

Landscape heterogeneity enhances Hymenoptera (Apoidea: Anthophila) abundance and diversity across Manitoba ecoregions

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ABSTRACT

Shukla-Bergen, Sydney Taylor. M.Sc., The University of Manitoba, June 2025. Landscape heterogeneity enhancing Hymenoptera (Apoidea: Anthophila) abundance and diversity in Manitoba ecoregions. Major Professor; Dr. Kyle Bobiwash.

As natural ecosystems across Canada continue to experience habitat loss, the need to understand the impacts of fragmentation on key members of the ecological community increases. In this study, I determine the influence of compositional and configurational landscape heterogeneity on bee communities through landscape characteristics in natural, semi-natural, and agricultural ecosystems in four Manitoba ecoregions. Additionally, I compare the use of roadside verges for foraging and provisioning of forage by bee indicator species across four Southern Manitoba ecoregions in natural, semi-natural, and agricultural landscapes. For the combined sampling period, 2021 and 2022, 8781 bees were captured using pan traps, blue vane traps, and aerial netting. Results varied year to year, suggesting the impacts of fragmentation vary depending on other abiotic or biotic factors not captured in this study. Urban land, pastureland, mixed wood, and shrubland were identified as key compositional heterogeneity variables shown to affect bee abundance, with no effect on bee diversity. Mean Shape Index and Patch Area were the only configurational heterogeneity metrics identified, with only Mean Shape Index showing a significant impact on bee abundance. Since bee diversity was not impacted by either compositional or configurational heterogeneity, further research is needed to understand the factors that determine diversity in Southern Manitoba. Indicator species analysis was inconclusive in determining a key indicator, highlighting the need for improved detection of species in sampling regimes, although some trends were identified. Recommendations to continue the use of *Bombus* as indicators, with the introduction of some medium-body sized bee species as indicators where identified.

INTRODUCTION

Bees are essential for the pollination of the world's animal-pollination-dependent flowering plant species (Winfree et al. 2008). Globally, 85% of flowering plant species are biotically pollinated by 20,000 species of bees in the world, contributing to maintaining angiosperm populations and diversity year over year (Michener 2007, Ollerton et al. 2011). Klein et al. (2007) showed that 35% of the world's food crops require animal-driven pollination for seed output and crop success, emphasizing bees as the most important pollinator for current cropping systems (Potts et al. 2016a). Bees support plant reproduction, diversity, and abundance, and improve overall ecosystem health via plant community development (Ollerton et al. 2011, Wilby and Orwin 2013). In addition to their role as pollinators, bees are provisioning sources to many predatory species in the ecosystem, such as spiders, amphibians, birds, wasps, and other bee species, all of which are key members of the ecosystem in their own right in particular as members of the secondary consumer trophic level (Dukas 2005, Potts et al. 2016a). Herbivorous primary consumers are consumed by secondary consumers, leading to a robust secondary consumer population that is consumed by tertiary consumers (Hooper et al. 2005, Wilby and Orwin 2013, Nether et al. 2019). If the population of bees were to be altered, reduced, or extirpated there would be severe and immediate consequences within our ecosystems starting with the loss of food crops, flowering plants, and species diversity in natural ecosystems (Kevan 1999, Klein et al. 2007, Ollerton et al. 2011, Potts et al. 2016a, Nether et al. 2019). This relationship to the trophic system makes bees an ideal candidate for indicator species analysis as a keystone species (Chowdhury et al. 2023). Currently habitat loss and fragmentation are the number one cause of declines in global animal and plant diversity, swiftly followed by climate

change, parasites, pathogens, and pesticides (Brittain et al. 2010, Potts et al. 2010, 2016a, Kerr et al. 2015, Yuan et al. 2024).

Bees' interdependency on plants is a relationship limited by the availability of natural ecosystems, where changes in the natural ecosystem cause knock-on effects to both the bees and plants, frequently resulting in losses of diversity on both sides (Dobson et al. 2006, Taki et al. 2007, Baldock et al. 2015, Xiao et al. 2016). A decrease in fitness in both plants and bees can be observed due to essential habitat degradation from disturbances, resulting in fewer seeds being produced by plants, or fewer offspring produced by bees, essentially jeopardizing future generations of both (Dukas 2005, Klein et al. 2007, Everaars et al. 2018). Examining habitat loss across Southern Manitoba, a decline in bee diversity and abundance related to the fragmentation of the landscape can be seen (Hanuschuk 2021, Olynyk et al. 2021, Martini 2022). The elements causing fragmentation within the landscape at the province-wide scale are roadside verges, agricultural practices, urbanization, powerline easements, and forestry (Hanuschuk 2021, Martini 2022). Increases in fragmentation caused by human intervention leads to a decline in natural habitat area, decreases in plant diversity and abundance, drainage of wetlands, and loss of connectivity between natural habitat patches (Steffan-Dewenter and Tschamtkke 1999, Fahrig 2003, Dobson et al. 2006, Yuan et al. 2024). When an increase in fragmentation is seen in natural ecosystems like forests, shrublands, or prairie landscapes in favor of urbanization, agricultural or wood harvesting, decreases in bee and plant diