

Zuur, A. F. and Ieno, E. N. (2016). A protocol for conducting and presenting results of regression-type analyses. *Methods in Ecology and Evolution*, *7*(6), 636-645.

Tables

Table 1: Generalized Linear Model summaries for each bee response variable per year - bee abundance, species richness, Shannon Diversity index. Results are from model averaging of 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. Significant predictors are shown at p<0.05 (*). For vineyard management categories, the reference value is "Conventional". Continuous predictors were standardized (z-scored) before analyses. On the right 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 R2 is for a model run with all variables included in the averaged model (significant or not).

Predictor(s)	Estimate	Standard Error	z value	p-value	AICc range	No. models	R2
Bee abundance 2021							
Intercept	**4.81**	**0.090**	**51.01**	**<2e-16 ***	217.28-219.18	4	0.56
Semi-natural	0.13	0.10	1.34	0.1795			
Annual crops	-0.12	0.10	1.20	0.2306			
Slope	**-0.21**	**0.10**	**2.06**	**0.0395 ***			
Texture	**0.24**	**0.10**	**2.41**	**0.016 ***			
Bee abundance 2022							
Intercept	**4.40**	**0.068**	**64.58**	**<2e-16 ***	231.0-232.69	4	0.55
Semi-natural	**0.16**	**0.071**	**2.24**	**0.0249 ***			
Texture	0.15	0.079	1.86	0.0626			
Vegetation height	**0.17**	**0.072**	**2.31**	**0.0207 ***			
Floral abundance	0.14	0.069	1.88	0.0602			
Species richness 2021							
Intercept	**3.12**	**0.15**	**21.04**	**<2e-16 ***	121.75-122.79	2	0.84
Semi-natural	**0.13**	**0.054**	**2.48**	**0.01309 ***			
Vegetation height	**0.17**	**0.062**	**2.76**	**0.00581 ***			
Management - Organic	**-0.33**	**0.15**	**2.25**	**0.02437 ***			
Management - Sustainable	**-0.35**	**0.16**	**2.15**	**0.03130 ***			
Species richness 2022							
Intercept	2.85	0.053	54.06	**<2e-16 ***	132.17-132.95	2	0.71
Semi-natural	0.091	0.052	1.75	0.07955			
Vegetation height	**0.17**	**0.050**	**3.47**	**0.00051***			
Shannon diversity (H) 2021							
Intercept	**2.08**	**0.064**	**32.69**	**<2e-16 ***	11.84-13.22	3	0.74
Semi-natural	0.11	0.068	1.55	0.12075			
Slope	-0.094	0.074	1.27	0.20295			
Texture	**-0.24**	**0.075**	**3.13**	**0.00177 ***			
Vegetation height	**0.24**	**0.066**	**3.60**	**0.00032 ***			
Shannon diversity (H) 2022							
Intercept	2.09	0.093	22.41	**0.00023 ***	21.03-22.58	6	0.64
Annual crops	0.10	0.072	1.45	0.14807			
Slope	0.084	0.074	1.14	0.25332			

Vegetation height	**0.27**	**0.089**	**3.06**	**0.00222 ***			
Management - Organic	0.13	0.18	0.73	0.46593			
Management - Sustainable	-0.30	0.18	1.68	0.09341			

Figures

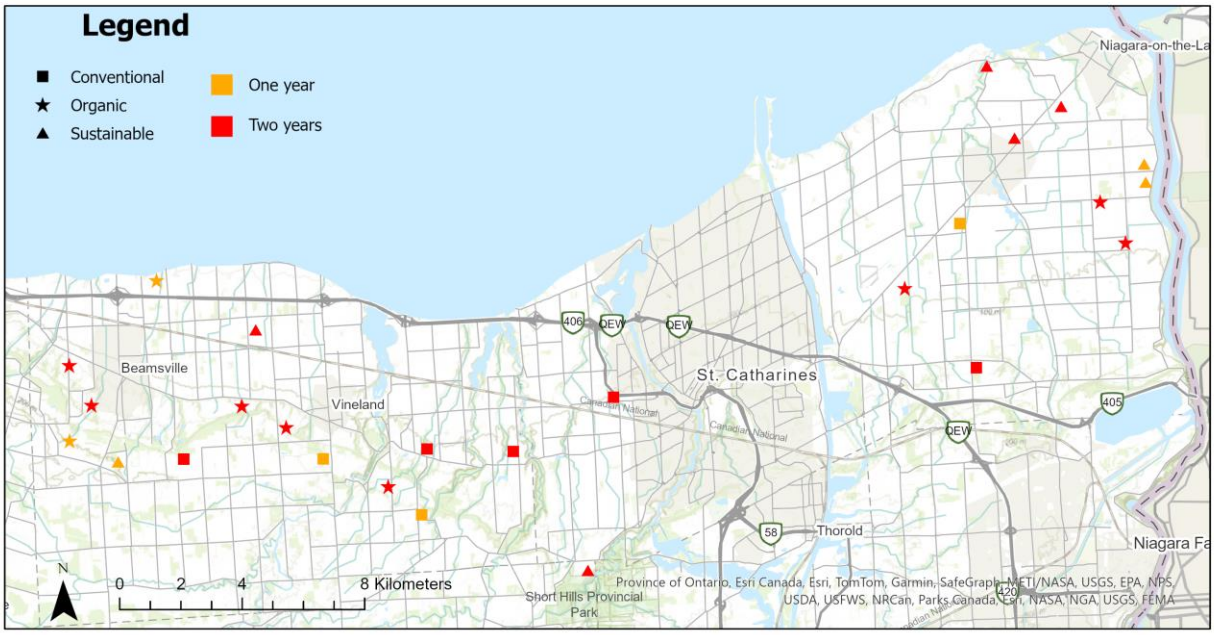

Figure 1: Vineyard sites for bee sampling across the Niagara Region, ON created in ArcMap Pro 3.0.2 (Esri, Redlands, CA) with the Canada Topographic, Canada Hillshade, and World Topographic Canadian Style basemaps. Different shapes indicate the vineyard management type at each site while different colours indicate whether the site was sampled for one year (2021 or 2022) or two years.

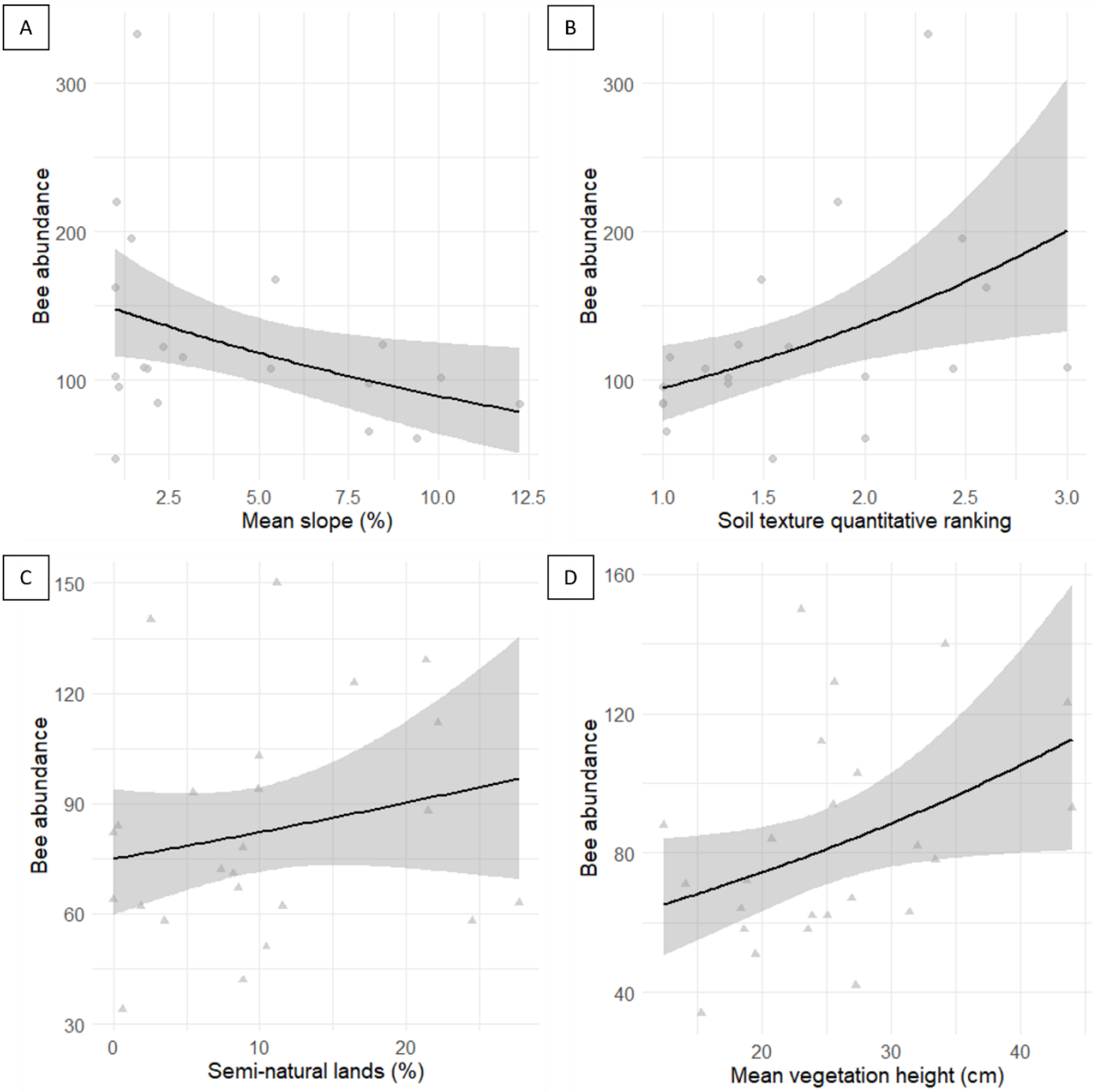

Figure 2: Significant ($p < 0.05$) landscape, soil, and vineyard management variables associated with bee abundance, identified through model averaging of the top Generalized Linear Models (ΔAICc < 2). Separate models were run for each year, with 2021 data shown as circles and 2022 data as triangles. In 2021, significant predictors were slope (A) and soil texture (B) and in 2022 they were the percent of semi-natural land (C) and between-row vegetation height (D). Soil and landscape variables were measured within a 300m radius of each site. Each graph shows raw data points of total bee abundance per site (y-axis) overlaid with fitted trendlines.

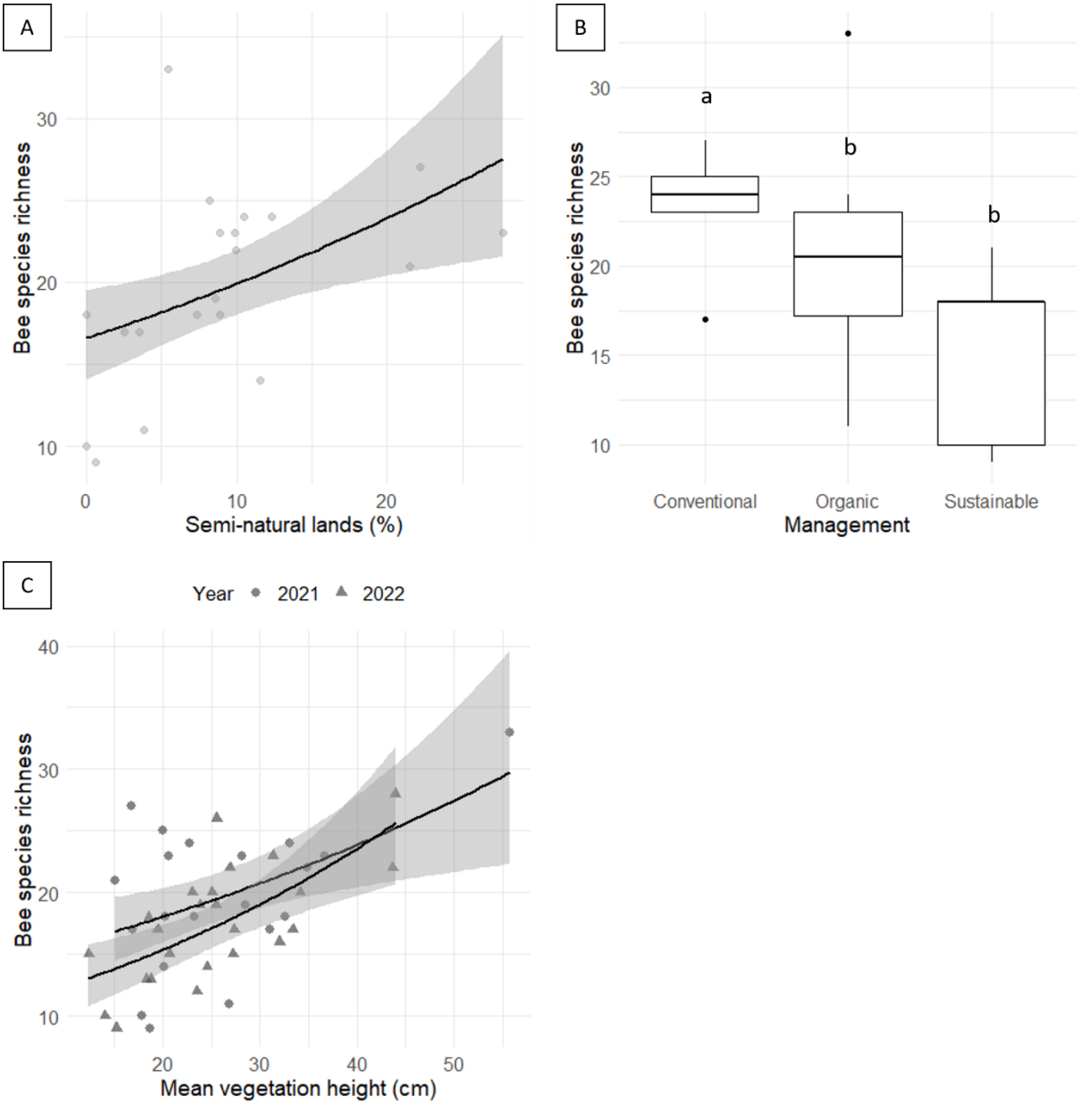

Figure 3: Significant ($p < 0.05$) landscape and vineyard management variables associated with bee species richness, identified through model averaging of the top Generalized Linear Models ($\Delta AICc < 2$). Separate models were run for each year, with 2021 data shown as circles and 2022 data as triangles. In 2021, significant predictors were the percentage of semi-natural lands (A) vineyard management type (B) and in both years between-row vegetation height (C). Landscape variables were measured within a 300m radius of each site. Each graph shows raw data points of total bee species richness per site (y-axis) overlaid with fitted trendlines for continuous predictors and as boxplots for categorical predictors. For

categorical variables, Tukey post-hoc comparisons based on model-estimated marginal means are indicated by different letters ($p<0.05$).

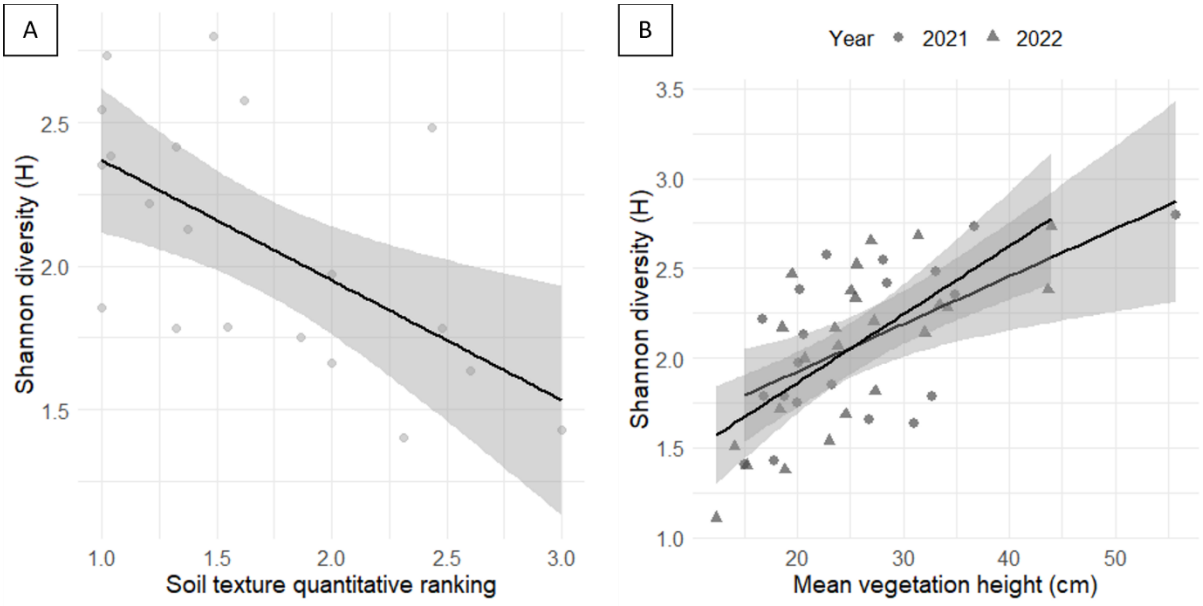

Figure 4: Significant ($p < 0.05$) soil and vineyard management variables associated with the Shannon diversity index of bee species, identified through model averaging of the top General Linear Models ($\Delta AICc < 2$). Separate models were run for each year, with 2021 data shown as circles and 2022 data as triangles. In 2021, significant predictors were soil texture (A) and in both years between-row vegetation height (B). Soil variables were measured within a 300m radius of each site. Each graph shows raw data points of Shannon diversity index per site (y-axis) overlaid with fitted trendlines.

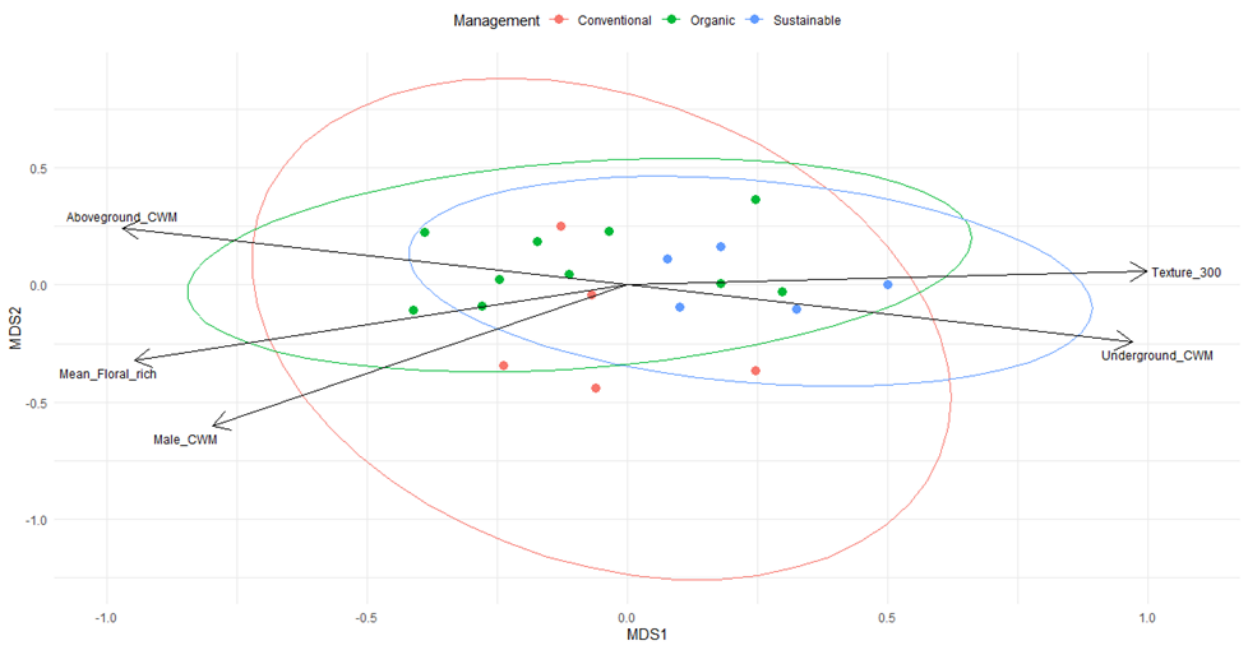

Figure 5: Non-metric multidimensional scaling (NMDS) of bee community composition at vineyard sites in 2021 (n=20) based on Bray-Curtis dissimilarity of Hellinger-transformed abundance data (stress=0.20). 95% confidence ellipses indicate different vineyard management categories (Permutational Multivariate Analysis of Variance $F=1.78$, $R^2= 0.17$, $p=0.009$). Vectors represent significantly correlated bee functional traits (community weighted means, CWM) and local, landscape, or soil variables ($p<0.05$, based on 999 permutations). Soil and landscape variables were taken from a 300m radius buffer around each site.

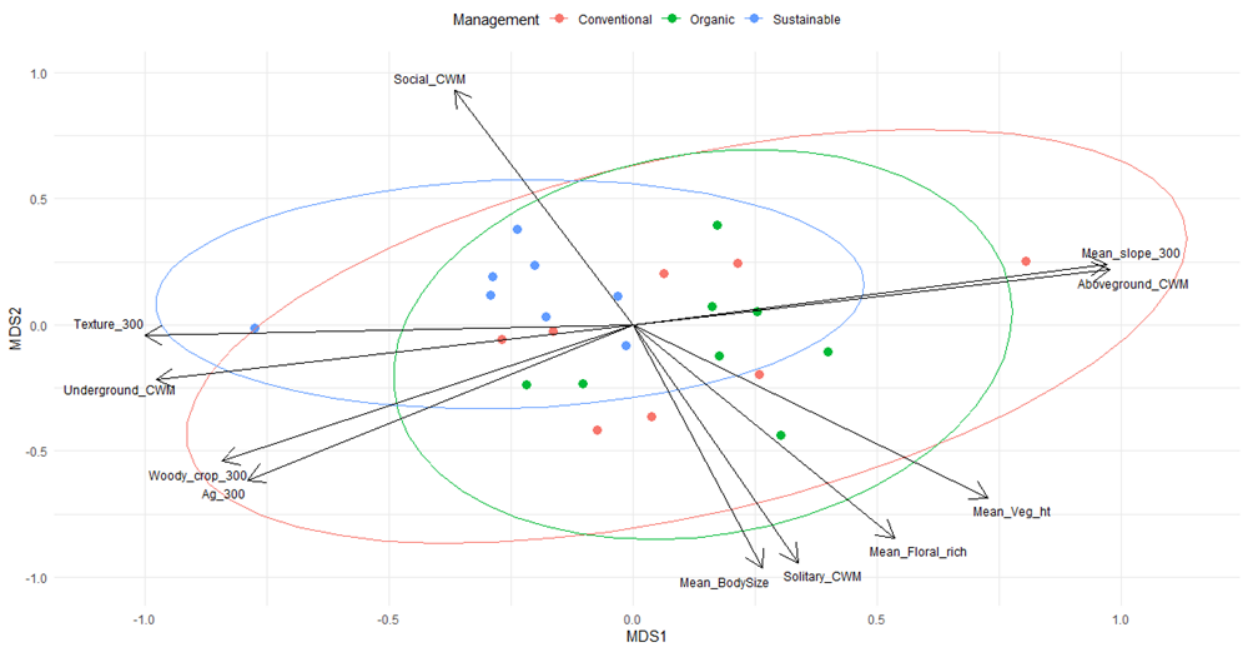

Figure 6: Non-metric multidimensional scaling (NMDS) of bee community composition at vineyard sites in 2022 (n=24) based on Bray-Curtis dissimilarity of Hellinger-transformed abundance data (stress=0.18). 95% confidence ellipses indicate different vineyard management categories (Permutational Multivariate Analysis of Variance F=1.92, R^2= 0.15, p=0.007). Vectors represent significantly correlated bee functional traits (community weighted means, CWM) and local, landscape, or soil variables (p<0.05, based on 999 permutations). Soil and landscape variables were taken from a 300m radius buffer around each site.

Chapter 4: Observations of wild bees foraging on wine grape (*Vitis vinifera* L.) flowers – first records and future research directions

Briann Dorin and Sheila Colla

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Author contributions: BD and SC conceived the project and methodology. BD collected the data and analyzed the results. SC provided supervision, guidance, and funding. BD led the writing of the manuscript. Both authors contributed to editing and gave final approval for publication to The Journal of the Entomological Society of Ontario and submission for this dissertation.

Abstract

While pollinator-independent crops do not require insect pollination for crop production, their flowers may still be used by bees for foraging resources. This study investigated if wild bees forage on *Vitis vinifera* (wine grape) flowers in commercial vineyards in Niagara, ON, Canada across ten common grape varieties. Over two years of observations during bloom, only ten bees were collected foraging on wine grape flowers, with additional incidental observations. Most were solitary, ground-nesting species from the Halictidae and Andrenidae families and were primarily observed on Gewürztraminer flowers. These results suggest that *V. vinifera* pollen is only occasionally used by wild bees and likely poses a low pesticide exposure risk. However, the limited food-resource value of wine grape flowers for wild bees reinforces the importance of maintaining diverse non-crop floral resources in vineyard-dominated landscapes to support wild bee communities.

Introduction

Pollinator-independent crops are not necessarily crops in which pollinators do not visit their flowers. Conversely, while a crop may not benefit from pollinators visiting their flowers in terms of crop production, pollinators may still use the pollen as a food resource. While pollinators include several taxa, bees (Hymenoptera: Apiformes) hold a significant role in the pollination of both wild and crop plants as they forage for pollen and nectar to meet their nutrient requirements (Kral-O'Brien *et al.* 2022). With documented declines for several bee species globally (Vanbergen and The Insect Pollinators Initiative 2013; Goulson *et al.* 2015), understanding the plant resources used by bees is important for directing conservation actions.

Agriculture-dominated landscapes may hold heightened risks for bees due to threats including habitat loss, pesticide exposure, and interactions with non-native species (Vanbergen and The Insect Pollinators Initiative 2013). Thus, it is especially important to understand the resources used by bees in agricultural lands and the potential benefits (e.g., nutritional quality) or risks (e.g., pesticide exposure) of foraging on crop flowers for pollen. Globally, 60% of food production comes from crops that are pollinator-independent, with 28 of the leading food crops showing no benefit from animal pollination (Klein *et al.* 2007). This represents a significant amount of land where bees may have limited food resources available to them. Very little is known about the role of pollinator-independent crops as a pollen resource for bees (reviewed in Kral-O'Brien *et al.* 2022). Most research on this topic comes from pollen collected from European honey bees (*Apis mellifera* L., 1758) (Saunders 2018; Kral-O'Brien *et al.* 2022), thus, more observational studies are needed to understand the breadth of bees that may use these food resources. The wine grape (*Vitis vinifera* L., 1753 (Vitaceae)) is a pollinator-independent crop for which we lack information about use by bees. With ~ 7.4 mha of global area planted with commercial grapevines (OIV 2019) more research is needed to understand to what extent bees use grapevine pollen and whether this pollen usage differs by variety or species.

Grapevine (*Vitis* spp. Linnaeus (Vitaceae)) pollination is highly variable with flowers ranging from self-compatible to self-incompatible and pollination mechanisms including insect, wind, and self-

pollination (Pratt 1971; McGregor 1976; Vasconcelos *et al.* 2009). Self-pollination may happen before or after capfall, which is when the fused petals, or calyptra, that cover the reproductive organs are shed, and cross-pollination may also occur with both wind and insect pollen vectors (Sampson *et al.* 2001; Vasconcelos *et al.* 2009). For domesticated grapevines, autogamy is thought of as the main route for pollination (Carmona *et al.* 2008). Still, there have been records of certain *V. vinifera* cultivated varieties benefiting from cross-pollination (McGregor 1976; Sabir 2015). For other grapevine species, including wild and dioecious species, diverse insect visitors to flowers have been documented (Carmona *et al.* 2008). This includes bees in the families Andrenidae, Megachilidae, Halictidae, Apidae (honey bees), as well as beetles (Coleoptera), wasps (Hymenoptera), and flies (Diptera) (Detjen 1917; Branties, 1978; Sampson *et al.* 2001; Martignago *et al.* 2017; Zito *et al.* 2018; Baronio *et al.* 2021). For *V. vinifera*, there are few studies on the topic of bee visitors to flowers and, of those that do exist, most focus solely on honey bees. Honey bees have been shown to forage on wine grape flowers, selectively foraging on inflorescences with high numbers of loose caps, however *V. vinifera* pollen often makes up a only small percentage of the total pollen they collect (Vorwohl 1977; Dimou and Thrasyvoulou 2007; Di Pasquale *et al.* 2016; Hogendoorn *et al.* 2016). With many gaps in knowledge regarding bee visitation to wine grape flowers, the goal of this study is to investigate the bee visitors to several varieties of *V. vinifera* in the Niagara Region, Ontario. Specifically, we aim to determine the role of wine grape flowers as a pollen resource for bees, which bees use the cultivated grapevine pollen as a food resource, and whether there are varietal differences in the frequency of pollen collection.

Methods

We observed bees visiting wine grape flowers during bloom in commercial vineyards throughout the Niagara Peninsula, Ontario, Canada in 2021 and 2022. Growing 46 varieties of grapes across 13,600 acres, the peninsula represents the largest planted area of vineyards in Canada (VQA. n.d.). We sampled ten of the most commonly grown *V. vinifera* varieties in the area, five white varieties: Chardonnay, Gewurztraminer, Pinot Grigio/Gris, Riesling, Sauvignon Blanc and five red varieties: Gamay Noir, Pinot

Noir, Merlot, Cabernet Franc, and Syrah (Table 1). Surveys were performed in 19 vineyards in 2021 and in 14 vineyards in 2022 (Fig. 1). At each site, we surveyed one block growing one variety and all sites were a minimum of 600 m apart to sample independent bee communities (Gathmann and Tscharntke 2002). All blocks were mature with the year of planting ranging from 1985-2017. Blocks varied in size, row spacing, and vineyard management practices.

Through communications with growers, we attempted to survey when vines were near 50% capfall which was expected to have the highest pollen availability (Hogendoorn *et al.* 2016). Sampling occurred between 12-17 June 2021 and 17-25 June 2022 on precipitation-free, low wind and low cloud cover days. To confirm the % capfall of each block, we visually estimated the open flowers from a subset of 50-100 inflorescences along the central vine row. Each inflorescence was categorised as: 0%, 1-30%, 31-69%, >70% capfall. This was estimated using 5 inflorescences per vine across 10-20 vines selecting inflorescences of similar size and location on the vine (Vasconcelos *et al.* 2009). In 2021, bees were collected during a 10-minute walked transect in the morning (9:00 am - 12:00 pm) while in 2022 the transect walk was performed both in the morning (as above) and in the afternoon (12:00 pm - 5:00 pm) for 20 total minutes of sampling in 2022. Sampling occurred across three neighboring vine rows using a ~400m^2 transect in the centre of the vineyard block. Transects were walked at a very slow pace, surveying for bees foraging on the vine flowers on either side for 5 minutes in each neighboring row. Bees that were observed foraging on flowers (gripping open anthers with their legs, moving from open flower to open flower) were collected using an aerial insect net, or, in year 2 of the project were also collected with a battery-operated insect vacuum (InsectaVac Aspirator, BioQuip Products, CA). Bees were initially placed in a killing jar containing ethyl acetate and later stored in a freezer at ~-18°C until processing. If a bee was observed foraging on grapevine flowers outside of timed transects attempts were made to photograph or video record the behavior. Frozen bees were later thawed, pinned, labelled and identified using a dissecting microscope and the Discover Life bee species and genera guides (Ascher and Pickering 2022). Specimens in the genus *Lasioglossum* Curtis, 1833 were identified only to subgenus for *Dialictus*

Robertson, 1902 bees (Gardner and Gibbs n.d.) due to the difficulty in identification to species level for this group of bees. Collected bees are stored in the Colla YorkU lab at York University, Toronto, Canada.

Results

In total, ten bees (Table 2) were collected foraging on *V. vinifera* flowers across all standardized surveys, while six low-quality photos were taken of bees foraging on wine grape flowers outside of timed transect sampling (Fig. 2). Very few bees (less than 10) were additionally visually observed foraging on grapevine flowers outside of timed transects and were unable to be photographed or collected. Most of these bees were bumble bees (*Bombus* spp. Latreille, 1802) as they were often first heard "buzzing" before being observed foraging on flowers tucked into the vine canopy. Most bees collected were from the Halictidae family followed by Andrenidae while a few observations and photos of bumble bees in the Apidae family were also made. The most common bees collected were *Lasioglossum* bees in the subgenus *Dialictus* followed by *Halictus confusus* Smith, 1853. Of the species identified, two are exotic to Ontario; *Andrena wilkella* Kirby, 1802 and *Lasioglossum zonulum* Smith, 1848. Most of the bees collected are solitary, polylectic, ground-nesting bees (Grixti and Packer 2006; Mackell *et al.* 2023). Bees were predominantly observed and collected foraging on Gewürztraminer flowers though they were also collected on Cabernet Franc and Sauvignon Blanc flowers (Table 2) and observed on Syrah and Pinot Gris/Grigio flowers (Fig. 2).

Discussion

After ~8 hours of observation over two years, only 10 bees were collected from *V. vinifera* grapevine flowers in this study. This may be due, in part, to the limited attraction and rewards for flower foraging insects (Carmona *et al.* 2008). Grapevine flower nectaries do not seem to produce nectar but only floral oils (Pratt 1971; Branties 1978) and after capfall pollen grains dry quickly and disperse (Hogendoorn *et al.* 2016). Interestingly, however, *V. vinifera* flowers have been shown to produce volatile organic compounds (VOCs) which may serve to attract pollinators (Martin *et al.* 2009; Barbagallo *et al.* 2014; Zito *et al.* 2016). In contrast with previous work (e.g., Hogendoorn *et al*. 2016), we did not observe

any honey bees foraging on *V. vinifera* flowers. This may be attributable to the timing of grapevine flowering in Niagara, Ontario which is past the bloom period for other bee-pollinated crops grown in the region where honey bee hives are often used (Niagara Region 2016). However, some grape growers reported keeping honey bees on the study sites and others noted neighbors in close proximity that were known to have hives. These sites likely had other available floral resources that were preferred over the grapevine flowers by honey bees. Seven of the 10 bees we collected were foraging on Gewürztraminer flowers while we never observed bees on varieties such as Riesling and Chardonnay despite the higher number of sites sampled for these varieties (Table 1). Volatile aroma compounds produced by *V. vinifera* flowers have been shown to significantly differ between cultivated varieties which may impact the attraction of bees to different varieties (Barbagallo *et al.* 2014). Varietal differences also exist for pollen viability and germination rates (Sabir 2015; Pereira *et al.* 2018) and the morphology of pollen grains (Marasali *et al.* 2005). More research is needed on the differences in bee attraction to grapevine flowers across cultivated varieties and the underlying reasons and ecological implications of these differences.

We faced several challenges observing and collecting bees foraging on cultivated grapevine flowers. The first challenge was the difficulty in netting bees from within the dense grapevine canopies. However, the use of an additional insect vacuum in year 2 was unhelpful as the sound of the battery-operated vacuum tended to scare off bees and the narrow tip of the vacuum made collection difficult. Another challenge was that bees would often forage across rows rather than along a single row, thus, we could not adequately follow the bee's foraging behavior due to the trellis system. Furthermore, in the winter of 2021/2022, the Niagara Region experienced its worst winter damage to grapevines in decades (Rosas 2022) and many of the vineyards had very few vines with flowers for observation, reducing the number of sites we were able to sample in 2022. Beyond methodologic challenges, more research is needed to understand the ideal conditions for observing bees foraging on wine grape flowers including the % capfall and time of day as we observed bees foraging at a higher % capfall and later in the day than anticipated (Hogendoorn *et al.* 2016). Lastly, future research should include pollen removal from

collected bees and identification of pollen by morphology or DNA sequencing to confirm the flower species being used and to avoid the issues associated with observing bees directly on grapevine flowers.

Based on the results of this study, the risk of bee exposure to pesticides by foraging on cultivated grapevine flowers is rather low due to the low foraging activity for grapevine pollen observed. It is likely that other floral resources within vineyards such as weeds and cover crops hold a higher risk of pesticide exposure for most bees (OMAFRA 2023a; 2023b). Thus, off-target drift and pesticide accumulation in the soils is still a concern regarding bee exposure to pesticides in vineyard agroecosystems. Our research demonstrates that few bees use wine grape pollen as a food resource and thus, in vineyard-dominated landscapes, it is important to provide other floral resources for bees such as through cover cropping, wildflower plantings, and semi-natural areas. For the bee species and genera observed foraging on wine grape flowers in this study, more research is needed to determine the percentage of their diet that comes from wine grape pollen and how this might be impacted by the availability of surrounding floral resources (Cane and Sipes 2006). In conclusion, native and exotic bees in at least three families forage at least occasionally on *Vitis vinifera* flowers during bloom in vineyards of the Niagara Region, ON, Canada. While this dataset is small, it provides the first records of non-honey bees foraging on cultivated *V. vinifera* flowers and highlights useful future research directions.

References

Ascher, J.S. and Pickering, J. 2022. Discover Life bee species guide and world checklist (Hymenoptera: Apoidea: Anthophila). Draft-55. http://www.discoverlife.org/mp/20q?guide=Apoidea_species [accessed May 2024].

Barbagallo, M. G., Pisciotta, A. and Saiano, F. 2014. Identification of aroma compounds of *Vitis vinifera* L. flowers by SPME GC-MS analysis. *Vitis Journal of Grapevine Research*, **53**:111–113.

Baronio, G. J., Souza, C. S., Silva, N. N. A., Moura, N. P., Leite, A.V., Santos, A. M. M., Maciel, M. I. S. and Castro, C. C. 2021. Different visitation frequencies of native and non-native bees to vines: how much vegetation is necessary to improve fruit production?. *Plant Biology*, **23**(6): 923–930. doi: 10.1111/plb.13327

Branties, N. B. M. 1978. Pollinator attraction of *Vitis vinifera* subsp. *silvestris*. *Vitis*, **17**: 229–233

Cane, J. H. and Sipes, S. 2006. Characterizing floral specialization by bees: analytical methods and a revised lexicon for oligolecty Pp. 99-122 In Waser, N. M. and Ollerton, J. (eds) Plant-pollinator interactions: from specialization to generalization, The University of Chicago Press, Chicago.

Carmona, M. J., Chaïb, J., Martínez-Zapater, J. M. and Thomas, M. R. 2008. A molecular genetic perspective of reproductive development in grapevine. *Journal of Experimental Botany*, **59**(10): 2579–2596. doi:10.1093/jxb/ern160

Detjen, L. R. 1917. Pollination of the rotundifolia grapes. *Journal of the Elisha Mitchell Scientific Society*, **33**(3): 120–127.

Dimou, M. and Thrasyvoulou, A. 2007. A comparison of three methods for assessing the relative abundance of pollen resources collected by honey bee colonies. *Journal of Apicultural Research*, **46**(3): 144–148. doi:10.1080/00218839.2007.11101385

Di Pasquale, G., Alaux, C., Le Conte, Y., Odoux, J. F., Pioz, M., Vaissière, B. E., Belzunces, L.P. and Decourtye, A. 2016. Variations in the availability of pollen resources affect honey bee health. *PloS one*, **11**(9): e0162818. doi:10.1371/journal.pone.0162818

Gardner, J. and Gibbs, J. n.d. Key to *Lasioglossum* subgenera in Canada. University of Manitoba. Unpublished key.

Gathmann, A. and Tscharntke, T. 2002. Foraging ranges of solitary bees. *Journal of Animal Ecology*, **71**(5): 757–764. doi:10.1046/j.1365-2656.2002.00641.x

Goulson, D., Nicholls, E., Botías, C. and Rotheray, E. L. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science*, **347**(6229): 1255957-1–9. doi:10.1126/science.1255957

Grixti, J. C. and Packer, L. 2006. Changes in the bee fauna (Hymenoptera: Apoidea) of an old field site in southern Ontario, revisited after 34 years. *The Canadian Entomologist*, **138**(2): 147–164. doi:10.4039/n05-034

Hogendoorn, K., Anantanawat, K. and Collins, C. 2016. Cap removal by honey bees leads to higher pollen rewards from grapevine flowers. *Apidologie*, **47**(5): 671–678. doi:10.1007/s13592-015-0419-1

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C. and Tscharntke, T. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the royal society B: biological sciences*, **274**(1608): 303–313. doi:10.1098/rspb.2006.3721

Kral-O'Brien, K. C., Hovick, T. J. and Harmon, J. P. 2022. Quid Pro Quo? A Review on Bee Utilization of Pollinator-Independent Crops. *Annals of the Entomological Society of America*, **115**(1): 1–9. doi:10.1093/aesa/saab029

MacKell, S., Elsayed, H. and Colla, S. 2023. Assessing the impacts of urban beehives on wild bees using individual, community, and population-level metrics. *Urban Ecosystems*, **26**(5): 1209–1223. doi:10.1007/s11252-023-01374-4

Marasali, B., Pinar, M. and Büyükkartal, H. N. 2005. Palynological study on the pollen grains of selected Turkish grape (*Vitis vinifera* L.) cultivars. *Turkish Journal of Agriculture and Forestry*, **29**(1): 75–81.

Martignago, M., Martins, R. and Harter-Marques, B. 2017. Honey bee contribution to 'Bordô' grapevine fruit production in southern Brazil. *Revista Brasileira de Fruticultura*, **39**(3): 1–6. doi:10.1590/0100-29452017155

Martin, D. M., Toub, O., Chiang, A., Lo, B. C., Ohse, S., Lund, S. T. and Bohlmann, J. 2009. The bouquet of grapevine (*Vitis vinifera* L. cv. Cabernet Sauvignon) flowers arises from the biosynthesis of sesquiterpene volatiles in pollen grains. *Proceedings of the National Academy of Sciences*, **106**(17): 7245–7250. doi:10.1073/pnas.0901387106

McGregor, S. E. 1976. Chapter 7: Small Fruits and Brambles In Insect Pollination of Cultivated Crop Plants (No. 496). Agricultural Research Service, US Department of Agriculture, Washington D.C. [online]. https://www.ars.usda.gov/ARSUserFiles/20220500/OnlinePollinationHandbook.pdf [accessed May 2024].

Niagara Region. 2016. Niagara Agricultural Profile [online]. https://www.niagararegion.ca/living/ap/pdf/niagara-agricultural-profile.pdf [accessed May 2024].

OIV (International Organisation of Vine and Wine). 2019. “2019 Statistical Report on World Vitiviniculture” [online]. https://www.oiv.int/public/medias/6782/oiv-2019-statistical-report-on-world-vitiviniculture.pdf [accessed May 2024].

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). 2023a. Cover crops: cover crop types [online]. https://www.ontario.ca/page/cover-crops-cover-crop-types [accessed February 2024].

OMAFRA (Ontario Ministry of Agriculture, Food, and Rural Affairs). 2023b. Weed identification guide for Ontario crops [online]. https://www.ontario.ca/document/weed-identification-guide-ontario-crops [accessed May 2024].

Pereira, M. R., Ribeiro, H., Cunha, M. and Abreu, I. 2018. Comparison of pollen quality in *Vitis vinifera* L. cultivars. *Scientia Horticulturae*, **227:** 112–116. doi:10.1016/j.scienta.2017.09.038

Pratt, C. 1971. Reproductive anatomy in cultivated grapes - A review. *American Journal of Enology and Viticulture*, **22**(2): 92–109. doi:10.5344/ajev.1971.22.2.92

Rosas, A. C. July 8, 2022. “Unpredictable winters causing significant damage to vineyards in Niagara region” CBC News [online]. https://www.cbc.ca/news/canada/hamilton/winter-damage-niagara-1.6513401 [accessed May 2024].

Sabir, A. 2015. Xenia and metaxenia in grapes: differences in berry and seed characteristics of maternal grape cv.‘Narince’(*Vitis vinifera* L.) as influenced by different pollen sources. *Plant Biology*, **17**(2): 567–573. doi:10.1111/plb.12266

Sampson, B., Noffsinger, S., Gupton, C. and Magee, J. 2001. Pollination biology of the muscadine grape. *HortScience*, **36**(1): 120–124.

Saunders, M. E. 2018. Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. *Insect Conservation and Diversity*, **11**(1): 13–31. doi:10.1111/icad.12243

Vanbergen, A. J. and The Insect Pollinators Initiative. 2013. Threats to an ecosystem service: Pressures on pollinators. *Frontiers in Ecology and the Environment*, **11**(5): 251–259. doi:10.1890/120126

Vasconcelos, M. C., Greven, M., Winefield, C. S., Trought, M. C. and Raw, V. 2009. The flowering process of *Vitis vinifera*: a review. *American Journal of Enology and Viticulture*, **60**(4): 411–434. doi:10.5344/ajev.2009.60.4.411

Vorwohl, G. 1977. The importance of the grapevine [*Vitis* spp.] as pollen-plant for the honeybee [*Apis mellifera* L]. *Apidologie*, **8**(3): 237–257.

VQA Ontario (Vintners Quality Alliance Ontario). n.d. The Niagara Peninsula Appellation Overview [online]. https://www.vqaontario.ca/Appellations/Niagara-Peninsula/ [accessed May 2024].

Zito, P., Scrima, A., Sajeva, M., Carimi, F. and Dötterl, S. 2016. Dimorphism in inflorescence scent of dioecious wild grapevine. *Biochemical Systematics and Ecology*, **66:** 58–62. doi:10.1016/j.bse.2016.03.003

Zito, P., Serraino, F., Carimi, F., Tavella, F. and Sajeva, M. 2018. Inflorescence-visiting insects of a functionally dioecious wild grapevine (*Vitis vinifera* subsp. *sylvestris*). *Genetic Resources and Crop Evolution*, **65**(5): 1329–1335. doi:10.1007/s10722-018-0616-7

Tables

Table 1: *Vitis vinifera* cultivated varieties surveyed for bee visitors to grapevine flowers including the number of sites sampled for each variety and the mean capfall (%) at the time of sampling. Dashed lines represent a variety not sampled in that year.

Variety	No. of sites		Mean capfall per variety (%)	
	2021	2022	2021	2022
Cabernet Franc	4	2	44	84
Chardonnay	3	3	25	69
Riesling	3	2	30	80
Merlot	2	1	60	64
Sauvignon Blanc	2	2	40	77
Gewürztraminer	1	2	21	74
Pinot Gris/Grigio	1	2	72	82
Syrah	1	0	42	------
Pinot Noir	1	0	55	------
Gamay Noir	1	0	42	------

Table 2: Bees collected foraging on *Vitis vinifera* flowers with their functional traits and the grape variety, sampling year, and mean capfall when collected.

Family	Genus	Species or subgenus(*)	Native or exotic [1]	Nesting[1]	Sociality [1]	Diet[1]	Variety	Year	Mean capfall per site (%)
Halictidae	*Agapostemon*	*sericeus* (Forster, 1771)	Native	Ground	Solitary	Polylectic	Gewürztraminer	2021	21
Halictidae	*Lasioglossum*	*zonulum* (Smith, 1848)	Exotic	Ground	Solitary	Polylectic	Gewürztraminer	2021	21
Halictidae	*Lasioglossum*	*Dialictus** (Robertson, 1902)	n/a	n/a	n/a	n/a	Gewürztraminer	2022	71
Halictidae	*Lasioglossum*	*Dialictus** (Robertson, 1902)	n/a	n/a	n/a	n/a	Gewürztraminer	2022	71
Halictidae	*Lasioglossum*	*Dialictus** (Robertson, 1902)	n/a	n/a	n/a	n/a	Gewürztraminer	2022	71
Halictidae	*Lasioglossum*	*Dialictus** (Robertson, 1902)	n/a	n/a	n/a	n/a	Gewürztraminer	2022	71
Halictidae	*Halictus*	*confusus* (Smith, 1853)	Native	Ground	Social	Polylectic	Gewürztraminer	2022	71
Halictidae	*Halictus*	*confusus* (Smith, 1853)	Native	Ground	Social	Polylectic	Cabernet Franc	2022	85
Andrenidae	*Andrena*	*miranda* (Smith, 1879)	Native	Ground	Solitary	Polylectic	Cabernet Franc	2022	82
Andrenidae	*Andrena*	*wilkella* (Kirby, 1802)	Exotic	Ground	Solitary	Polylectic	Sauvignon blanc	2022	78

[1] Grixti and Packer (2006); MacKell *et al*. (2023). *Bees in the subgenus *Dialictus* were not identified to species, thus, functional traits could not be determined.

Figures

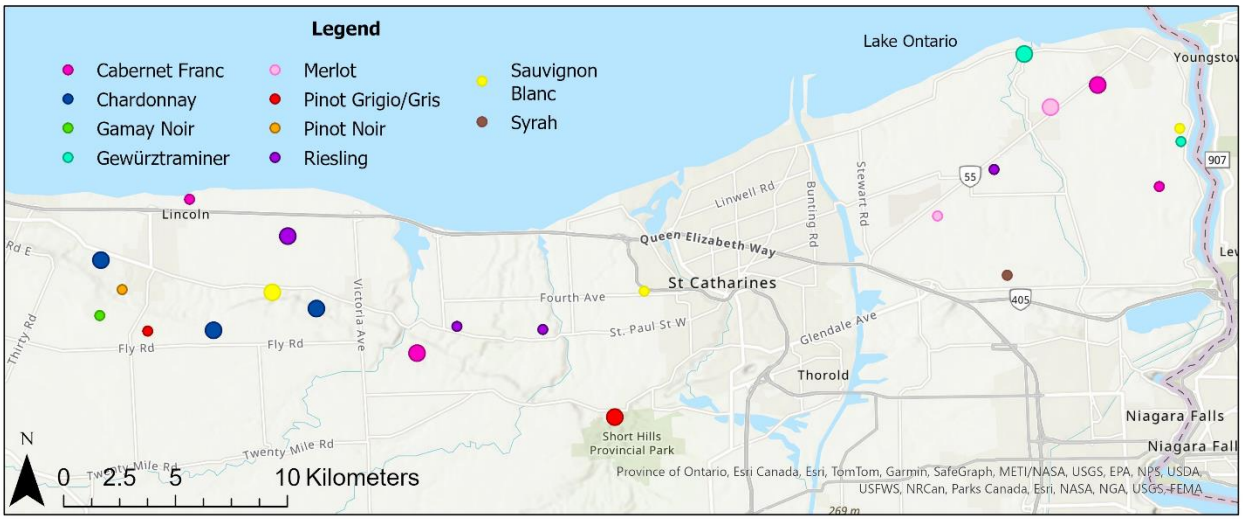


Figure 1: Site locations of vineyards where observations of the bee visitors to *Vitis vinifera* flowers occurred. At each site, one cultivated variety was observed as indicated by the different colours. Sites were sampled in either 2021 (9 sites), 2022 (4 sites), or in both years (10 sites). Sites sampled in both years are represented by larger circles whereas smaller circles represent sites sampled in only one year (either 2021 or 2022).

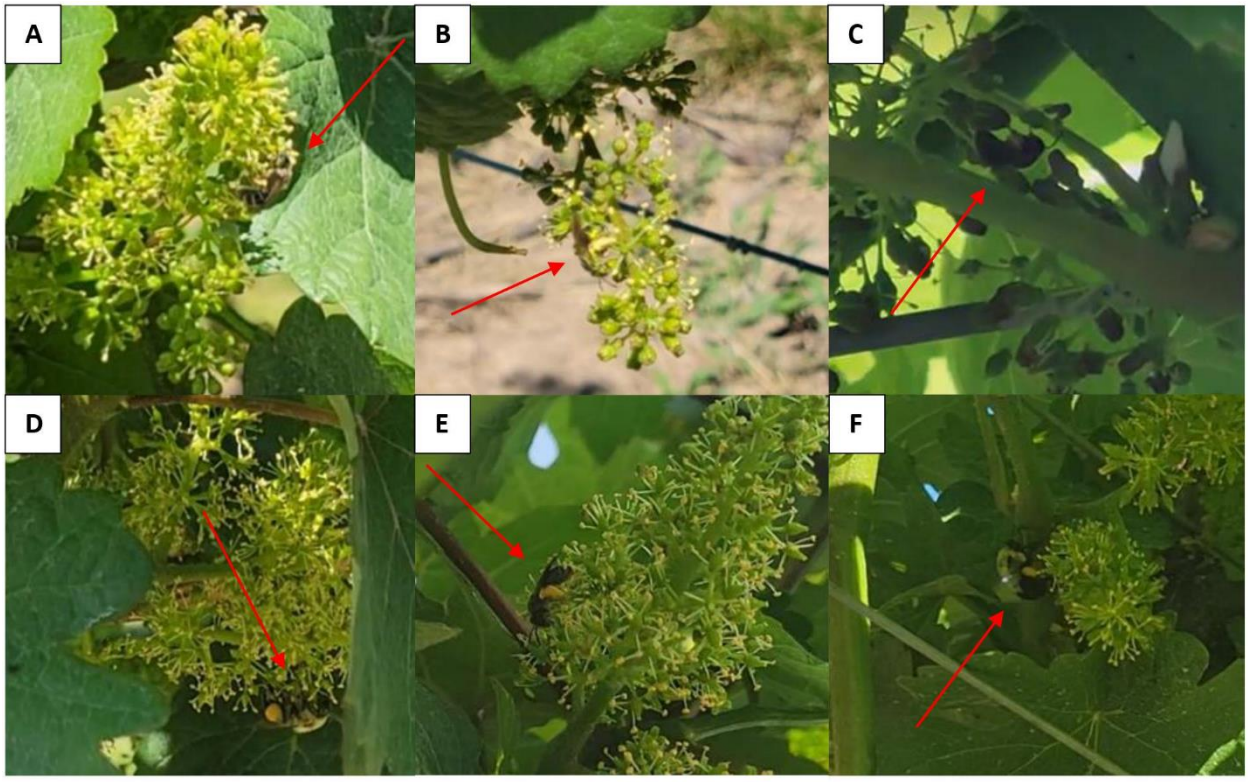


Figure 2: Images captured of bees foraging on *Vitis vinifera* flowers outside of timed transects. Images were taken as either a still photograph or a screenshot from a video recording. The year and variety associated with each image from top-left to bottom-right are as follows; A: 2021 Gewürztraminer, B: 2021 Gewürztraminer, C: 2021 Syrah, D: 2021 Gewürztraminer, E: 2022 Gewürztraminer, F: 2021 Pinot Gris/Grigio. Photos by Briann Dorin and Ryanna Baich.

Chapter 5: Conclusion and recommendations

The overall objective of this thesis was to better understand the role of pollinator-independent crops in wild bee conservation. Agricultural lands cover 5 billion hectares globally or 38% of the world's land area (FAO, 2020) and agricultural land use is considered the leading global driver of biodiversity loss (Newbold et al., 2015; Kehoe et al., 2017). One group of animals with evidence of declines are pollinators - associated with several threats including habitat loss, pesticide exposure, climate change, and interactions with non-native and managed species such as pest and disease spread (Cane & Tepedino, 2001; Potts et al., 2010). Animal pollinators provide an essential ecosystem service in the form of pollinating ~87% of global flowering plant species (Ollerton et al., 2011) and further pollinating 87 of the leading global food crops (Klein et al., 2007). The economic value of crop pollination services globally ranges from $195-$387 billion USD depending on the valuation methods used (Porto et al., 2020). A large percentage of this animal pollination is from bees (Hymenoptera: Apoidea: Apiformes) with ~1/3 of human diets coming from bee-pollinated crops specifically (Thapa, 2006; Klein et al., 2007; Khalifa et al., 2021). For monoculture crop production, one bee species in particular, the European honey bee (*Apis mellifera*), is highly relied upon for crop pollination where wild pollinator populations may not be sufficient to provide this service (Klein et al., 2007). However, several crops have been shown to be better pollinated by wild bees or other non-honey bee pollinators and many crops benefit when a diversity of bees visit their flowers (Klein et al., 2007; Reilly et al., 2024). Thus, concerns exist regarding a loss of wild pollinators and the crop pollination services they provide (Steffan-Dewenter et al., 2005; Artamendi et al., 2025). And with the alarming losses of honey bee colonies being experienced by beekeepers since the early 2000s (Aurell et al., 2024), this may lead to an increased dependence on wild pollinators to provide this essential ecosystem service if bee keeping becomes increasingly less viable (Klein et al., 2007). Declines in wild bee species can also have negative implications for natural ecosystems and flora

as bee declines can negatively influence animal-pollinated plant reproductive success if plants are unable to adapt (Artamendi et al., 2025; Thomann, 2013).

Many economically important crops globally do not require animal pollination, instead, being self-fertile or pollinated by abiotic factors such as wind (Klein et al., 2007). While these crops lack the economic driver of crop pollination to motivate actions that support pollinator populations, pollinator-independent crop fields may still hold significant capacity to help conserve and protect wild pollinators within the greater landscape (Saunders, 2018). In Chapter 1, I reviewed the current state of knowledge on primary research projects examining wild bee responses to local and/or landscape factors in the top global pollinator-independent crops. One major finding from this review was the large crop and geographic discrepancy across studies. Previous research has shown that crops differ in their biodiversity pressures (Chapman et al., 2025) and in their wild bee visitors and communities as well as factors such as their risks to pollinators from pesticide exposure (Martins et al., 2018; Rondeau et al., 2022; French et al., 2024). More research is needed on the topic of bee conservation in crops with low or no pollinator-dependence that accounts for differences in crop management across crop types. The geographic bias in current research highlights the importance of also expanding this research to understudied global areas, as biodiversity pressures from agricultural land-use differ across regions, associated with factors such as the overlap of agricultural land area with species ranges, crop production volumes, national consumption and global food trade (Chapman et al., 2025). A recent global analysis of 303 studies demonstrated that land-use intensity in cropland had differing impacts on pollinators in tropical vs. temperate lands such that cropland use, compared to a primary vegetation baseline, negatively impacted pollinator total abundance and species richness in tropical areas but not in temperate areas (Millard et al., 2021). This demonstrates the importance of expanding our current state of knowledge on the topic of bee conservation in agricultural lands to understudied crops and regions, as biodiversity losses tend to be concentrated in biodiverse but economically poor countries (Newbold et al., 2015). These regions may not be supported

by conservation programs or spending and are at a heightened risk of biodiversity losses under future agricultural intensification and expansion forecasting (Kehoe et al., 2017).

The level of pollinator dependence or independence of crops can have mixed evidence based on factors such as study design and crop genotypes regarding the level of yield or other crop benefits from animal pollination (Tamburini et al., 2019; Bishop and Nakagawa, 2021; Esquivel et al., 2021). Several crops are deemed highly reliant on animal pollination, such as almonds, where growers often pay for honey bee colonies during crop bloom to ensure sufficient crop pollination (Goodrich et al., 2019). Yet, with current breeding programs, even these highly animal-pollinator reliant crops are now producing varieties with lowered pollinator dependence (Sáez et al., 2020). According to Sáez, et al., (2020) the deemed pollinator-independent almond variety Independence is the fastest growing variety in California - the world's largest almond producing region. Thus, pollinator-dependence is a complicated categorisation for crops and while historically, pollinator research may have focused primarily on highly pollinator-dependent crops, even crops with deemed little or moderate benefit from animal pollination such as soybean, coffee, and canola may have greater benefits than previously considered (Esquivel et al., 2021). These crops should have increased research on the crop benefits of animal pollination as well as greater involvement in pollinator conservation programs and policies. This should be supplemented with social science research regarding farmers' perceptions and their willingness to change behaviours for pollinator health. This information can help inform policies and programs aimed at collaborating with farmers to support pollinator conservation efforts by identifying motivations and barriers and understanding how this differs by crop type and geographic location (Hall and Martins, 2020).

In Chapter 2, I focused on the farm management practices that support abundant and diverse bee communities in a pollinator-independent crop, the wine grape. A major finding was the importance of between-row vegetation height for both bee abundance and diversity metrics. While planting flowers for bees is a commonly promoted farmland pollinator conservation action (Wood et al., 2017), which this thesis also supports by demonstrating a positive relationship between bees and floral abundance, allowing

the between-row vegetation to grow taller was the strongest predictor out of all the measured local floral and vegetation variables. Vegetation height is a less commonly recorded, measured, or reported variable in other studies on this topic. This chapter emphasizes the importance of this variable when researching wild bee responses to land management practices, both in rural and non-rural contexts. Mowing frequency research in other fields, such as in road-side verges and rights-of-ways, can help inform this research in a cropland context (Du Clos et al., 2021). Interestingly, there was limited evidence to support the benefits of several other sustainable vineyard management practices for supporting diverse and abundant bee communities in Chapter 2, particularly cover cropping, organic management, and a regional vineyard sustainability certification. The limited support may reflect the study's methodological approach, particularly the extent to which spatio-temporal dynamics of practice adoption, such as pesticide exposure, were considered. Wild bees are exposed to pesticides in agricultural landscapes through various routes and across different life stages (Raine and Rundlöf, 2024). From exposure in nest sites, such as in underground nests through pesticide soil accumulation, to direct and indirect exposure to sprays and pesticides across crop and non-crop plants when foraging, detecting responses of wild bees to organic management at the site-level is challenging. Without accounting for the management practices of neighbouring crop fields, it is difficult to assess realistic pesticide exposure levels when only considering site-level organic management. Furthermore, in this study, time under organic management was not obtained from producers and thus, not included in analyses, although different pesticides have varying degradation behaviours (Lonsdorf et al., 2024). Future research should examine landscape-scale adoption of organic practices within the foraging ranges of different bee species, alongside the temporal dynamics of organic management to better understand the time needed for impacts to become detectable in bee communities (Lonsdorf et al., 2024).

Another important factor is the wide range in functional traits and taxonomy among the bees collected in this study. Such variability suggests that some bees may have responded more strongly than others to different management practices, depending on their life history traits, functional traits, and

ecology. For example, although cover cropping was not shown to benefit site-level bee abundance or diversity metrics, positive effects might have been detected for certain bee groups or taxa, such as bumble bees, which are known to forage on the dominant cover crops of clover found in Niagara vineyards (Kanduth et al., 2021). This echoes other research that has shown that agri-environment schemes that promote floral plantings only benefit a limited suite of bee species (Wood et al., 2017). It is possible that uniform solutions applied across farmlands may be less beneficial for bees than diverse management practices across farms. Thus, while site-level alpha bee diversity may not uniformly benefit from certain practices, having multiple farms under varying management regimes could be more beneficial overall to the regional beta- and gamma- diversity. More research is needed on the matrix of farm management practices across farmland and on farm-to-farm interactions and their impacts on bees (Tsang et al., 2025). This also requires an understanding of how policies and programs can account for landscape-scale management of farmland for biodiversity including farmer-to-farmer cooperation and trust (Sutherland et al, 2012). The community composition analyses in Chapter 2 demonstrated that the bee communities in vineyards differed significantly between conventional, organic, and certified sustainable sites. The reasons behind this variability were further highlighted in Chapter 3 where I investigated the multi-scale drivers of vineyard bee communities, including vineyard management practices, surrounding land-uses, and soils.

In Chapter 3, in addition to highlighting the importance of semi-natural lands for bees, I show that bee nesting traits are strongly associated with the grouping of bee communities and that soil texture is important for shaping these patterns. Given the ground-nesting nature of ¾ of all bees (Antoine and Forrest, 2021), it is concerning that soils are less often considered in both research and conservation planning for bees in farmlands (as discussed in Antoine et al., 2025). Despite the vast amount of research on bee conservation that has been produced over the last decade, there is a glaring gap in knowledge on bee nesting habitat for most species (Antoine and Forrest, 2021). This is primarily due to difficulty in detecting underground bee nests (Antoine and Forrest, 2021). This thesis adds to the evidence that nest site availability is a key habitat variable for bee conservation, highlighting the need for fundamental

research on bee nesting in farmlands and how it is shaped by farm management practices and surrounding land uses.

Another important consideration is the interpretation of large-scale field studies on bee communities when soils are not accounted for. If bee communities are largely shaped by nest site availability, such as soil texture, then in areas where soils differ significantly across landscapes, such as the Niagara Region (Haynes, 2000), this should be accounted for in study design and interpretation. For instance, if underground-nesting bees are more common in sandier soils, then comparing bee abundance or diversity between sandier and less-sandy sites in response to management practices could yield misleading conclusions. A paired-site design would help control for soil variables, although this was not feasible here due to the limited availability of certified organic and sustainable vineyards at the start of the study. Still, this thesis highlights the important role of soil variables in large-scale region-wide studies on bee responses to land management and surrounding land uses. Future research should place significant emphasis on measuring soil variables or using publicly available soil data in analyses. Further disentangling of the effects of soils and slopes on qualities like plant composition, and not just on bee nest site availability, remains a challenge and requires additional experimental approaches (Antoine et al., 2025).

Lastly, in Chapter 4, the bee visitors to wine grape flowers during bloom were surveyed to understand if bees use wine grape pollen as a food resource. Several challenges with this study were discussed in the Chapter, however, the results do show that some bees will use this pollen, albeit at very low levels. The limited data makes it difficult to determine why this pollen was used at some sites and for some bees. Possible explanations include a lack of alternative resources at these sites, the proximity to nests, or the nutritional qualities of grapevine pollen which may benefit certain bees. Although research on plant-pollinator networks is increasing (Bascompte and Scheffer, 2023), there remains a critical need to better understand the nutritional aspects of these interactions and the quality of floral resources for bees (Crone et al., 2022). Fundamental data on the nutritional profiles of crop flowers, including those

considered to have low pollinator dependence (Esquival et al., 2021), as well as common non-crop, weedy and planted species, are essential for assessing the risks and benefits of foraging for a diversity of wild bee species and life stages (Filipiak, 2018). Bee nutrition in agricultural landscapes is still poorly understood and warrants further investigation.

Overall, this thesis adds to the literature on important facets of wild bee conservation in agricultural lands, with a focus on pollinator-independent crops. With almost half the world's habitable land in use for agriculture, these landscapes represent a significant capacity for supporting conservation efforts. With growing political emphasis and support for bee conservation in farmland (Jones Ritten et al., 2017; Cole et al., 2020), scientific evidence is needed to inform these programs and guide effective conservation actions. This thesis demonstrates the importance of crop- and location-specific research on this topic and a highlights a large number of understudied crop types and regions globally. This thesis also highlights the importance of multi-scale research on the topic to understand how both local and landscape factors influence wild bees. Specifically, further emphasis should be placed on understanding bee nesting behaviours in agricultural landscapes and identifying key nesting habitat variables for a variety of taxa and functional traits across wild bees. Longer-term studies are also necessary to detect the impacts of pesticide exposure at the field-level such as organic farm management. Further research into how sustainable farming practices can be enhanced to better support wild bees, including mowing frequencies, sustainability certifications, and floral plantings is necessary to ensure pollinators are considered in agri-environmental-type programs. Lastly, more research is needed on the nutritional value of crop and non-crop floral resources to expand our understanding of not only which floral resources are being used by bees, but also the implications for population health among species.

References

Antoine, C. M., & Forrest, J. R. (2021). Nesting habitat of ground-nesting bees: a review. *Ecological Entomology*, *46*(2), 143-159.

Antoine, C. M., Normandin, E., & Forrest, J. R. (2025). Associations between soil characteristics and ground-nesting bees on farms. *Insect Conservation and Diversity*.

Artamendi, M., Martin, P. A., Bartomeus, I., & Magrach, A. (2025). Loss of pollinator diversity consistently reduces reproductive success for wild and cultivated plants. *Nature Ecology & Evolution*, *9*(2), 296-313.

Aurell, D., Bruckner, S., Wilson, M., Steinhauer, N., & Williams, G. R. (2024). A national survey of managed honey bee colony losses in the USA: results from the Bee Informed Partnership for 2020–21 and 2021–22. *Journal of Apicultural Research*, *63*(1), 1-14.

Bascompte, J., & Scheffer, M. (2023). The resilience of plant–pollinator networks. *Annual Review of Entomology*, *68*(1), 363-380.

Bishop, J., & Nakagawa, S. (2021). Quantifying crop pollinator dependence and its heterogeneity using multi-level meta-analysis. *Journal of Applied Ecology*, *58*(5), 1030-1042.

Cane, J. H., & Tepedino, V. J. (2001). Causes and extent of declines among native North American invertebrate pollinators: detection, evidence, and consequences. *Conservation Ecology*, *5*(1).

Chapman, A. S., Green, R., Hadida, G., Kennard, H., Mabhaudhi, T., Scheelbeek, P., & Dalin, C. (2025). Biodiversity pressure from fruit and vegetable consumption in the United Kingdom, India and South Africa varies by product and growing location. *Nature food*, 1-14.

Cole, L. J., Kleijn, D., Dicks, L. V., Stout, J. C., Potts, S. G., Albrecht, M., Balzan, M. V., Bartomeus, I., Bebeli, P. J., & Bevk, D. (2020). A critical analysis of the potential for EU Common Agricultural Policy measures to support wild pollinators on farmland. J. Appl. Ecol., 57(4), 681–694.

Crone, M. K., Biddinger, D. J., & Grozinger, C. M. (2022). Wild bee nutritional ecology: Integrative strategies to assess foraging preferences and nutritional requirements. *Frontiers in Sustainable Food Systems*, *6*, 847003.

Du Clos, B., deMaynadier, P., Drummond, F., & Loftin, C. (2021). Roadside rights-of-way as pollinator habitat: A literature review. Technical Report 21-01, MaineDOT, Research and Innovation Office, Augusta, ME. Retrieved from: https://rosap.ntl.bts.gov/view/dot/62729

Esquivel, I. L., Parys, K. A., & Brewer, M. J. (2021). Pollination by non-Apis bees and potential benefits in self-pollinating crops. *Annals of the Entomological Society of America*, *114*(2), 257-266.

FAO (2020, May 7). “Land use in agriculture by the numbers”. Food and Agriculture Organization of the United Nations. Retrieved from: https://www.fao.org/sustainability/news/detail/en/c/1274219/

Filipiak, M. (2018). A better understanding of bee nutritional ecology is needed to optimize conservation strategies for wild bees—the application of ecological stoichiometry. *Insects*, *9*(3), 85.

French, S. K., Pepinelli, M., Conflitti, I. M., Jamieson, A., Higo, H., Common, J., ... & Zayed, A. (2024). Honey bee stressor networks are complex and dependent on crop and region. *Current Biology*, *34*(9), 1893-1903.

Goodrich, B. K., Williams, J. C., & Goodhue, R. E. (2019). The great bee migration: supply analysis of honey bee colony shipments into California for almond pollination services. American Journal of Agricultural Economics, *101*(5), 1353-1372.

Hall, D. M., & Martins, D. J. (2020). Human dimensions of insect pollinator conservation. *Current opinion in insect science*, *38*, 107-114.

Haynes, S. J. (2000). Geology and Wine 2. A geological foundation for terroirs and potential sub-appellations 1063 of Niagara Peninsula wines, Ontario, Canada. Geoscience Canada 27:67-87.

Jones Ritten, C., Bastian, C., Shogren, J. F., Panchalingam, T., Ehmke, M. D., & Parkhurst, G. (2017). Understanding pollinator habitat conservation under current policy using economic experiments. Land, 6(3), 57.

Kanduth, L., Chartier, M., Schönenberger, J., & Dellinger, A. S. (2021). Red and white clover provide food resources for honeybees and wild bees in urban environments. *Nordic Journal of Botany*, *39*(3).

Kehoe, L., Romero-Muñoz, A., Polaina, E., Estes, L., Kreft, H., & Kuemmerle, T. (2017). Biodiversity at risk under future cropland expansion and intensification. *Nature ecology & evolution*, *1*(8), 1129-1135.

Khalifa, S. A., Elshafiey, E. H., Shetaia, A. A., El-Wahed, A. A. A., Algethami, A. F., Musharraf, S. G., ... & El-Seedi, H. R. (2021). Overview of bee pollination and its economic value for crop production. *Insects*, *12*(8), 688.

Klein, A. M., Vaissière, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings of the royal society B: biological sciences*, *274*(1608), 303-313.

Lonsdorf, E. V., Rundlöf, M., Nicholson, C. C., & Williams, N. M. (2024). A spatially explicit model of landscape pesticide exposure to bees: Development, exploration, and evaluation. *Science of the Total Environment*, *908*, 168146.

Martins, K. T., Albert, C. H., Lechowicz, M. J., & Gonzalez, A. (2018). Complementary crops and landscape features sustain wild bee communities. *Ecological Applications*, *28*(4), 1093-1105.

Millard, J., Outhwaite, C. L., Kinnersley, R., Freeman, R., Gregory, R. D., Adedoja, O., ... & Newbold, T. (2021). Global effects of land-use intensity on local pollinator biodiversity. *Nature communications*, *12*(1), 2902.

Newbold, T., Hudson, L. N., Hill, S. L., Contu, S., Lysenko, I., Senior, R. A., ... & Purvis, A. (2015). Global effects of land use on local terrestrial biodiversity. *Nature*, *520*(7545), 45-50.

Ollerton, J., Winfree, R., & Tarrant, S. (2011). How many flowering plants are pollinated by animals?. *Oikos*, *120*(3), 321-326.

Porto, R. G., de Almeida, R. F., Cruz-Neto, O., Tabarelli, M., Viana, B. F., Peres, C. A., & Lopes, A. V. (2020). Pollination ecosystem services: A comprehensive review of economic values, research funding and policy actions. *Food Security*, *12*(6), 1425-1442.

Potts, S. G., Biesmeijer, J. C., Kremen, C., Neumann, P., Schweiger, O., & Kunin, W. E. (2010). Global pollinator declines: trends, impacts and drivers. *Trends in ecology & evolution*, *25*(6), 345-353.

Raine, N. E., & Rundlöf, M. (2024). Pesticide exposure and effects on non-Apis bees. *Annual review of entomology*, *69*(1), 551-576.

Reilly, J., Bartomeus, I., Simpson, D., Allen-Perkins, A., Garibaldi, L., & Winfree, R. (2024). Wild insects and honey bees are equally important to crop yields in a global analysis. *Global Ecology and Biogeography*, *33*(7), e13843.

Rondeau, S., Willis Chan, D. S., & Pindar, A. (2022). Identifying wild bee visitors of major crops in North America with notes on potential threats from agricultural practices. *Frontiers in Sustainable Food Systems*, *6*, 943237.

Sáez, A., Aizen, M. A., Medici, S., Viel, M., Villalobos, E., & Negri, P. (2020). Bees increase crop yield in an alleged pollinator-independent almond variety. *Scientific reports*, *10*(1), 3177.

Saunders, M. E. (2018). Insect pollinators collect pollen from wind-pollinated plants: implications for pollination ecology and sustainable agriculture. *Insect conservation and diversity*, *11*(1), 13-31.

Steffan-Dewenter, I., Potts, S. G., & Packer, L. (2005). Pollinator diversity and crop pollination services are at risk. *Trends in ecology & evolution*, *20*(12), 651-652.

Sutherland, L. A., Gabriel, D., Hathaway-Jenkins, L., Pascual, U., Schmutz, U., Rigby, D., ... & Stagl, S. (2012). The 'Neighbourhood Effect': A multidisciplinary assessment of the case for farmer co-ordination in agri-environmental programmes. *Land Use Policy*, *29*(3), 502-512.

Tamburini, G., Bommarco, R., Kleijn, D., van der Putten, W. H., & Marini, L. (2019). Pollination contribution to crop yield is often context-dependent: A review of experimental evidence. *Agriculture, ecosystems & environment*, *280*, 16-23.

Thapa, R. B. (2006). Honeybees and other insect pollinators of cultivated plants: a review. *Journal of the Institute of Agriculture and Animal Science*, *27*, 1-23.

Thomann, M., Imbert, E., Devaux, C., & Cheptou, P. O. (2013). Flowering plants under global pollinator decline. *Trends in plant science*, *18*(7), 353-359.

Tsang, T. P., De Santis, A. A., Armas-Quiñonez, G., Ascher, J. S., Ávila-Gómez, E. S., Báldi, A., ... & Bonebrake, T. C. (2025). Land use change consistently reduces α-but not β-and γ-diversity of bees. *Global change biology*, *31*(1), e70006.

Wood, T. J., Holland, J. M., & Goulson, D. (2017). Providing foraging resources for solitary bees on farmland: current schemes for pollinators benefit a limited suite of species. *Journal of Applied Ecology*, *54*(1), 323-333.

Supplemental Tables

Chapter 2

Supplemental Table 1: Site information for the commercial vineyard blocks used for data collection including their management category (Organic, Sustainable, or Conventional), the Vintners Quality Alliance (VQA) [now the Ontario Wine Appellation Authority] sub-appellation (https://vqaontario.ca/ontario-appellations/niagara-peninsula/), the *Vitis vinifera* L. cultivated variety, year of planting, and the size of the block sampled as well as the years sampled for this project (2021, 2022, or both years). Sustainable sites are those certified through the Sustainable Winegrowing Ontario certification program (https://sustainablewinegrowingontario.ca/).

Site management	Sub-appellation	Variety	Year planted	Block size (acres)	Years sampled
Organic 1	Beamsville Bench	Chardonnay	1991	1.42	Both
Organic 2	Beamsville Bench	Pinot Noir	2009	1.30	Both
Organic 3	Twenty Mile Bench	Chardonnay	2006	0.96	Both
Organic 4	Beamsville Bench	Sauvignon Blanc	1993	0.97	Both
Organic 5	Twenty Mile Bench	Cabernet Franc	1999	9.84	Both
Organic 6	Four Mile Creek	Merlot	2017	1.98	Both
Organic 7	Four Mile Creek	Chardonnay	2013	1.35	Both
Organic 8	Four Mile Creek	Cabernet Franc	1998	1.66	Both
Organic 9	Vinemount Ridge	Gamay Noir	2014	4.2	2021
Organic 10	Lincoln Lakeshore	Cabernet Franc	1996	3.0	2021
Conventional 1	Vinemount Ridge	Chardonnay	2000	2.01	Both
Conventional 2	Creek Shores	Riesling	2009	1.89	Both
Conventional 3	Creek Shores	Riesling	2015	4.67	Both
Conventional 4	Creek Shores	Sauvignon Blanc	2017	2.97	Both
Conventional 5	St. David's Bench	Syrah	2001	5.19	Both
Conventional 6	Vinemount Ridge	Pinot Gris	2002	1.44	2022
Conventional 7	Vinemount Ridge	Gewürztraminer	2003	2.2	2022
Conventional 8	Four Mile Creek	Riesling	1998	3.88	2022

Sustainable 1	Lincoln Lakeshore	Riesling	2006	3.2	Both
Sustainable 2	Short Hills Bench	Pinot Grigio	2015	6.56	Both
Sustainable 3	Niagara Lakeshore	Merlot	1990	1.77	Both
Sustainable 4	Niagara Lakeshore	Cabernet Franc	2001	1.56	Both
Sustainable 5	Niagara Lakeshore	Gewürztraminer	1997	1.2	Both
Sustainable 6	Vinemount Ridge	Gamay Noir	2013	3.4	2022
Sustainable 7	Niagara River	Sauvignon Blanc	1999	4.3	2022
Sustainable 8	Niagara River	Gewürztraminer	1985	1.3	2022

Supplemental Table 2: Open flower species recorded in vineyards. Flowers were considered cover crops if a grower noted planting it as a cover crop or if it is recommended as a cover crop (OMAFRA, 2023b). All other flowers were considered weeds per OMAFRA (2009; 2023a) or simply due to them not being knowingly planted as a cover crop (as indicated by *). The average abundance (number of flowering units) per species across sites and years is shown as well as the frequency (number of sites where present). Plant taxonomy was taken from the USDA PLANTS Database (https://plants.sc.egov.usda.gov/home/plantProfile?symbol=TRRE3)

Common name	Family	Genus	Species	Cover crop or weed	Abundance	Frequency
Redroot amaranth	Amaranthaceae (amaranth)	Amaranthus	retroflexus L.	Weed	9.00	17
Annual ragweed	Asteraceae (aster)	Ambrosia	artemisiifolia L.	Weed	0.54	2
Scarlet pimpernel	Primulaceae (primrose)	Anagallis	arvensis L.	Weed	0.27	1
Stinking chamomile	Asteraceae (aster)	Anthemis	cotula L.	Weed*	0.38	1
Hairy rockcress	Brassicaceae (mustard)	Arabis	hirsuta (L.) Scop.	Weed*	0.15	1
Common milkweed	Asclepiadoideae (milkweed)	Asclepias	syriaca L.	Weed	0.02	1
Spear saltbush	Chenopodiaceae (goosefoot)	Atriplex	patula L.	Weed	3.00	4
Garden yellowrocket	Brassicaceae (mustard)	Barbarea	vulgaris W.T. Aiton	Weed	0.02	1
Field mustard	Brassicaceae (mustard)	Brassica	rapa L.	Cover crop	0.04	1
Shepherd's-purse	Brassicaceae (mustard)	Capsella	bursa-pastoris (L.) Medik.	Weed	15.81	16
Common mouse-ear chickweed	Caryophyllaceae (pink)	Cerastium	fontanum Baumg.	Weed	1.19	5
Lambsquarters	Chenopodioideae	Chenopodium	album L.	Weed	14.27	13
Chicory	Asteraceae (aster)	Cichorium	intybus L.	Weed	1.77	3
Canada thistle	Asteraceae (aster)	Cirsium	arvense (L.) Scop.	Weed	2.40	9

Field bindweed	Convolvulaceae (morning-glory)	Convolvulus	arvensis L.	Weed	45.77	15
Queen Anne's lace	Apiaceae (carrot)	Daucus	carota L.	Weed	15.77	10
Spring draba	Brassicaceae (mustard)	Draba	verna L.	Weed	0.08	1
Eastern daisy fleabane	Asteraceae (aster)	Erigeron	annuus (L.) Pers.	Weed	0.38	2
Redstem stork's bill	Geraniaceae (geranium)	Erodium	cicutarium (L.) L'Hér. ex Aiton	Weed*	0.17	2
Buckwheat	Polygonaceae (buckwheat)	Fagopyrum	esculentum Moench	Cover crop	0.35	2
Shaggy soldier	Asteraceae (aster)	Galinsoga	quadriradiata Cav.	Weed*	1.42	1
Small geranium	Geraniaceae (geranium)	Geranium	pusillum L.	Weed*	4.94	6
Ground ivy	Lamiaceae (mint)	Glechoma	hederacea L.	Weed	0.13	1
Common hawkweed	Asteraceae (aster)	Hieracium	lachenalii C.C. Gmel.	Weed*	0.87	1
Purple deadnettle	Lamiaceae (mint)	Lamium	purpureum L.	Weed	38.94	11
Field pepperweed	Brassicaceae (mustard)	Lepidium	campestre (L.) W.T. Aiton	Weed	0.10	1
Ox-Eye Daisy	Asteraceae (aster)	Leucanthemum	vulgare Lam.	Weed	0.13	1
Butter and eggs	Scrophulariaceae (figwort)	Linaria	vulgaris Mill.	Weed*	0.25	1
Indian-tobacco	Campanulaceae (bellflower)	Lobelia	inflata L.	Weed*	0.04	1
Bird's-foot trefoil	Fabaceae (pea)	Lotus	corniculatus L.	Cover crop	6.62	5
Common mallow	Malvaceae (mallow)	Malva	neglecta Wallr.	Weed	0.98	5
Wild chamomile	Asteraceae (aster)	Matricaria	chamomilla L.	Weed*	0.13	2
Black medick	Fabaceae (pea)	Medicago	lupulina L.	Weed	130.27	24
Alfalfa	Fabaceae (pea)	Medicago	sativa L.	Cover crop	10.98	5
White sweetclover	Fabaceae (pea)	Melilotus	albus Medik.	Cover crop	0.12	1
Yelllow sweetclover	Fabaceae (pea)	Melilotus	officinalis (L.) Lam.	Cover crop	6.38	4
Common yellow oxalis	Oxalidaceae (wood-sorrel)	Oxalis	stricta L.	Weed	1.13	7
Narrowleaf plantain	Plantaginaceae (plantain)	Plantago	lanceolata L.	Weed	13.44	11
Common plantain	Plantaginaceae (plantain)	Plantago	major L.	Weed	6.94	19
Prostrate knotweed	Polygonaceae (buckwheat)	Polygonum	aviculare L.	Weed	329.06	26
Spotted ladysthumb	Polygonaceae (buckwheat)	Polygonum	persicaria L.	Weed	16.00	7
Little hogweed	Portulacaceae (purslane)	Portulaca	oleracea L.	Weed	3.73	3
Common selfheal	Lamiaceae (mint)	Prunella	vulgaris L.	Weed*	1.21	3

Radish	Brassicaceae (mustard)	Raphanus	sp.	Cover crop	3.06	3
Old-man-in-the-Spring	Asteraceae (aster)	Senecio	vulgaris L.	Weed	10.00	12
Hedgemustard	Brassicaceae (mustard)	Sisymbrium	officinale (L.) Scop.	Cover crop	0.21	1
Field sowthistle	Asteraceae (aster)	Sonchus	arvensis L.	Weed	14.96	8
Common chickweed	Caryophyllaceae (pink)	Stellaria	media (L.) Vill.	Weed	52.10	14
Dandelion	Asteraceae (aster)	Taraxacum	officinale F.H. Wigg.	Weed	144.13	25
Field pennycress	Brassicaceae (mustard)	Thlaspi	arvense L.	Weed*	0.63	2
Aslike clover	Fabaceae (pea)	Trifolium	hybridum L.	Cover crop	17.96	11
Crimson clover	Fabaceae (pea)	Trifolium	incarnatum L.	Cover crop	0.29	3
Red clover	Fabaceae (pea)	Trifolium	pratense L.	Cover crop	17.13	18
White clover	Fabaceae (pea)	Trifolium	repens L.	Cover crop	116.63	23
Wild tulip	Liliaceae (lily)	Tulipa	sylvestris L.	Weed*	0.27	1
Corn speedwell	Scrophulariaceae (figwort)	Veronica	arvensis L.	Weed	0.73	1
Neckweed	Scrophulariaceae (figwort)	Veronica	peregrina L.	Weed	0.46	1
Bird's-Eye Speedwell	Scrophulariaceae (figwort)	Veronica	persica Poir.	Weed	0.37	2
Thymeleaf speedwell	Scrophulariaceae (figwort)	Veronica	serpyllifolia L.	Weed*	6.42	3
Bird vetch	Fabaceae (pea)	Vicia	cracca L.	Weed	3.73	7

Supplemental Table 3: Summary of the global Generalized Linear Mixed Models used for model selection for each bee response variable. Models were run for the entire growing season (Full model, May-August) and for mid-summer months only (Mid-summer model, June-July). For each response variable, the model family and link function, fixed effects (X + X), random effects (1 | X), and interaction terms (*) are shown.

Response variable	Family, link function	Full model	Mid-summer model
Bee abundance	Negative Binomial (1), log	~ Floral abundance * month + floral richness + vegetation cover + vegetation height * month + vineyard management + year + (1 | Site)	~ Floral abundance + floral richness + vegetation cover + vegetation height + cover crop percentage + alternate row +
Bee abundance	Negative Binomial (1), log		

collected by netting			vineyard management + month + year + (1 | Site)
Bee abundance collected by pan traps	Negative Binomial (1), log		
Bee species richness	Poisson, log	~ Floral abundance + floral richness + vegetation cover + vegetation height + vineyard management + month + year + (1 | Site)	
Shannon Diversity Index - Species	Gaussian, identity		
Bee genus richness	Conway-Maxwell-Poisson, log		
Shannon Diversity Index - Genus	Gaussian, identity		
Lasioglossum (*Dialictus*) abundance	Negative Binomial (2), log		

Supplemental Table 4: Summary of the genus-level diversity of bees collected across all sites and years. The number of sites where the genus was collected as well as the total number of bees, species richness, and individuals collected by net vs. pan trap methods are shown. Authority information for each genera were taken from the Discover Life Bee Genera Guide (Ascher and Pickering, 2022). Genera where all bees were not identified to species level (ex. sub-genera or species-groups) are identified by *.

		Frequency	Abundance	Richness	Collection method	
Genus	Authority	Number of sites	Number of individuals	Number of species	Net abundance	Pan trap abundance
Lasioglossum *	Curtis	26	1958	8	208	1750
Agapostemon	Guerin-Meneville	25	450	3	52	398
Andrena	Fabricius	25	246	23	205	41
Augochlorella	Sandhouse	25	336	1	89	247
Bombus	Latreille 1802	25	331	7	323	8
Halictus	Latreille	25	531	3	172	359
Ceratina	Latreille	23	177	3	72	105
Hylaeus *	Fabricius	21	110	6	16	94
Hoplitis	Klug	19	54	1	23	31
Osmia	Panzer	19	64	6	8	56

Augochlora	(Say, 1837)	15	47	1	28	19
Calliopsis	Smith	14	28	1	2	26
Megachile	Latreille	13	36	8	20	16
Xylocopa	Latreille	12	20	1	20	0
Sphecodes *	Latreille	11	23	6	3	20
Melissodes	Latreille	10	25	2	10	15
Stelis	Panzer	8	17	2	2	15
Nomada	Scopoli	5	10	2	3	7
Anthidium	Fabricius	3	10	1	8	2
Anthophora	Latreille	3	3	1	1	2
Coelioxys	Latreille	3	3	2	2	1
Augochloropsis	Cockerell	2	2	1	2	0
Heriades	Spinola	2	2	2	1	1
Peponapis	(Say, 1837)	2	2	1	0	2
Colletes	Latreille	1	2	1	2	0
Holcopasites	Ashmead	1	2	1	0	2
Pseudoanthidium	Friese	1	1	1	1	0
				Total:	1273	3217

Supplemental Table 5: Generalized Linear Mixed Model summaries for genus level bee response variables with site as a random effect. Model summaries are from model averaging of the top models with the lowest AICc (Akaike Information Criterion, corrected) within delta AICc<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. Significant predictors are shown at p<0.05 (**) and nearly significant at p<0.1 (*). Bolded predictors are significant (p<0.1) 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 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 predictors included in the averaged model (significant or not).

Predictor(s)	Estimate	Standard Error	z value	p-value	AICc range	No. models	R2m	R2c
Bee genus richness								
Intercept	**1.72**	**0.081**	**21.20**	**< 2e-16 ****		4	0.09	0.15

Year – 2022	**-0.20**	**0.053**	**3.70**	**0.0002 ****				
Month – May	**-0.15**	**0.081**	**1.86**	**0.0636 ***				
Month – June	**0.25**	**0.073**	**3.46**	**0.0005 ****				
Month – July	**0.27**	**0.068**	**3.92**	**8.8e-05 ****				
Vegetation height	0.026	0.035	0.76	0.4501				
Vegetation cover	-0.017	0.035	0.50	0.6173				
Management – Organic	-0.018	0.11	0.16	0.8726				
Management – Sustainable	-0.18	0.12	1.49	0.1376	740.38-742.34			
Floral richness	**0.064**	**0.033**	**1.93**	**0.0548 ***				
Shannon genus diversity index (H')								
Intercept	**1.21**	**0.10**	**12.06**	**< 2e-16 ****				
Year – 2022	-0.088	0.058	1.50	0.1326				
Month – May	-0.085	0.084	1.01	0.3114				
Month – June	**0.35**	**0.082**	**4.23**	**2.31e-0.5 ****				
Month – July	**0.13**	**0.076**	**1.72**	**0.0859 ***	172.8-174.8	7	0.25	0.44
Floral abundance (log)	***0.066***	***0.034***	***1.93***	***0.0540 ****				
Management – Organic	0.12	0.11	1.05	0.2932				
Management – Sustainable	***-0.21***	***0.12***	***1.80***	***0.0721 ****				
Floral richness	0.072	0.044	1.63	0.1022				

Supplemental Table 6: Generalized Linear Mixed Model summaries for genus level bee response variables for models run with June and July data only to include cover crop percentage and alternate row management as additional predictors. All models had site as a random effect. Model summaries are from model averaging of the top models with the lowest AICc (Akaike Information Criterion, corrected) within delta AICc<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. Significant predictors are shown at $p<0.05$ (**) and nearly significant at $p<0.1$ (*). Bolded predictors are significant ($p<0.1$) 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 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).

Predictor(s)	Estimate	Standard Error	z value	p-value	AICc range	No. models	R2m	R2c
Bee genus richness								
Intercept	**1.96**	**0.078**	**25.07**	**< 2e-16 ****	396.74-398.70	14	0.04	0.09
Year – 2022	**-0.17**	**0.072**	**2.31**	**0.0208 ****				
Month – June	-0.050	0.065	0.77	0.4409				
Vegetation height	***0.070***	***0.043***	***1.65***	***0.0992 ****				
Management – Organic	-0.074	0.13	0.58	0.5608				
Management – Sustainable	***-0.22***	***0.13***	***1.74***	***0.0811 ****				
Vegetation cover	0.061	0.046	1.31	0.1918				
Floral abundance (log)	0.067	0.045	1.50	0.1349				
Floral richness	0.053	0.045	1.18	0.2374				
Shannon genus diversity index (H')								
Intercept	**1.31**	**0.068**	**19.35**	**< 2e-16 ****	81.97-83.64	4	0.15	0.50
Month – June	**0.19**	**0.068**	**2.76**	**0.0057 ****				
Vegetation height	**0.11**	**0.046**	**2.28**	**0.0227 ****				
Floral richness	0.053	0.049	1.09	0.2777				
Floral abundance (log)	***0.082***	***0.047***	***1.75***	***0.0798 ****				
Vegetation cover	-0.053	0.052	1.07	0.2870				

Supplemental Table 7: Generalized Linear Mixed Model summaries for models of the abundance of *Lasioglossum* (*Dialictus*) bees across all months (full) and for mid-summer months only (mid-summer, June and July), the latter included cover cropping and alternate row management as fixed effects. All models had site as a random effect. Model summaries are from model averaging of the top models with the lowest AICc (Akaike Information Criterion, corrected) within delta AICc<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. 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 (full) or "July" (mid-summer), and "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).

Predictor(s)	Estimate	Standard Error	z value	p-value	AICc range	No. models	R2m	R2c
Lasioglossum (*Dialictus*) abundance - full								
Intercept	**2.28**	**0.27**	**8.44**	**< 2e-16 ****	1101.32-1103.15	4	0.35	0.58
Year – 2022	**-0.58**	**0.14**	**4.13**	**3.66e-05 ****				
Month – May	-0.099	0.19	0.53	0.597159				
Month – June	**-0.45**	**0.19**	**2.36**	**0.018232 ****				
Month – July	**0.62**	**0.18**	**3.44**	**0.000576 ****				
Floral abundance (log)	***-0.17***	***0.081***	***2.06***	***0.039722 *****				
Vegetation cover	0.13	0.096	1.41	0.159715				
Vegetation height	-0.13	0.11	1.16	0.244776				
Management – Organic	-0.41	0.30	1.39	0.163603				
Management – Sustainable	0.50	0.31	1.62	0.105572				
Lasioglossum (*Dialictus*) abundance - mid-summer								
Intercept	**3.24**	**0.23**	**14.01**	**< 2e-16 ****	552.65-554.27	10	0.56	0.70
Year – 2022	**-0.81**	**0.16**	**5.14**	**3.0e-07 ****				
Month – June	**-1.02**	**0.15**	**6.66**	**< 2e-16 ****				
Vegetation cover	**0.24**	**0.11**	**2.18**	**0.0292 ****				
Management – Organic	**-0.66**	**0.28**	**2.37**	**0.0180 ****				
Management – Sustainable	0.12	0.29	0.41	0.6806				
Cover crop percentage	-0.11	0.081	1.33	0.1850				
Vegetation height	-0.14	0.11	1.26	0.2096				
Floral richness	-0.17	0.11	1.49	0.1354				
Floral abundance (log)	-0.13	0.10	1.34	0.1819				

Supplemental Table 8: Generalized Linear Mixed Model summaries for models of the abundance of bees based on capture-method of netted bees and pan trap-collected bees across all months (full) and for mid-summer months only (mid-summer, June and July), the latter included cover cropping and alternate row management as additional fixed effects. All models had site as a random effect. Model summaries are from model averaging of the top models with the lowest AICc (Akaike Information Criterion, corrected) within delta AICc<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. 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 (full) or “July” (mid-summer), and “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).

Predictor(s)	Estimate	Standard Error	z value	p-value	AICc range	No. models	R2m	R2c
Net abundance - full								
Intercept	**1.90**	**0.15**	**12.65**	**< 2e-16 ****	1015.56-1017.43	6	0.30	0.39
Month - July	0.22	0.14	1.53	0.1274				
Month – June	0.12	0.16	0.75	0.4553				
Month - May	-0.13	0.17	0.73	0.4636				
Vegetation height	**0.24**	**0.07**	**3.57**	**0.0004 ****				
Floral richness	**0.23**	**0.06**	**3.82**	**0.0001 ****				
Vegetation cover	-0.08	0.08	1.06	0.2887				
Management - Organic	-0.16	0.17	0.91	0.3605				
Management - Sustainable	***-0.38***	***0.20***	***1.86***	***0.0630 ****				
Net abundance – mid-summer								
Intercept	**1.97**	**0.12**	**16.91**	**< 2e-16 ****	515.48-517.27	10	0.19	0.28
Month - June	-0.24	0.15	1.62	0.1049				
Year - 2022	0.13	0.14	0.92	03565				
Vegetation height	**0.22**	**0.07**	**3.20**	**0.0014 ****				
Floral richness	***0.18***	***0.08***	***2.28***	***0.0228 *****				
Floral abundance (log)	***0.17***	***0.09***	***1.82***	***0.0689 ****				
Cover crop percentage	0.10	0.07	1.33	0.1827				
Pan trap abundance - full								
Intercept	**2.92**	**0.13**	**22.47**	**< 2e-16 ****	1318.11-1319.75	4	0.39	0.61
Month - July	**0.61**	**0.13**	**4.69**	**2e-16 ****				
Month – June	0.09	0.15	0.59	0.5561				
Month - May	**-0.32**	**0.16**	**1.91**	**0.0556 ***				
Year - 2022	**-0.49**	**0.10**	**4.86**	**1.2e-06 ****				
Vegetation height	-0.09	0.12	0.77	0.4443				
Floral richness	***-0.17***	***0.08***	***2.10***	***0.0360 *****				
Vegetation cover	***0.14***	***0.07***	***1.94***	***0.0519 ****				
Floral abundance (log)	-0.11	0.07	1.47	0.1429				
May:Vegetation height	-0.002	0.17	0.01	0.9886				
June:Vegetation height	-0.041	0.13	0.31	0.7574				
July:Vegetation height	**0.29**	**0.12**	**2.46**	**0.0140 ****				
Pan trap abundance – mid-summer								
Intercept	**3.75**	**0.10**	**36.28**	**< 2e-16 ****	664.14-666.11	2	0.43	0.58
Month - June	**-0.47**	**0.10**	**4.62**	**3.90e-06 ****				
Year – 2022	**-0.84**	**0.11**	**7.71**	**< 2e-16 ****				
Vegetation cover	**0.24**	**0.08**	**3.01**	**0.0026 ****				

Floral richness	**-0.17**	**0.08**	**2.08**	**0.0374 ****				
Alternate row - Yes	0.12	0.17	0.71	0.4778				
Cover crop percentage	**-0.22**	**0.05**	**4.12**	**3.81e-05 ****				

Supplemental Table 9: Comparison of the Estimated Marginal Means (Emmean) from Generalized Linear Models comparing the abundance of select genera between the three vineyard management types. Model estimated marginal means (log scale) and standard errors (SE) were compared using Tukey post-hoc tests, as indicated with different letters. Significance is shown for GLMs and for post-hoc testing at $p<0.05$ and $p<0.1$ using bolding and grey shading.

		Organic		Conventional		Sustainable		Model significance	R^2	Pairwise significance
Genus	Year	Emmean	SE	Emmean	SE	Emmean	SE			
Bombus	2021	1.31	0.41	2.05	0.55	1.28	0.58		0.10	
Bombus	**2022**	**2.53 a**	**0.27**	**2.54 a**	**0.27**	**1.50 b**	**0.30**	**p<0.05**	**0.38**	**p<0.05**
Andrena	2021	1.96	0.26	1.72	0.37	1.28	0.40		0.13	
Andrena	**2022**	**2.08 a**	**0.20**	**1.42 b**	**0.23**	**1.39 b**	**0.24**	**p<0.05**	**0.33**	**p<0.1**
Ceratina	2021	1.61	0.22	1.53	0.31	0.88	0.37		0.20	
Ceratina	**2022**	**1.18 ab**	**0.46**	**1.89 a**	**0.44**	**0.49 b**	**0.50**	**p<0.05**	**0.24**	**p<0.1**
Lasioglossum	**2021**	**3.75 a**	**0.19**	**4.01 ab**	**0.26**	**4.57 b**	**0.26**		**0.40**	**p<0.05**
Lasioglossum	**2022**	**3.07 a**	**0.21**	**3.34 ab**	**0.21**	**3.85 b**	**0.21**	**p<0.1**	**0.35**	**p<0.05**
Hylaeus	2021	1.61	0.28	1.03	0.43	0.79	0.45		0.19	
Hylaeus	**2022**	**0.97 a**	**0.31**	**0.41 a**	**0.37**	**-1.39 b**	**0.74**	**p<0.05**	**0.51**	**p<0.05, p<0.1**
Agapostemon	2021	2.25	0.35	2.72	0.48	3.01	0.48		0.12	
Agapostemon	2022	2.34	0.39	1.68	0.40	1.87	0.39		0.09	
Augochlorella	**2021**	**2.69 a**	**0.21**	**1.39 b**	**0.35**	**1.57 b**	**0.33**	**p<0.05**	**0.62**	**p<0.05**
Augochlorella	**2022**	**2.35 a**	**0.35**	**1.73 ab**	**0.37**	**0.69 b**	**0.41**	**p<0.1**	**0.41**	**p<0.05**
Halictus	2021	2.65	0.28	2.94	0.40	2.75	0.40		0.03	
Halictus	2022	2.37	0.27	2.15	0.27	2.03	0.28		0.05	

Supplemental Table 10: Summary of Generalized Linear Mixed Models to determine how local vegetation and floral resources differ by vineyard management type. Model type and response variables are along the left and included predictors are on the right with their model estimate (E) and p-values (p). Categorical reference values in the models are Conventional (Management category), 2021 (Year), and August (Month). Significance is indicated by bolding for $p<0.05$ and by * for nearly significant at $p<0.1$. Grey boxes indicate predictor variables that are significant or nearly significant ($p<0.1$).

Model family (link function)	Response variable	Intercept		Organic		Sustainable		Year – 2022		May		June		July	
		E	p	E	p	E	p	E	p	E	p	E	p	E	p

Gamma (log)	Floral abundance	**3.73**	**0.00**	0.11	0.69	-0.15	0.61	0.12	0.50	-0.36	0.11	**-0.58**	**0.00**	**-0.60**	**0.00**
Gaussian (identity)	Floral richness	**2.39**	**0.00**	0.07	0.79	**-0.70**	**0.02**	**0.35**	**0.01**	**-1.04**	**0.00**	**-0.92**	**0.00**	**-0.53**	**0.00**
Gaussian (identity)	Vegetation cover	**64.28**	**0.00**	1.42	0.78	-6.37	0.25	2.71	0.25	-2.01	0.51	**-7.55**	**0.02**	**-6.68**	**0.03**
Gaussian (identity)	Vegetation height	**24.14**	**0.00**	6.18	0.09 *	-4.07	0.28	0.013	0.99	-0.79	0.67	2.04	0.27	0.64	0.73

Chapter 3

Supplemental Table 1: Landscape categories used to determine the impact of landscape composition on vineyard bee communities at three levels of refinement (Refined, Medium, Broad). Landscape data were taken from Agriculture and Agri-Food Canada Annual Crop Inventory (AAFC, 2023). Category descriptions are shown with definitions pertaining to the Niagara Region.

Refined	**Water**	**Developed**	**Exposed**	**Treed**	**Wetland**	**Pasture**	**Annual crops**	**Orchards**	**Vineyards**
Definition	Water bodies (ex. lakes, rivers)	Predominantly built-up (ex. roads, buildings) + greenhouses	Predominately non-vegetated and non-developed (ex. rock, mines, rubble)	Predominantly woody vegetation of shrubland (+/-2 meters height) or forest (coniferous, broadleaf, mixed wood)	Water table near, at, or above soil surface (ex. fens, bogs, marshes)	Periodically cultivated (ex. tame grasses, alfalfa, clover mixtures for hay, pasture or seed)	Any non-perennial crop (ex. oats, rye, wheat, corn, soy, other vegetables)	Any orchard crop (ex. tender fruit, apple, pear, nuts)	Any vine crop (ex. grapes)
Medium	**Water**	**Impervious**		**Treed**	**Wetland**	**Pasture/annual crops**		**Woody perennials**	
Definition	Water bodies (ex. lakes, rivers)	Combined developed land + greenhouses + exposed land		Same as above	Same as above	Combined pasture + annual crops		Combined orchards + vineyards	
Broad	**Water**	**Impervious**		**Semi-natural**		**Agriculture**			
Definition	Water bodies (ex. lakes, rivers)	Same as above		Combined treed + wetland		Combined pasture/annual crops + woody perennials			

*AAFC [Agriculture and Agri-Food Canada]. (2023). ISO 19131 Annual Crop Inventory – Data Product Specifications Revision: A. https://agriculture.canada.ca/atlas/data_donnees/annualCropInventory/supportdocument_documentdesupport/en/ISO%2019131_AAFC_Annual_Crop_Inventory_Data_Product_Specifications.pdf

Supplemental Table 2: Global model fixed effects and their hypotheses and predicted effects on bees (abundance and diversity). References underlying hypotheses are provided in brackets and are listed below the table.

Effect types	Fixed effect	Hypothesis	Predicted impact on bees
Landscape factors	Semi-natural lands	Provide undisturbed nesting and floral habitat (1)	Positive
	Vineyards	Larger field sizes (vineyard blocks and sites) require increased foraging range to access natural habitat (2)	Negative
	Annual crops	Represent pulsed floral resources and increased exposure to pesticides (3)	Negative
	Impervious surfaces	Impervious surfaces remove nesting sites especially for ground-nesting bees (4)	Negative
Soils	Slope	Some ground-nesting bees may prefer sloping ground due to impacts on nest temperature and drainage/soil moisture (5)	Positive
	Soil texture	Some ground-nesting bees may prefer soils with higher sand content and higher drainage capacities (5)	Positive
Local management	Vegetation height	Taller vegetation height indicates lower mowing frequencies which can be beneficial for flowering plants and bees (6, 7)	Positive
	Floral abundance	Higher floral abundance increases the pollen and nectar resources for bees (8)	Positive
	Management type	Organic and sustainable vineyards may use less-toxic pesticides for bees and provide more floral resources (9)	Positive

References:

1) Holland, J. M., Douma, J. C., Crowley, L., James, L., Kor, L., Stevenson, D. R., & Smith, B. M. (2017). Semi-natural habitats support biological control, pollination and soil conservation in Europe. A review. *Agronomy for Sustainable Development*, *37*, 1-23.
2) Fahrig, L., Girard, J., Duro, D., Pasher, J., Smith, A., Javorek, S., ... & Tischendorf, L. (2015). Farmlands with smaller crop fields have higher within-field biodiversity. *Agriculture, Ecosystems & Environment*, *200*, 219-234.
3) Lau, P. W., Esquivel, I. L., Parys, K. A., Hung, K. L. J., & Chakrabarti, P. (2023). The nutritional landscape in agroecosystems: a review on how resources and management practices can shape pollinator health in agricultural environments. *Annals of the Entomological Society of America*, *116*(5), 261-275.
4) Ayers, A. C., & Rehan, S. M. (2021). Supporting bees in cities: how bees are influenced by local and landscape features. *Insects*, *12*(2), 128.

5) Antoine, C. M., & Forrest, J. R. (2021). Nesting habitat of ground-nesting bees: a review. *Ecological Entomology*, *46*(2), 143-159.
6) Proske, A., Lokatis, S., & Rolff, J. (2022). Impact of mowing frequency on arthropod abundance and diversity in urban habitats: a meta-analysis. *Urban Forestry & Urban Greening*, *76*, 127714.
7) Morrison, M. A., & Bright, A. (2025). Reduced mowing frequencies increase pollinator abundance in urban lawns in the UK. *Conservation Evidence*, *22*, 1.
8) Fowler, R. E., Rotheray, E. L., & Goulson, D. (2016). Floral abundance and resource quality influence pollinator choice. *Insect Conservation and Diversity*, *9*(6), 481-494.
9) Walker, E., Wooliver, R., Russo, L., & Jagadamma, S. (2025). The context-dependent benefits of organic farming on pollinator biodiversity: A meta-analysis. *Journal of Applied Ecology*, *62*(1), 41-52.

Supplemental Table 3: List of all bee species (or subgenera, morphospecies, or species-groups (indicated by *)) that were collected over two years from 26 commercial vineyards. The number of individuals [Ab.] collected over the two years are shown and their functional traits of Diet (P = polylectic, O = oligolectic, C = cleptoparasite), Nest (U = underground, A = aboveground), Sociality [Soc] (SC = social, SL = solitary, C = cuckoo), body size [TD] (as the distance across the tegula in mm), Rarity [Rar] (R = rare species represent <1% of non-honey bees collected across sites and years, A = abundant), and Native [Nat] (N = native to North America, E = exotic) from which the data were obtained from the following references [Ref] 1) MacKell et al., 2023, 2) Onuferko et al., 2015, 3) Grixti & Packer, 2006, 4) Normandin et al., 2017, 5) Gibbs et al., 2017, 6) Gibbs & Dathe, 2017, 7) Gibbs et al., 2023, 8) Gutierrez et al., 2023, 9) Willis Chan et al., 2019, 10) Portman et al., 2019. Full references are provided below the table. TD was measured when data were not available from MacKell et al., (2023) as indicated by *. For non-species groups, the most common functional trait and average TD were taken for bees from the Niagara Region per (Onuferko et al., 2015) or were unable to be determined (N/A).

Genus	Species or subgenera/groups/morphospecies (*)	Authority	Ab.	Diet	Nest	Soc	TD (mm)	Nat	Rar	Ref
Lasioglossum	Dialictus *	Robertson	1708	P	U	SC	1.61	N	N/A	1,2
Agapostemon	virescens	(Fabricius)	418	P	U	SL	3.37	N	A	1,2
Augochlorella	aurata	(Smith)	336	P	U	SC	2.22	N	A	1,2
Halictus	confusus	Smith	308	P	U	SC	2.00	N	A	1,2
Bombus	impatiens	Cresson	224	P	U	SC	3.97	N	A	1,2
Halictus	ligatus	Say	192	P	U	SC	2.24	N	A	1,2
Andrena	wilkella	(Kirby)	160	P	U	SL	3.05	E	A	1,2
Lasioglossum	zonulum	(Smith)	142	P	U	SL	2.6	E	A	1,2

Ceratina	calcarata	Robertson	108	P	A	SL	1.79	N	A	1,2
Hylaeus	affinis/modestus/ illinoisensis *	N/A	92	P	A	SL	1.33	N	A	1,2
Ceratina	mikmaqi	Rehan	60	P	A	SL	1.79	N	A	1,2
Hoplitis	producta	(Cresson)	54	P	A	SL	2.05	N	A	1,2
Bombus	bimaculatus	Cresson	51	P	U	SC	4.64	N	A	1,2
Augochlora	pura	(Say)	47	P	A	SL	2.4	N	A	1,2
Lasioglossum	leucozonium	(Schrank)	38	P	U	SL	2.59	E	R	1,2
Agapostemon	sericeus	(Förster)	31	P	U	SL	1.89	N	R	1,3
Halictus	rubicundus	(Christ)	31	P	U	SC	2.89	N	R	1,2
Lasioglossum	coriaceum	(Smith)	30	P	U	SL	2.59	N	R	1,2
Osmia	atriventris	Cresson	30	P	A	SL	2.87*	N	R	2,3
Bombus	griseocollis	(DeGeer)	28	P	U	SC	6.00	N	R	1,2
Calliopsis	andreniformis	Smith	28	P	U	SL	1.86	N	R	1,2
Andrena	carlini	Cockerell	24	P	U	SL	3.63	N	R	1,2
Osmia	conjuncta	Cresson	24	P	A	SL	2.91	N	R	1,2
Melissodes	subillatus	LaBerge	22	O	U	SL	2.79	N	R	1,7
Xylocopa	virginica	(Linnaeus)	20	P	A	SC	7.72	N	R	1,2
Lasioglossum	cinctipes	(Provancher)	19	P	U	SC	2.3	N	R	1,2
Lasioglossum	pectorale	(Smith)	17	P	U	SL	1.56	N	R	1,3
Sphecodes	atlantis/cressonii *	N/A	15	C	U	C	1.26*	N	R	2,3
Stelis	lateralis	Cresson	15	C	A	C	1.94	N	R	1,3
Megachile	texana	Cresson	14	P	U	SL	4.36	N	R	1,2
Andrena	cressonii	Robertson	13	P	U	SL	2.8	N	R	1,2
Bombus	fervidus	(Fabricius)	13	P	U	SC	6.05	N	R	1,2
Andrena	nasonii	Robertson	12	P	U	SL	2.26	N	R	1,2
Bombus	rufocinctus	Cresson	11	P	U	SC	4.2	N	R	1,2
Anthidium	oblongatum	(Illiger)	10	P	A	SL	3.86	E	R	1,2
Hylaeus	mesillae	(Cockerell)	10	P	A	SL	1.19	N	R	1,2
Ceratina	dupla	Say	9	P	A	SL	1.42	N	R	1,2
Nomada	articulata	Smith	9	C	U	C	2.35	N	R	1,2
Megachile	brevis	Say	6	P	A	SL	3.66	N	R	1,2
Megachile	rotundata	(Fabricius)	6	P	A	SL	2.73	E	R	1,2
Osmia	pumila	Cresson	6	P	A	SL	2.68	N	R	1,2
Andrena	vicina	Smith	5	P	U	SL	3.36	N	R	1,2
Andrena	arabis	Robertson	4	O	U	SL	2.27	N	R	1,2
Andrena	hippotes	Robertson	4	P	U	SL	3.06*	N	R	2
Hylaeus	leptocephalus	(Morawitz)	4	P	A	SL	1.52	E	R	1,4
Andrena	imitatrix	Cresson	3	P	U	SL	2.92	N	R	1,3
Anthophora	terminalis	Cresson	3	P	A	SL	4.17	N	R	1,2
Bombus	vagans	Smith	3	P	U	SC	4.67	N	R	1,2
Megachile	latimanus	Say	3	P	U	SL	4.34	N	R	1,2
Megachile	mendica	Cresson	3	P	A	SL	3.97	N	R	1,2
Melissodes	desponsus	Smith	3	O	U	SL	3.81	N	R	1,2
Sphecodes	illinoensis	(Robertson)	3	C	U	C	2.38	N	R	1,3
Andrena	barbilabris	(Kirby)	2	P	U	SL	2.7	N	R	1,3
Andrena	brevipalpis	Cockerell	2	P	U	SL	2.8	N	R	1,4
Andrena	erigeniae	Robertson	2	O	U	SL	2.51*	N	R	2
Andrena	miranda	Smith	2	P	U	SL	3.09	N	R	1,3
Andrena	perplexa	Smith	2	P	U	SL	3.6	N	R	1,4
Andrena	regularis	Malloch	2	P	U	SL	3.93*	N	R	3
Augochloropsis	metallica	(Fabricius)	2	P	U	SL	2.95	N	R	1,2
Coelioxys	rufitarsis	Smith	2	C	A	C	3.91*	N	R	2,3

Colletes	inaequalis	Say	2	P	U	SL	3.54	N	R	1,3
Holcopasites	calliopsidis	(Linsley)	2	C	U	C	1.5	N	R	1,3
Hylaeus	pictipes	Nylander	2	P	A	SL	1.2*	E	R	6
Lasioglossum	foxii	(Robertson)	2	P	U	SL	1.59	N	R	1,2
Lasioglossum	quebecense	(Crawford)	2	P	U	SL	2.02	N	R	1,2
Megachile	centuncularis	(Linnaeus)	2	P	A	SL	4.08*	E	R	2,4
Osmia	taurus	Smith	2	P	A	SL	3.59*	E	R	4,8
Peponapis	pruinosa	(Say)	2	O	U	SL	4.31*	N	R	3,9
Sphecodes	clematidis	Robertson	2	C	U	C	2.5	N	R	1,3
Stelis	permaculata	Cockerell	2	C	A	C	1.37*	N	R	7
Agapostemon	texanus	Cresson	1	P	U	SL	2.51	N	R	1,2
Andrena	commoda	Smith	1	P	U	SL	3.89	N	R	1,3
Andrena	dunningi	Cockerell	1	P	U	SL	3.21	N	R	1,2
Andrena	erythronii	Robertson	1	O	U	SL	3.43*	N	R	2
Andrena	mandibularis	Robertson	1	P	U	SL	2.17	N	R	1,2
Andrena	miserabilis	Cresson	1	P	U	SL	2.02	N	R	1,2
Andrena	nida	Mitchell	1	O	U	SL	2.44*	N	R	5
Andrena	robertsonii	Dalla Torre	1	P	U	SL	2.12*	N	R	3,4
Andrena	rugosa	Robertson	1	P	U	SL	2.89	N	R	1,3
Andrena	wheeleri	Graenicher	1	P	U	SL	2.48	N	R	1,2
Bombus	ternarius	Say	1	P	U	SC	4.73*	N	R	2
Coelioxys	sayi	Robertson	1	C	A	C	3.55	N	R	1,2
Heriades	carinata	Cresson	1	P	A	SL	2.07	N	R	1,2
Heriades	leavitti	Crawford	1	P	A	SL	1.62	N	R	1,2
Hylaeus	annulatus	(Linnaeus)	1	P	A	SL	1.32	N	R	1,2
Hylaeus	hyalinatus	Smith	1	P	A	SL	1.56	E	R	1,2
Megachile	ericetorum	Lepeletier	1	P	A	SL	5.31*	E	R	2
Megachile	sculpturalis	Smith	1	P	A	SL	4.29	E	R	1,2
Nomada	imbricata	Smith	1	C	U	C	3.26*	N	R	2,3
Osmia	caerulescens	Linnaeus	1	P	A	SL	3.1	E	R	1,4
Osmia	simillima	Smith	1	P	A	SL	3.38	N	R	1,2
Pseudoanthidium	nanum	(Mocsáry)	1	O	A	SL	2.97*	E	R	10
Sphecodes	coronus	Mitchell	1	C	U	C	1.93	N	R	1,3
Sphecodes	ranunculi	Robertson	1	C	U	C	2.83	N	R	1,3
Sphecodes	sp. (morphospecies 1) *	N/A	1	C	U	C	2.17*	N	R	1,2, 3

Full references:

1) MacKell, S., Elsayed, H., & Colla, S. (2023). Assessing the impacts of urban beehives on wild bees using individual, community, and population-level metrics. *Urban Ecosystems*, *26*(5), 1209-1223.

2) Onuferko, T. M., Kutby, R., & Richards, M. H. (2015). A list of bee species (Hymenoptera: Apoidea) recorded from three municipalities in the Niagara region of Ontario, including a new record *of Lasioglossum furunculum* Gibbs (Halictidae) in Canada. *The Journal of the Entomological Society of Ontario*, *146*.

3) Grixti, J. C., & Packer, L. (2006). Changes in the bee fauna (Hymenoptera: Apoidea) of an old field site in southern Ontario, revisited after 34 years. *The Canadian Entomologist*, *138*(2), 147-164.

4) Normandin, É., Vereecken, N. J., Buddle, C. M., & Fournier, V. (2017). Taxonomic and functional trait diversity of wild bees in different urban settings. *PeerJ*, *5*, e3051.

5) Gibbs, J., Ascher, J. S., Rightmyer, M. G., & Isaacs, R. (2017). The bees of Michigan (Hymenoptera: Apoidea: Anthophila), with notes on distribution, taxonomy, pollination, and natural history. *Zootaxa*, *4352*(1), 1-160.

6) Gibbs, J., & Dathe, H. H. (2017). First records of *Hylaeus* (Paraprosopis) *pictipes* Nylander, 1852 (Hymenoptera: Colletidae) in North America. *Check List*, *13*(3), 2116-2116.
7) Gibbs, J., Hanuschuk, E., Miller, R., Dubois, M., Martini, M., Robinson, S., ... & Onuferko, T. M. (2023). A checklist of the bees (Hymenoptera: Apoidea) of Manitoba, Canada. *The Canadian Entomologist*, *155*, e3.
8) Gutierrez, G. M., LeCroy, K. A., Roulston, T. A. H., Biddinger, D. J., & López-Uribe, M. M. (2023). *Osmia taurus* (Hymenoptera: Megachilidae): A non-native bee species with invasiveness potential in North America. *Environmental entomology*, *52*(2), 149-156.
9) Willis Chan, D. S., Prosser, R. S., Rodríguez-Gil, J. L., & Raine, N. E. (2019). Assessment of risk to hoary squash bees (*Peponapis pruinosa*) and other ground-nesting bees from systemic insecticides in agricultural soil. *Scientific Reports*, *9*(1), 11870.
10) Portman, Z. M., Burrows, S. J., Griswold, T., Arduser, M., Irber, A. J., Tonietto, R. K., & Cariveau, D. P. (2019). First records of the adventive *Pseudoanthidium nanum* (Mocsáry)(Hymenoptera: Megachilidae) in Illinois and Minnesota, with notes on its identification and taxonomy. *The Great Lakes Entomologist*, *52*(1), 6.

Supplemental Table 4: Generalized Linear Model summaries for each bee response variable per year for genus-level results as well as *Lasioglossum* (*Dialictus*) abundance. Model summaries are from model averaging of the top models within delta AICc<2. On the left are predictors included in the conditional averaged models alongside their estimates, standard errors (adjusted for averaged models), absolute z values, and p-values. Significant predictors are shown at p<0.05 (*). Continuous predictors were standardized (z-scored) before analyses. For vineyard management categories, the reference value is "Conventional". On the right 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 R2 is for a model run with all variables included in the averaged model (significant or not).

Predictor(s)	Estimate	Standard Error	z value	p-value	AICc range	No. models	R2
Genus richness 2021							
Intercept	**2.50**	**0.094**	**26.59**	**<2e-16 ***	101.87-103.74	6	0.66
Semi-natural	**0.12**	**0.051**	**2.39**	**0.0167 ***			
Vineyard	0.058	0.054	1.07	0.2827			
Annual crops	-0.093	0.065	1.43	0.1533			
Vegetation height	0.058	0.051	1.15	0.2517			
Management – Organic	-0.14	0.11	1.27	0.2056			
Management - Sustainable	**-0.36**	**0.15**	**2.39**	**0.0169 ***			
Genus richness 2022							
Intercept	**2.39**	**0.054**	**44.49**	**<2e-16 ***	110.17-112.15	6	0.50
Semi-natural	**0.086**	**0.040**	**2.12**	**0.0339 ***			
Impervious	0.057	0.038	1.49	0.1353			

Vegetation height	**0.086**	**0.039**	**2.20**	**0.0276 ***			
Management – Organic	0.037	0.093	0.40	0.6908			
Management - Sustainable	**-0.20**	**0.10**	**2.01**	**0.0445 ***			
Shannon diversity genus (H') 2021							
Intercept	**1.67**	**0.066**	**25.56**	**<2e-16 ***	11.96-13.74	5	0.68
Semi-natural	0.082	0.071	1.16	0.2456			
Slope	-0.086	0.075	1.15	0.2517			
Texture	**-0.25**	**0.072**	**3.46**	**0.0005 ***			
Vegetation height	**0.15**	**0.077**	**1.96**	**0.0498 ***			
Floral abundance	-0.12	0.081	1.43	0.1526			
Shannon diversity genus (H') 2022							
Intercept	**1.78**	**0.10**	**17.26**	**<2e-16 ***	12.82-14.78	3	0.55
Vegetation height	0.15	0.081	1.89	0.0584			
Management – Organic	0.080	0.15	0.52	0.6047			
Management - Sustainable	**-0.38**	**0.15**	**2.51**	**0.0120 ***			
Lasioglossum (*Dialictus*) abundance 2021							
Intercept	**3.75**	**0.13**	**29.69**	**<2e-16 ***	189.8	1	0.54
Texture	**0.41**	**0.13**	**3.20**	**0.0014 ***			
Vegetation height	**-0.40**	**0.13**	**3.07**	**0.0022**			
Lasioglossum (*Dialictus*) abundance 2022							
Intercept	**3.33**	**0.18**	**18.54**	**<2e-16 ***	209.38-211.33	5	0.31
Slope	-0.15	0.14	1.06	0.2909			
Texture	0.14	0.15	0.92	0.3597			
Vegetation height	-0.29	0.15	1.94	0.0529			
Management – Organic	-0.32	0.34	0.94	0.3478			
Management - Sustainable	0.52	0.33	1.57	0.1174			

Supplemental Table 5: Comparison of the median, interquartile range (IQR), and range of values (minimum and maximum) for landscape, soil, and local vegetation variables between vineyard management types: Conv – Conventional, Org – Organic, Sust – Sustainable. Local vegetation variables were averaged across months and years for sites sampled in multiple years. Kruskal-Wallis chi-squared (Chi) and p-value results are shown on the right comparing vineyard types (Df=2) and significance ($p<0.05$) is noted with * beside the p-value. Different letters under the median values indicate significantly different categories from a Dunn's post-hoc test.

	Median (IQR)			Range (min. – max.)			Kruskal-Wallis	
Variable	Conv	Org	Sust	Conv	Org	Sust	Chi	p-value
Semi-natural (%)	9.7 (10.7)	9.4 (4.9)	4.0 (13.5)	1.9-22.2	2.6-27.7	0-24.5	1.52	0.47
Vineyard (%)	69.6 (17.6)	63.7 (14.7)	69.8 (39.5)	34.1-85.5	26.6-80.5	31.8-88.5	0.55	0.76
Annual crops (%)	2.5 (6.6)	0 (6.0)	0 (0)	0-14.3	0-35.1	0-17.4	3.63	0.16

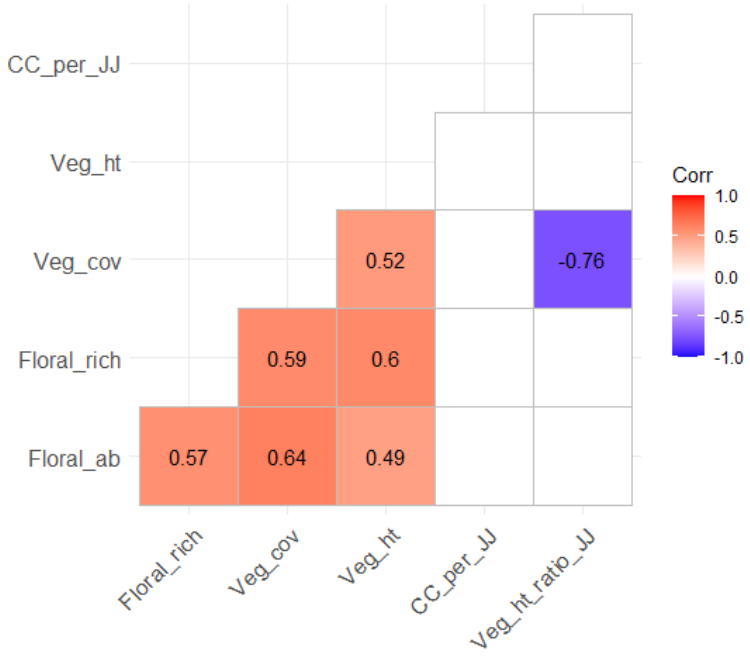
Impervious (%)	12.5 (9.9)	11.6 (8.2)	12.1 (14.7)	1.0-62.1	0.6-28.1	4.2-26.4	0.18	0.91
Slope (%)	3.0 (3.7)	4.2 (6.8)	1.5 (1.3)	1-10.1	1-9.4	1-12.2	1.80	0.41
Texture	1.4 (0.3)	1.4 (0.9)	2.0 (0.9)	1-1.9	1-2.6	1-3	3.31	0.19
Floral abundance	32.2 (18.5)	28.7 (22.5)	25.9 (8.7)	11.4-72	13.5-91.2	10.0-87.6	0.61	0.74
Vegetation height (cm)	22.5 (5.6) ab	29.4 (6.2) a	19.6 (3.7) b	17.0-43.7	22.6-49.9	13.7-32.4	10.1	0.006*
Floral richness	1.99 (0.8) a	1.8 (0.4) a	1.39 (0.4) b	1.12-3.14	1.27-3.06	0.9-1.6	9.36	0.009*
Vegetation cover (%)	63.6 (17.4)	60.2 (20.8)	57.8 (10.9)	45.1-77.1	50.2-77.3	35.9-67.0	1.62	0.44

Supplemental Table 6: Generalized Linear Models for underground and aboveground nesting bees. Results are from model averaging of 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. Significant predictors are shown at $p<0.05$ (*). Continuous predictors were standardized (z-scored) before analyses. On the right 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 R2 is for a model run with all variables included in the averaged model (significant or not).

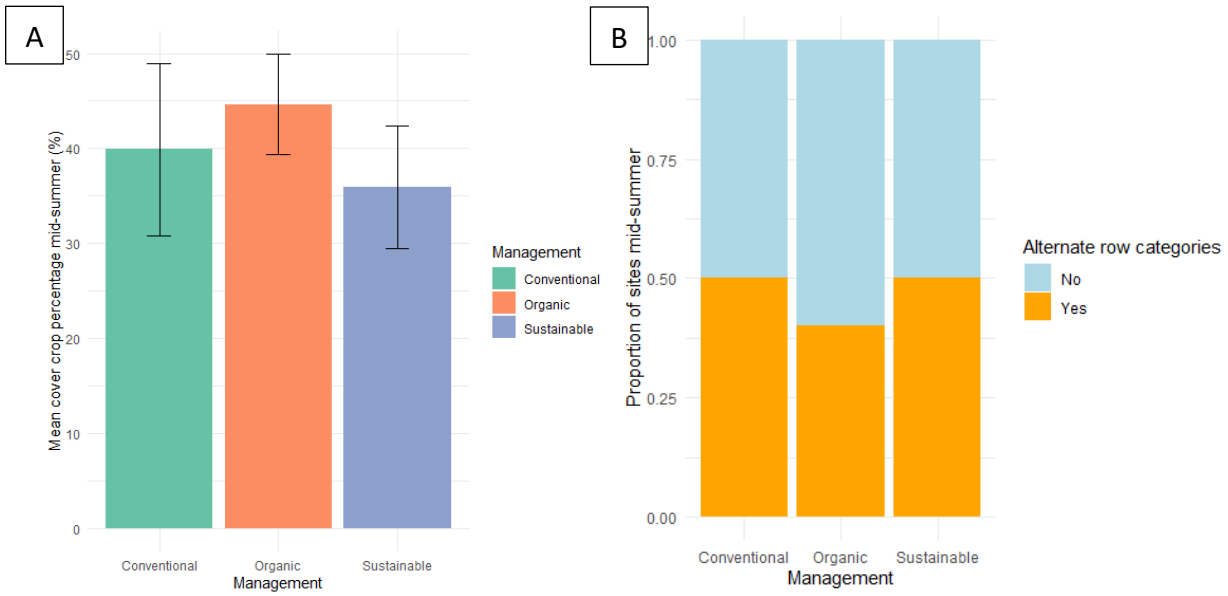
Predictor(s)	Estimate	Standard Error	z value	p-value	AICc range	No. models	R2
Underground abundance 2021							
Intercept	**4.67**	**0.10**	**48.52**	**<2e-16 ***	213.08-215.03	3	0.62
Semi-natural	0.13	0.10	1.29	0.1973			
Annual crops	-0.12	0.099	1.18	0.2383			
Texture	**0.31**	**0.10**	**3.02**	**0.0025 ***			
Underground abundance 2022							
Intercept	**4.26**	**0.076**	**56.06**	**<2e-16 ***	228.73-230.49	8	0.59
Semi-natural	**0.18**	**0.082**	**2.14**	**0.0325 ***			
Vineyard	0.11	0.075	1.43	0.1538			
Texture	0.17	0.093	1.85	0.0649			
Vegetation height	0.15	0.077	1.93	0.0532			
Floral abundance	0.12	0.079	1.56	0.1187			
Aboveground abundance 2021							
Intercept	**2.52**	**0.13**	**19.77**	**<2e-16 ***	138.39-140.22	4	0.70
Semi-natural	0.17	0.13	1.36	0.1738			
Texture	**-0.40**	**0.14**	**2.90**	**0.0037 ***			
Vegetation height	0.22	0.12	1.88	0.0595			
Floral abundance	0.18	0.13	1.39	0.1661			
Aboveground abundance 2022							
Intercept	**2.21**	**0.14**	**16.29**	**<2e-16 ***	159.4-161.4	6	0.80
Semi-natural	**0.29**	**0.14**	**2.04**	**0.0414 ***			
Annual crops	0.22	0.14	1.67	0.1077			
Vineyard	**-0.36**	**0.16**	**2.33**	**0.0199 ***			
Impervious	**0.35**	**0.13**	**2.68**	**0.0073 ***			
Texture	-0.27	0.16	1.67	0.0945			
Vegetation height	**0.40**	**0.14**	**2.88**	**0.0040 ***			

Supplemental Figures

Chapter 2

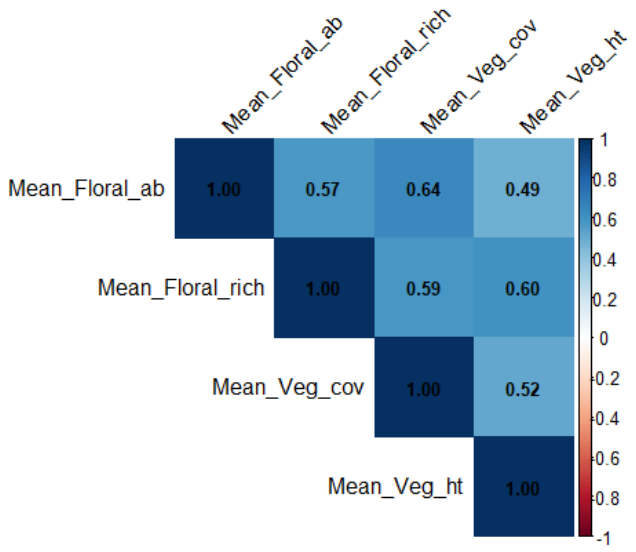


Supplemental Figure 1: Shows the significant ($p<0.05$) Spearman's correlation coefficients (r) for vineyard vegetation and floral resources from 26 commercial vineyards averaged across months and years. Floral and vegetation variables are; Floral_ab = Floral abundance, Floral_rich = Floral species richness, Veg_cov = Vegetation percent cover, Veg_ht = Vegetation height, CC_per_JJ = the percent of flowers that were cover crop species in June and July, Veg_ht_ratio_JJ = the ratio of vegetation height between alternate rows in June and July, as a proxy for alternate row management.

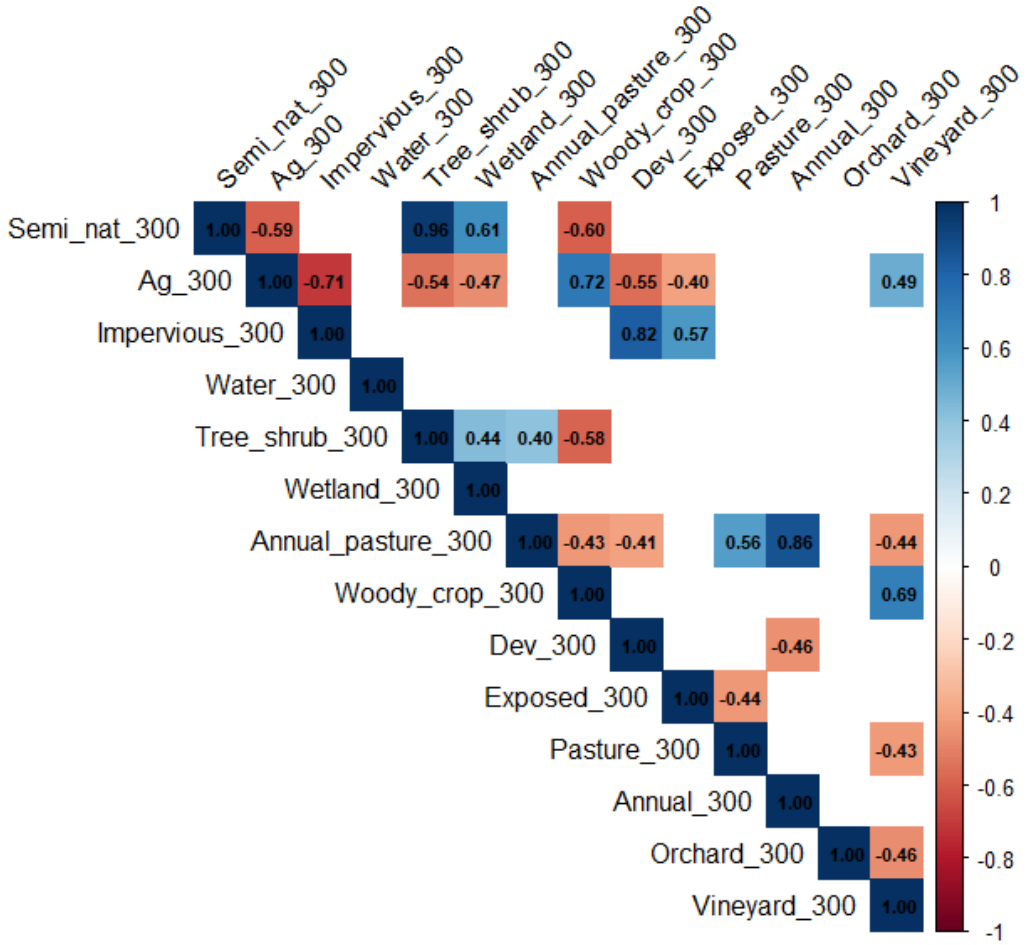


Supplemental Figure 2: Shows the differences in the percentage of flowers that are from cover crop species (A) and the frequency of alternate row management use (B) in commercial vineyards under different management types. Data are from mid-summer, averaged per site across months (June and July) and years. Differences between management types were not significant for cover crop percentage (Analysis of variance, ANOVA $F(2,23)= 0.42$, $p= 0.662$) or alternate row frequency (Fisher's Exact test, two sided, $p= 1$).

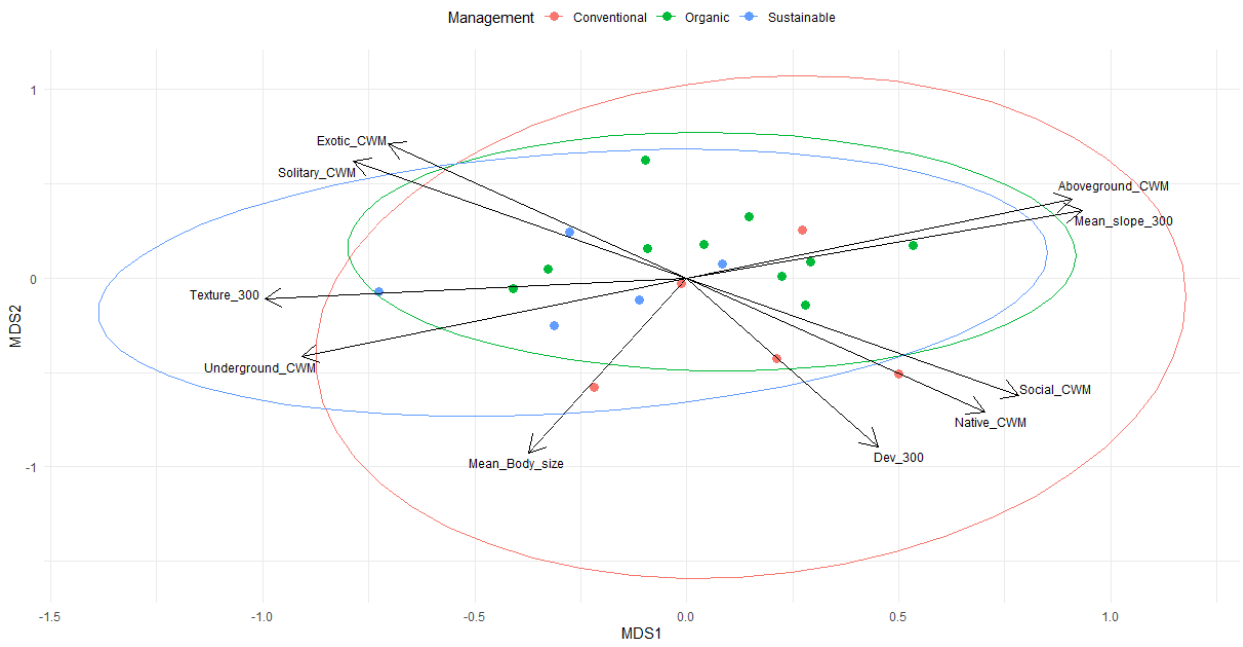
Chapter 3



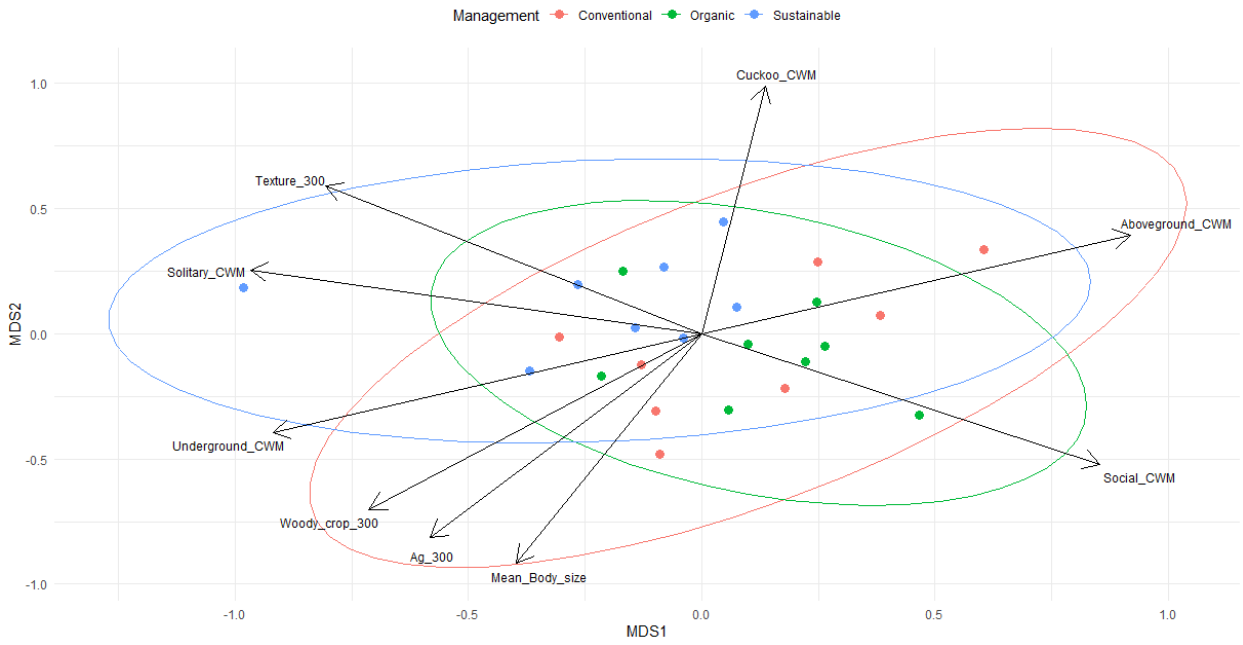
Supplemental Figure 1: Shows the significant ($p<0.05$) Spearman's correlation coefficients (r) for vineyard vegetation and floral resources from 26 commercial vineyards taking the mean across months and years per site. Floral and vegetation variables are; Floral_ab = Floral abundance, Floral_rich = Floral species richness, Veg_cov = Vegetation percent cover, Veg_ht = Vegetation height.



Supplemental Figure 2: Shows the significant ($p<0.05$) Spearman's correlation coefficients (r) for the percentage of surrounding landscape categories taken from a 300m radius circular buffer around 26 commercial vineyards. Categories include: Semi_nat = semi-natural lands, Ag = agricultural lands, Impervious = impervious surfaces, Water = open water, Tree_shrub = treed and shrub lands, Wetland = wetlands, Annual_pasture = annual crops and pasture fields, Woody_crop = perennial woody crops, Dev = developed land, Exposed = barren land such as mines and rubble, Pasture = pasture fields, Annual = annual crops, Orchard = orchards, Vineyard = vineyards.



Supplemental Figure 3: Non-metric multidimensional scaling (NMDS) of bee community composition at vineyard sites in 2021 (n=20) based on Bray-Curtis dissimilarity of Hellinger-transformed abundance data excluding *Lasioglossum* (*Dialictus*) (stress=0.18). 95% confidence ellipses indicate different vineyard management categories (Permutational Multivariate Analysis of Variance $F=1.76$, $R^2= 0.17$, $p=0.014$). Vectors represent significantly correlated bee functional traits (community weighted means, CWM) and local, landscape, or soil variables ($p<0.05$, based on 999 permutations). Soil and landscape variables were taken from a 300m radius buffer around each site.



Supplemental Figure 4: Non-metric multidimensional scaling (NMDS) of bee community composition at vineyard sites in 2022 (n=24) based on Bray-Curtis dissimilarity of Hellinger-transformed abundance data excluding *Lasioglossum* (*Dialictus*) (stress=0.20). 95% confidence ellipses indicate grouping of sites by vineyard management categories though they did not significantly differ (Permutational Multivariate Analysis of Variance $F=1.35$, $R^2= 0.11$, $p=0.064$). Vectors represent significantly correlated bee functional traits (community weighted means, CWM) and local, landscape, or soil variables ($p<0.05$, based on 999 permutations). Soil and landscape variables were taken from a 300m radius buffer around each site.

Appendices:

Chapter 1

Appendix A: Systematic review search terms

Web of Science Core Collection search:

Data range (Publication Date): 2005-01-01 – 2024-12-31

Document type: Article

Language: English

Crop-specific search:

Title = ("bee" OR "bees" OR "pollinat*" OR "flower visit*" OR "flower-visit*" OR "Apoidea" OR "Apiformes" OR "Anthophila" OR "Hymenoptera" OR "insect*" OR "arthropod*" OR "wildlife" OR "diversity" OR "animal*" OR "taxa" OR "taxon" OR "functional" OR "community")

AND

("pesticide*" OR "friendly" OR "practice*" OR "ecosystem service*" OR "agroecolog*" OR "catch crop*" OR "buffer*" OR "connectivity" OR "conservation" OR "management" OR "cover crop*" OR "vegetation" OR "nest*" OR "till*" OR "organic" OR "biodynamic" OR "integrated pest management" OR "IPM" OR "integrated pest and pollinator management" OR "IPPM" OR "conventional" OR "weed*" OR "sown" OR "habitat*" OR "margin*" OR "edge*" OR "agroforestry" OR "intercropping*" OR "rotation*" OR "planting*" OR "floral" OR "wildflower*" OR "flower*" OR "mowing" OR "landscape*" OR "land use*" OR "land-use*" OR "semi-natural" OR "natural" OR "patch*" OR "artificial" OR "crop*" OR "fallow*" OR "hedgerow*" OR "tree*" OR "soil*" OR "shrub*" OR "ecological infrastructure" OR "ecological intensification" OR "sustainab*")

AND

Abstract = ("bee" OR "bees" OR "Apoidea" OR "Apiformes" OR "Anthophila")

AND

("Cicer" OR "C. arietinum" OR "chickpea*" OR "gram" OR "garbanzo bean*" OR "Pisum" OR "P.

sativum" OR "P. arvense" OR "pea" OR "peas" OR "Vitis" OR "V. vinifera" OR "grape" OR "grapes" OR "vineyard*" OR "vine*" OR "viticult*" OR "Olea" OR "O. europaea" OR "olive*" OR "grove*" OR "Saccharum" OR "S. officinarum" OR "sugar cane*" OR "sugarcane*" OR "Zea" OR "Z. mays" OR "maize" OR "corn" OR "Triticum" OR "T. aestivum" OR "T. durum" OR "T. spelta" OR "wheat" OR "spelt" OR "Oryza" OR "O. sativa" OR "rice" OR "paddy" OR "paddies" OR "Beta vulgaris" OR "B. vulgaris" OR "sugar beet*" OR "Hordeum" OR "H. disticum" OR "H. distichon" OR "H. distichum" OR "H. vulgare" OR "barley" OR "Sorghum" OR "S. guineense" OR "S. vulgare" OR "S. dura" OR "S. bicolor" OR "sorghum" OR "Echinochloa" OR "E. frumentacea" OR "Eleusine" OR "E. coracana" OR "Eragrostis" OR "E. abyssinica" OR "Panicum" OR "P. miliaceum" OR "Paspalum" OR "P. scrobiculatum" OR "Pennisetum" OR "P. glaucum" OR "Setaria" OR "S. italica" OR "millet" OR "Avena" OR "A. sativa" OR "oat*" OR "Lactuca" OR "L. sativa" OR "lettuce*" OR "Secale" OR "S. cereale" OR "rye*" OR "Triticosecale" OR "T. rimpaui" OR "triticale" OR "Spinacia" OR "S. oleracea" OR "spinach*" OR "Phoenix" OR "P. dactylifera" OR "date palm*")

General pollinator-independent crop search:

Title = ("bee" OR "bees" OR "pollinat*" OR "flower visit*" OR "flower-visit*" OR "Apoidea" OR "Apiformes" OR "Anthophila" OR "Hymenoptera" OR "insect*" OR "arthropod*" OR "wildlife" OR "diversity" OR "animal*" OR "taxa" OR "taxon" OR "functional" OR "community")

AND

("pesticide*" OR "friendly" OR "practice*" OR "ecosystem service*" OR "agroecolog*" OR "catch crop*" OR "buffer*" OR "connectivity" OR "conservation" OR "management" OR "cover crop*" OR "vegetation" OR "nest*" OR "till*" OR "organic" OR "biodynamic" OR "integrated pest management" OR "IPM" OR "integrated pest and pollinator management" OR "IPPM" OR "conventional" OR "weed*" OR "sown" OR "habitat*" OR "margin*" OR "edge*" OR "agroforestry" OR "intercropping*" OR "rotation*" OR "planting*" OR "floral" OR "wildflower*" OR "flower*" OR "mowing" OR "landscape*" OR "land use*" OR "land-use*" OR "semi-natural" OR "natural" OR "patch*" OR "artificial" OR "crop*"

OR "fallow*" OR "hedgerow*" OR "tree*" OR "soil*" OR "shrub*" OR "ecological infrastructure" OR "ecological intensification" OR "sustainab*")

AND

Abstract = ("bee" OR "bees" OR "Apoidea" OR "Apiformes" OR "Anthophila")

AND

("grain*" OR "cereal*" OR "pollinator-independent" OR "pollinator independent" OR "pollination-independent" OR "pollination independent" OR "self-pollinat*" OR "self pollinat*" OR "selfing" OR "self-reproducing" OR "wind-pollinat*" OR "wind pollinat*" OR "parthenocarpic" OR " non-insect-pollinat*" OR "not pollination-dependent" OR "non-pollination-dependent" OR "self-fertile" OR "self-compatible" OR "self compatible" OR "autogamous" OR "cleistogamous" OR "abiotic pollination" OR "abiotic reproduction" OR " asexual reproduction" OR "non-entomophilous" OR "anemophilous" OR "autogamous")

AND ("crop" OR "crops" OR "crop species" OR "field*" OR "agricultural plant*" OR "cultivated plant*" OR "cultivated land*" OR "agricultural land*" OR "farmland*" OR "food crop*" OR "cropland*" OR "orchard*" OR "vineyard*" OR "grove*" OR "paddy" OR "paddies" OR "agroecosystem*" OR "agricultural system*" OR "farming system*")

NOT ("pollen grain*" OR "pollen*")

Appendix B: List of papers included in the systematic literature review

Adhikari, S., Burkle, L. A., O'Neill, K. M., Weaver, D. K., Delphia, C. M., & Menalled, F. D. (2019). Dryland organic farming partially offsets negative effects of highly simplified agricultural landscapes on forbs, bees, and bee–flower networks. *Environmental Entomology*, *48*(4), 826-835.

Amy, C., Noël, G., Hatt, S., Uyttenbroeck, R., Van de Meutter, F., Genoud, D., & Francis, F. (2018). Flower strips in wheat intercropping system: effect on pollinator abundance and diversity in Belgium. *Insects*, *9*(3), 114.

Blaise, C., Mazzia, C., Bischoff, A., Millon, A., Ponel, P., & Blight, O. (2022). Vegetation increases abundances of ground and canopy arthropods in Mediterranean vineyards. *Scientific reports*, *12*(1), 3680.

Boetzl, F. A., Krimmer, E., Holzschuh, A., Krauss, J., & Steffan-Dewenter, I. (2022). Arthropod overwintering in agri-environmental scheme flowering fields differs among pollinators and natural enemies. *Agriculture, Ecosystems & Environment*, *330*, 107890.

Bosco, L., Moser, V., Jones, M. M., Opedal, Ø., Ovaskainen, O., Sonja, G., ... & Jacot, A. (2023). Habitat area and local habitat conditions outweigh fragmentation effects on insect communities in vineyards. *Ecological Solutions and Evidence*, *4*(1), e12193.

Brittain, C. A., Vighi, M., Bommarco, R., Settele, J., & Potts, S. G. (2010). Impacts of a pesticide on pollinator species richness at different spatial scales. *Basic and Applied Ecology*, *11*(2), 106-115.

Bryan, C. J., Sipes, S. D., Arduser, M., Kassim, L., Gibson, D. J., Scott, D. A., & Gage, K. L. (2021). Efficacy of cover crops for pollinator habitat provision and weed suppression. *Environmental Entomology*, *50*(1), 208-221.

Campbell, J. W., Rand, T. A., West, N. M., Morphew, A., Allen, B. L., Jabro, J. D., & Dangi, S. R. (2024). Pollinators and Other Beneficial Insects Within Two Brassicaceous Oilseeds and a Cover Crop Mix Under Evaluation as Fallow Surrogates for Dryland Production Systems of the Northern Great Plains. *Journal of the Kansas Entomological Society*, *96*(3), 78-92.

Carrié, R., Lopes, M., Ouin, A., & Andrieu, E. (2018). Bee diversity in crop fields is influenced by remotely-sensed nesting resources in surrounding permanent grasslands. *Ecological Indicators*, *90*, 606-614.

Happe, A. K., Riesch, F., Rösch, V., Gallé, R., Tscharntke, T., & Batáry, P. (2018). Small-scale agricultural landscapes and organic management support wild bee communities of cereal field boundaries. *Agriculture, Ecosystems & Environment*, *254*, 92-98.

Hass, A. L., Liese, B., Heong, K. L., Settele, J., Tscharntke, T., & Westphal, C. (2018). Plant-pollinator interactions and bee functional diversity are driven by agroforests in rice-dominated landscapes. *Agriculture, Ecosystems & Environment*, *253*, 140-147.

Holzschuh, A., Steffan-Dewenter, I., Kleijn, D., & Tscharntke, T. (2007). Diversity of flower-visiting bees in cereal fields: effects of farming system, landscape composition and regional context. *Journal of Applied Ecology*, *44*(1), 41-49.

Holzschuh, A., Steffan-Dewenter, I., & Tscharntke, T. (2010). How do landscape composition and configuration, organic farming and fallow strips affect the diversity of bees, wasps and their parasitoids?. *Journal of Animal Ecology*, *79*(2), 491-500.

Hüber, C., Zettl, F., Hartung, J., & Müller-Lindenlauf, M. (2022). The impact of maize-bean intercropping on insect biodiversity. *Basic and Applied Ecology*, *61*, 1-9.

Kaczmarek, M., Entling, M. H., & Hoffmann, C. (2024). Wild Bee Conservation in Viticulture: Effects of Semi-Natural Habitats, Organic Management, and Fungicide Reduction. *Ecology and Evolution*, *14*(10), e70378.

Karamaouna, F., Kati, V., Volakakis, N., Varikou, K., Garantonakis, N., Economou, L., ... & Edwards, M. (2019). Ground cover management with mixtures of flowering plants to enhance insect pollinators and natural enemies of pests in olive groves. *Agriculture, ecosystems & environment*, *274*, 76-89.

Kehinde, T., & Samways, M. J. (2012). Endemic pollinator response to organic vs. conventional farming and landscape context in the Cape Floristic Region biodiversity hotspot. *Agriculture, ecosystems & environment*, *146*(1), 162-167.

Kehinde, T., & Samways, M. J. (2014). Management defines species turnover of bees and flowering plants in vineyards. *Agricultural and Forest Entomology*, *16*(1), 95-101.

Kehinde, T., von Wehrden, H., Samways, M., Klein, A. M., & Brittain, C. (2018). Organic farming promotes bee abundance in vineyards in Italy but not in South Africa. *Journal of Insect Conservation*, *22*, 61-67.

Kovács-Hostyánszki, A., Batáry, P., & Báldi, A. (2011). Local and landscape effects on bee communities of Hungarian winter cereal fields. *Agricultural and Forest Entomology*, *13*(1), 59-66.

Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guernion, M., Burel, F., ... & Winter, S. (2018). Tillage intensity or landscape features: What matters most for wild bee diversity in vineyards?. *Agriculture, Ecosystems & Environment*, *266*, 142-152.

Kratschmer, S., Pachinger, B., Schwantzer, M., Paredes, D., Guzmán, G., Goméz, J. A., ... & Winter, S. (2019). Response of wild bee diversity, abundance, and functional traits to vineyard inter-row management intensity and landscape diversity across Europe. *Ecology and Evolution*, *9*(7), 4103-4115.

Kratschmer, S., Pachinger, B., Gaigher, R., Pryke, J. S., van Schalkwyk, J., Samways, M. J., ... & Winter, S. (2021). Enhancing flowering plant functional richness improves wild bee diversity in vineyard inter-rows in different floral kingdoms. *Ecology and Evolution*, *11*(12), 7927-7945.

Magagnoli, S., Bosi, S., Negri, L., Dinelli, G., Burgio, G., & Masetti, A. (2024). Flowering areas enhance insect pollinators and biological control agents in wheat intensive agro-ecosystems. *Insect Conservation and Diversity*, *17*(5), 884-893.

Martínez-Núñez, C., Manzaneda, A. J., Isla, J., Tarifa, R., Calvo, G., Molina, J. L., ... & Rey, P. J. (2020). Low-intensity management benefits solitary bees in olive groves. *Journal of Applied Ecology*, *57*(1), 111-120.

Meagher Jr, R. L., Watrous, K. M., Fleischer, S. J., Nagoshi, R. N., Brown, J. T., & Westbrook, J. K. (2021). Comparison of bee composition in sunn hemp and other cover crops. *Florida Entomologist*, *103*(4), 419-424.

Pascual, S. (2022). Landscape composition and configuration affect bees in the olive agroecosystem. *Journal of Applied Entomology*, *146*(1-2), 1-18.

Rasran, L., Diener, A., Pachinger, B., & Bernhardt, K. G. (2018). Diversity of Flower Visiting Insects in Dry Grasslands and Vineyards Close to the City of Vienna with Special Focus on Wild Bees. *Sociobiology*, *65*(4), 603-611.

Shankar, U., & Mukhtar, Y. (2024). Empirical studies of integrated pest and pollinator management (IPPM) in chickpea (Cicer arietinum L.). *Journal of Plant Diseases and Protection*, *131*(1), 201-208.

Stavrianakis, G., Sentas, E., Stattegger, S. R., Tscheulin, T., & Kizos, T. (2024). Effect of olive grove's understorey management on arthropod diversity. *Agroecology and Sustainable Food Systems*, *48*(8), 1115-1138.

Tscheulin, T., Neokosmidis, L., Petanidou, T., & Settele, J. (2011). Influence of landscape context on the abundance and diversity of bees in Mediterranean olive groves. *Bulletin of Entomological Research*, *101*(5), 557-564.

Uzman, D., Reineke, A., Entling, M. H., & Leyer, I. (2020). Habitat area and connectivity support cavity-nesting bees in vineyards more than organic management. *Biological Conservation*, *242*, 108419.

Wersebeckmann, V., Warzecha, D., Entling, M. H., & Leyer, I. (2023). Contrasting effects of vineyard type, soil and landscape factors on ground-versus above-ground-nesting bees. *Journal of Applied Ecology*, *60*(4), 601-613.

Wilson, H., Wong, J. S., Thorp, R. W., Miles, A. F., Daane, K. M., & Altieri, M. A. (2018). Summer flowering cover crops support wild bees in vineyards. *Environmental Entomology*, *47*(1), 63-69.

Chapter 2

Supplemental methods

Site selection:

Grapes are the 3rd largest fruit crop grown in Canada by total acreage, with Ontario representing 68% of Canada's wine grape production in 2020 (Agriculture and Agri-Food Canada, 2021). Within Ontario, the Niagara Region is the largest planted area with vineyards covering 13,600 acres (VQA, n.d.). Commercial vineyard blocks of mature *Vitis vinifera* (minimum three years since planting) were selected across the Niagara Region. Sites were selected that were managed conventionally, organically, or certified sustainably per the Sustainable Winegrowing Ontario certification program (SWO, n.d.). This program requires that vineyard management considers factors such as biodiversity, water use, and soil health among others and recommends practices such as cover cropping and integrated pest management (IPM). Sites that were managed organically and were also certified sustainable were categorized as organic for this study due to the often more stringent environmental regulations for organic management (Seufert et al., 2017) and the goal to investigate the sustainability certification in isolation. In Year 1, 20 sites were sampled: ten managed organically, five under conventional management and five under certified sustainable management. In Year 2, 24 sites were sampled, eight organic, eight conventional, and eight certified sustainable (Supplemental Table 1). Thus, some sites were sampled for only one year and some for two years due to changes in grower availability and increased research capacity in Year 2 (Figure 1). Vineyard blocks were selected in collaboration with grape growers encompassing a variety of surrounding landscape compositions and grape growing sub-appellations. These sub-appellations vary slightly from one another in growing degree days, average precipitation, frost-free days, soil type, and physical geography/topography (VQA, n.d.). Vineyard blocks varied in size and planting year. All sites were at minimum 600 m apart to enable the independent sampling of bee communities at each site (Gathmann and Tscharntke, 2002). While some wild bees can forage greater distances, most foraging occurs within a smaller geographic range (Knight et al., 2005; Zurbuchen et al., 2010).

Bee surveys:

Data were collected over two field seasons in 2021 and 2022. Bees were sampled approximately every four weeks from May through August corresponding roughly with the grape phenology stages of leaf out, flowering, bunch closure, and veraison (colour development) (Schindler et al., 2013). Sites were

sampled in a random order during each sampling campaign 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 centre of each vineyard block which spanned across two neighbouring between-row spaces to account for possible alternate row management. Transect length, marked along the central vine row, was adjusted to the different row spacing between sites to ensure consistent total area sampled (Kratschmer et al., 2018). Aerial netting was performed for 30 minutes in the morning and afternoon, 15 min per alternate row, using collecting jars with ethyl acetate (BioQuip 1121 Series Collecting Jars). Pan traps were made of 3.25 oz (96 mL) plastic cups painted with UV-fluorescent yellow, blue, or white paint (New Horizons bee bowls, Maryland). Twenty-four pan traps, eight of each colour, were placed underneath the central vine row within the same 400m^2 area, spaced ~3 m apart with alternating colours. If the under-vine area consisted of tall vegetation, then traps were raised using commercial garden stakes, which were dark green in colour, at a height of ~15-30 cm depending on the height of the vegetation. Pan traps were filled with water and a small amount of unscented dishwashing soap to break the surface tension. Pan traps were placed prior to 9:00 am and collected after 5:00 pm on the same day, removing bees using a fine-mesh sieve. All collected bees were stored in labelled plastic bags in a standard freezer at approximately -18°C.

Vegetation and floral surveys:

On the same days that bees were sampled, vineyard floral resources and vegetation characteristics were also recorded. A 1 m^2 quadrat was semi-randomly placed on the ground eight times along the 400 m^2 sampling area, with four quadrats per alternate row. 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 inside the quadrat (excluding grasses, rushes and sedges) regardless of their known pollinator-attraction or pollination systems (Baldock et al., 2019). Abundances were recorded as the number of open 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) common weed identification resources (OMAFRA, 2009; 2023a). Flowering species were further classified as either cover crops or weeds based on OMAFRA resources and grower-reported planting of specific species as cover crops (OMAFRA, 2023a; 2023b, Supplemental Table 2). 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 was measured, as a proxy for mowing frequency, in each quadrat by dividing each quadrat into four equal sections and measuring the tallest piece of vegetation in each section. The mean vegetation height, floral abundance, floral richness, and vegetation cover were calculated per site and sampling round, the latter using the median value of the DAFOR scale. The percentage of flowers that were from cover crop species was also calculated as well as the vegetation height ratio between the two neighbouring rows as a proxy for alternate row management. This ratio was then transformed into a binary variable where a height ratio of 2:1 or greater was considered "yes" for alternate row management based on quadrat photos and field notes at varying ratios.

Bee identification:

Washed and pinned bees were identified using a dissecting microscope and several identification guides and keys (Packer et al., 2007; see Appendix for the list of published keys 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* sub-genus Dialictus, *Hylaeus affinis/modesutus/illinoinesis*, *Sphecodes atlantis/cressonii*, and one distinct morphospecies of *Sphecodes* sp. All results and discussion at the "species" level here forth include these sub-genus level identifications unless otherwise specified. Identifications were verified by fellow graduate students in York University's Centre for Bee Ecology, Evolution, and Conservation for a subset of three males and three females, where available, per species.

Statistical analyses:

All analyses were performed in R v.4.4.2 (R Core Team, 2014) and excluded honey bees due to inconsistent information on hive presence across sites (Kratschmer et al., 2018). To determine which vineyard management variables influence bee abundance, species richness, and Shannon diversity index Generalized Linear Mixed Models (GLMM) were run and the model(s) with the best fit selected per the Akaike Information Criterion (AIC) using the packages "lme4" (Bates et al. 2014), "lmerTest" (Kuznetsova et al., 2017), "glmmTMB" (Brooks et al., 2017), and "MuMIn" (Bartoń, 2024) following Zuur and Ieno (2016) and Harrison et al. (2018). The fixed effects included in the models were management type (organic, conventional, or certified sustainable), floral abundance, floral species richness, vegetation height, and vegetation percent cover. The temporal variables of month (May, June, July, August) and year (2021, 2022) were also included as fixed effects to account for variation in both bee communities and vineyard floral resources and vegetation over time. Lastly, site was included as a random effect (intercept only) to account for site-level factors that may occur outside of modeled variables and due to the non-independent repeat sampling of sites over time (Bolker, 2015).

Before running models, data were checked for outliers and distributions using graphical tools (box plots and histograms) and Shapiro Wilk tests for normality (Zuur et al., 2010). One variable, floral abundance, was highly skewed and was log(x+1) transformed. Before running models, all numeric explanatory variables were scaled and centred (z-score standardized) (Harrison et al., 2018). Multicollinearity between explanatory variables was checked using Variance Inflation Factors (VIF) by running a linear model with all possible explanatory variables with the package "car" (Fox and Weisberg, 2019). All variables had an adjusted VIF <2 and were included in model selection (Zuur et al., 2010). Relationships between bee response variables and explanatory factors were visualized using scatterplots and box plots of raw data using the package "ggplot2" (Wickham, 2016). To determine if the relationships between bee response variables and vineyard management practices change over the growing season, co-plots were created to visualize possible interactions with month (Zuur et al., 2010). Interactions were then included in model selection procedures only when the relationship differed drastically across months due to interaction terms being especially demanding for model performance (Harrison et al., 2018). Global

models (models with all fixed effects and interaction terms) were fitted with the appropriate family and link function (Supplemental Table 3) and were assessed for model fit and diagnostics (Harrison et al., 2018) using the R package "performance" (Lüdecke et al., 2021). Pearson's residuals were plotted against fitted values, against all explanatory variables, and for each random factor (site) (Harrison et al., 2018; Zuur and Ieno, 2016). Model overdispersion, R^2, and intra-class correlation (ICC) were also assessed. Additionally, the packages "gstat" (Gräler et al., 2016) and "sp" (Bivand et al., 2013) were used to create spatial variograms with site spatial coordinates (UTM Zone 17N) to check for spatial dependency of model residuals (Zuur and Ieno, 2016).

Model selection was based on the second order Akaike Information Criterion (AICc) which is corrected for a small sample size relative to the number of model parameters (Harrison et al., 2018). The function *dredge* from the MuMIn package was used to rank all possible models, as all fixed effects in the global models were hypothesized to impact bee abundance or diversity. When there was model uncertainty with multiple top models having delta AICc<2 model averaging was performed to get model estimates for the fixed effects across all top models (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 R2 values for averaged models, a GLMM was run with all fixed effects included in the final averaged model, significant or not. Model diagnostics were also run on this model using the "DHARMa" package (Hartig, 2024). When categorical variables were significant in averaged models, the "emmeans" package (Lenth, 2024) was used to obtain back-transformed estimated marginal means (EMMs) and to perform Tukey-adjusted pairwise comparisons. To determine if cover cropping and alternate row management impacts bee abundance and diversity, mid-summer models were run with data from June and July only as cover crops were blooming primarily during these months and alternate row management was most detectable during these months. All modelling procedures were the same as above, including all the above variables as well as cover crop

percentage and alternate row management (binary, yes or no) as additional fixed effects (Supplemental Table 3). Due to some bee groups not being identified to species level, three further groups of bee data were modelled as above. First, models were run with genus-level bee richness and Shannon diversity index to check if results were similar at the genus level. Secondly, *Lasioglossum* (*Dialictus*) bees, which were highly abundant, were modelled to see if the abundance of this group of bees was associated with certain vineyard management factors. Lastly, bee abundances were modelled separately for pan trap and net-collected data to account for methodological differences in sampling effectiveness for bees (Supplemental Table 3).

To determine how local vegetation and floral resources differed between vineyard management categories of organic, conventional and certified sustainable, GLMMs were performed each 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 categories 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 vineyard categories using a one-way analysis of variance (ANOVA) or Fischer's Exact test.

To investigate how bee community composition was influenced by vineyard management practices, bee abundances per species were summed for each site across months and averaged across years. Hellinger transformations were performed on the bee abundance data to account for the many zero values and to downweigh the effect of highly abundant species (Zuur et al., 2007). Non-metric multidimensional scaling (NMDS) was performed on these data using the "vegan" package (Oksanen et al. 2022) with Bray-Curtis distances and 2-dimensional solutions applying convex hulls around vineyard management categories. A permutational multivariate analysis of variance (PERMANOVA) was

performed to see if the management categories differed. To see how individual bee species as well as vineyard floral and vegetation data associate with the bee community composition, the *envfit* function was used to determine correlations with the NMDS ordination using random permutations (999) (Kratschmer et al., 2018). Significant ($p<0.05$) floral variables, vegetation characteristics, and bee species were then added to the NMDS plot for visualization. Additionally, for each year, Generalized Linear Models (GLMs) were run on the total abundance of select genera to further investigate how bee communities differed between vineyard management types. Negative binomial models with a log-link were run using the "MASS" package (Venables & Ripley, 2002). Genera were selected for modelling if they were abundant and widespread across sites (Supplemental Table 4) and if at least one species was associated with the NMDS of bee community composition. Models of the total abundance, per year, were run for Andrena, Agapostemon, Augochlorella, Bombus, Ceratina, Halictus, Hylaeus, and Lasioglossum with management type as the fixed effect. Lastly, to investigate if floral community composition differed between sites and if this difference associated with vineyard management, the same NMDS analyses as above were performed using Hellinger transformed abundances of each flower species. Convex hulls were used to visualize differences between vineyard management categories. Floral and vegetation variables and individual flower species that were significantly correlated with the NMDS axes ($p < 0.05$), were added to the final plot to visualize key characteristics and flower species associated with community patterns.

Appendix C: List of published identification guides used for bee identifications

Agapostemon, Augochlora, Augochlorella, Augochloropsis:

Portman, Z. M., Arduser, M., Lane, I. G., & Cariveau, D. P. (2022). A review of the Augochloropsis (Hymenoptera, Halictidae) and keys to the shiny green Halictinae of the midwestern United States. *ZooKeys*, *1130*, 103.

Andrena:

LaBerge, W. E. (1980). A revision of the bees of the genus Andrena of the western hemisphere. Part X. Subgenus Andrena. *Transactions of the American Entomological Society (1890-)*, *106*(4), 395-525.

LaBerge, W. E. (1985). A revision of the bees of the genus Andrena of the western hemisphere. Part XI. Minor subgenera and subgeneric key. *Transactions of the American Entomological Society (1890-)*, *111*(4), 441-567.

LaBerge, W. E. (1986). A revision of the bees of the genus Andrena of the Western Hemisphere. Part XII. Subgenera Leucandrena, Ptilandrena, Scoliandrena and Melandrena. *Transactions of the American Entomological Society (1890-)*, *112*(3), 191-248.

LaBerge, W. E. (1989). A revision of the bees of the genus Andrena of the Western Hemisphere. Part XIII. Subgenera Simandrena and Taeniandrena. *Transactions of the American Entomological Society (1890-)*, *115*(1), 1-56.

Bombus:

Williams, P. H., Thorp, R. W., Richardson, L. L., & Colla, S. R. (2014). Bumble Bees of North America. In *Bumble Bees of North America*. Princeton University Press.

Ceratina:

Rehan, S. M., & Sheffield, C. S. (2011). Morphological and molecular delineation of a new species in the *Ceratina dupla* species-group (Hymenoptera: Apidae: Xylocopinae) of eastern North America. *Zootaxa*, *2873*(1), 35-50.

Halictus:

Mitchell, T. B. (1960). Bees of the eastern United States, Vol. 1. Family Halictidae, pp 331-521. North Carolina Agricultural Experimental Station Technical Bulletin, Raleigh, NC.

Heriades:

Michener, C. D. (1938). American bees of the genus Heriades. *Annals of the Entomological Society of America*, *31*(4), 514-531.

Hylaeus:

Gibbs, J., & Dathe, H. H. (2017). First records of *Hylaeus* (Paraprosopis) *pictipes* Nylander, 1852 (Hymenoptera: Colletidae) in North America. *Check List*, *13*(3), 2116-2116.

Romankova, T.G. (2007). Bees of the Genus Hylaeus of Ontario (Hymenoptera: Apoidea: Colletidae). J Entomol Soc Ont 138: 137-154.

Lasioglossum:

Gibbs, J. (2010). Revision of the metallic species of Lasioglossum (Dialictus) in Canada (Hymenoptera, Halictidae, Halictini). Zootaxa 2591: 1–382.

Gibbs, J., Packer, L., Dumesh, S., Danforth, B.N. (2013). Revision and reclassification of Lasioglossum (Evylaeus), L. (Hemihalictus) and L. (Sphecodogastra) in eastern North America (Hymenoptera: Apoidea: Halictidae). Zootaxa 3672(1): 1–117.

McGinley, R.J. (1986). Studies of Halictinae (Apoidea: Halictidae), I: Revision of New World Lasioglossum Curtis. Smithson Contr Zool 429: 1-294.

Megachile:

Sheffield, C.S., Ratti, C., Packer, L., Griswold, T. (2011). Leafcutter and Mason Bees of the Genus Megachile Latreille (Hymenoptera: Megachilidae) in Canada and Alaska. Can J Arthropod Identif 18:1–107. https://doi.org/10.3752/cjai.2011.18

Melissodes:

LaBerge, W. E. (1961). A Revision of the Bees of the Genus Melissodes in North and Central America. Part III (Hymenoptera, Apidae). Univ Kansas Sci Bullietin XLII:283–663

Pseudoanthidium:

Portman, Z. M., Burrows, S. J., Griswold, T., Arduser, M., Irber, A. J., Tonietto, R. K., & Cariveau, D. P. (2019). First records of the adventive *Pseudoanthidium nanum* (Mocsáry)(Hymenoptera: Megachilidae) in Illinois and Minnesota, with notes on its identification and taxonomy. *The Great Lakes Entomologist*, *52*(1), 6.

Chapter 3

Appendix D: List of published identification guides used for bee identifications and resources used for bee functional traits

Agapostemon, Augochlora, Augochlorella, Augochloropsis identifications:

Portman, Z. M., Arduser, M., Lane, I. G., & Cariveau, D. P. (2022). A review of the Augochloropsis (Hymenoptera, Halictidae) and keys to the shiny green Halictinae of the midwestern United States. *ZooKeys*, *1130*, 103.

Andrena identifications:

LaBerge, W. E. (1980). A revision of the bees of the genus Andrena of the western hemisphere. Part X. Subgenus Andrena. *Transactions of the American Entomological Society (1890-)*, *106*(4), 395-525.

LaBerge, W. E. (1985). A revision of the bees of the genus Andrena of the western hemisphere. Part XI. Minor subgenera and subgeneric key. *Transactions of the American Entomological Society (1890-)*, *111*(4), 441-567.

LaBerge, W. E. (1986). A revision of the bees of the genus Andrena of the Western Hemisphere. Part XII. Subgenera Leucandrena, Ptilandrena, Scoliandrena and Melandrena. *Transactions of the American Entomological Society (1890-)*, *112*(3), 191-248.

LaBerge, W. E. (1989). A revision of the bees of the genus Andrena of the Western Hemisphere. Part XIII. Subgenera Simandrena and Taeniandrena. *Transactions of the American Entomological Society (1890-)*, *115*(1), 1-56.

Bombus identifications:

Williams, P. H., Thorp, R. W., Richardson, L. L., & Colla, S. R. (2014). Bumble Bees of North America. In *Bumble Bees of North America*. Princeton University Press.

Ceratina identifications:

Rehan, S. M., & Sheffield, C. S. (2011). Morphological and molecular delineation of a new species in the *Ceratina dupla* species-group (Hymenoptera: Apidae: Xylocopinae) of eastern North America. *Zootaxa*, *2873*(1), 35-50.

Halictus identifications:

Mitchell, T. B. (1960). Bees of the eastern United States, Vol. 1. Family Halictidae, pp 331-521. North Carolina Agricultural Experimental Station Technical Bulletin, Raleigh, NC.

Heriades identifications:

Michener, C. D. (1938). American bees of the genus Heriades. *Annals of the Entomological Society of America*, *31*(4), 514-531.

Hylaeus identifications:

Gibbs, J., & Dathe, H. H. (2017). First records of *Hylaeus* (Paraprosopis) *pictipes* Nylander, 1852 (Hymenoptera: Colletidae) in North America. *Check List*, *13*(3), 2116-2116.

Romankova, T.G. (2007). Bees of the Genus Hylaeus of Ontario (Hymenoptera: Apoidea: Colletidae). J Entomol Soc Ont 138: 137-154.

Lasioglossum identifications:

Gibbs, J. (2010). Revision of the metallic species of Lasioglossum (Dialictus) in Canada (Hymenoptera, Halictidae, Halictini). Zootaxa 2591: 1–382.

Gibbs, J., Packer, L., Dumesh, S., Danforth, B.N. (2013). Revision and reclassification of Lasioglossum (Evylaeus), L. (Hemihalictus) and L. (Sphecodogastra) in eastern North America (Hymenoptera: Apoidea: Halictidae). Zootaxa 3672(1): 1–117.

McGinley, R.J. (1986). Studies of Halictinae (Apoidea: Halictidae), I: Revision of New World Lasioglossum Curtis. Smithson Contr Zool 429: 1-294.

Megachile identifications:

Sheffield, C.S., Ratti, C., Packer, L., Griswold, T. (2011). Leafcutter and Mason Bees of the Genus Megachile Latreille (Hymenoptera: Megachilidae) in Canada and Alaska. Can J Arthropod Identif 18:1–107. https://doi.org/10.3752/cjai.2011.18

Melissodes identifications:

LaBerge, W. E. (1961). A Revision of the Bees of the Genus Melissodes in North and Central America. Part III (Hymenoptera, Apidae). Univ Kansas Sci Bullietin XLII:283–663

Pseudoanthidium identifications:

Portman, Z. M., Burrows, S. J., Griswold, T., Arduser, M., Irber, A. J., Tonietto, R. K., & Cariveau, D. P. (2019). First records of the adventive *Pseudoanthidium nanum* (Mocsáry)(Hymenoptera: Megachilidae) in Illinois and Minnesota, with notes on its identification and taxonomy. *The Great Lakes Entomologist*, *52*(1), 6.

List of resources used for bee functional traits:

*References used for majority of functional traits are noted with (*)

Gibbs, J., Ascher, J. S., Rightmyer, M. G., & Isaacs, R. (2017). The bees of Michigan (Hymenoptera: Apoidea: Anthophila), with notes on distribution, taxonomy, pollination, and natural history. *Zootaxa*, *4352*(1), 1-160.

Gibbs, J., & Dathe, H. H. (2017). First records of *Hylaeus* (Paraprosopis) *pictipes* Nylander, 1852 (Hymenoptera: Colletidae) in North America. *Check List*, *13*(3), 2116-2116.

Gibbs, J., Hanuschuk, E., Miller, R., Dubois, M., Martini, M., Robinson, S., ... & Onuferko, T. M. (2023). A checklist of the bees (Hymenoptera: Apoidea) of Manitoba, Canada. *The Canadian Entomologist*, *155*, e3.

Grixti, J. C., & Packer, L. (2006). Changes in the bee fauna (Hymenoptera: Apoidea) of an old field site in southern Ontario, revisited after 34 years. *The Canadian Entomologist*, *138*(2), 147-164.

Gutierrez, G. M., LeCroy, K. A., Roulston, T. A. H., Biddinger, D. J., & López-Uribe, M. M. (2023). *Osmia taurus* (Hymenoptera: Megachilidae): A non-native bee species with invasiveness potential in North America. *Environmental entomology*, *52*(2), 149-156.

*MacKell, S., Elsayed, H., & Colla, S. (2023). Assessing the impacts of urban beehives on wild bees using individual, community, and population-level metrics. *Urban Ecosystems*, *26*(5), 1209-1223.

Normandin, É., Vereecken, N. J., Buddle, C. M., & Fournier, V. (2017). Taxonomic and functional trait diversity of wild bees in different urban settings. *PeerJ*, *5*, e3051.

*Onuferko, T. M., Kutby, R., & Richards, M. H. (2015). A list of bee species (Hymenoptera: Apoidea) recorded from three municipalities in the Niagara region of Ontario, including a new record *of Lasioglossum furunculum* Gibbs (Halictidae) in Canada. *The Journal of the Entomological Society of Ontario*, *146*.

Willis Chan, D. S., Prosser, R. S., Rodríguez-Gil, J. L., & Raine, N. E. (2019). Assessment of risk to hoary squash bees (*Peponapis pruinosa*) and other ground-nesting bees from systemic insecticides in agricultural soil. *Scientific Reports*, *9*(1), 11870.

Chapter 4

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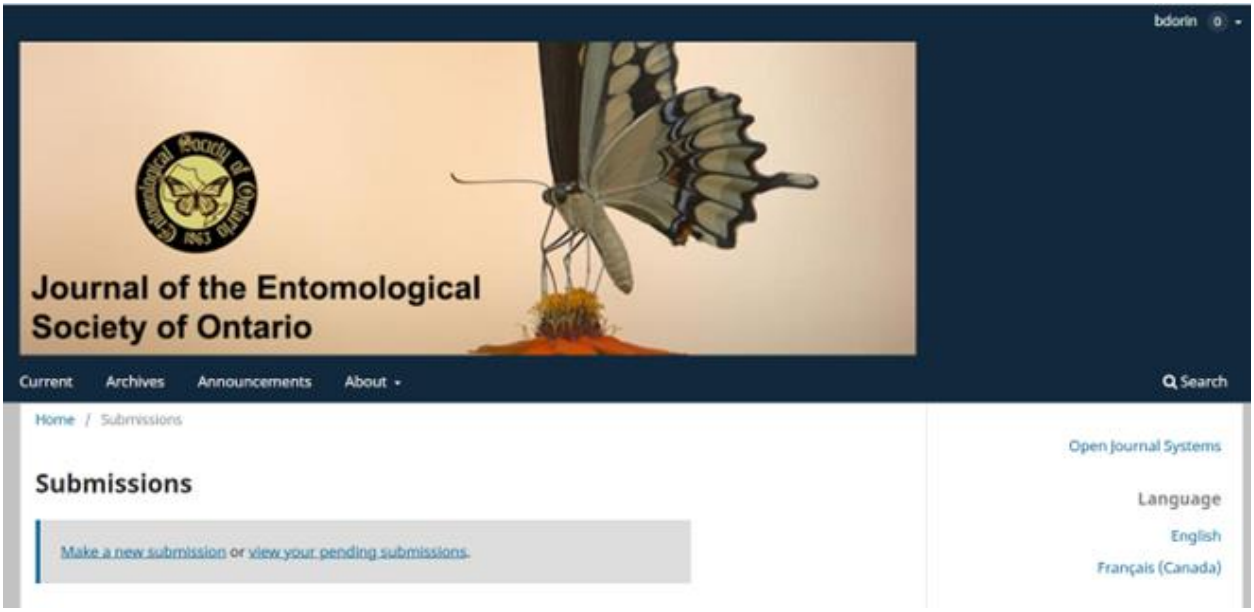

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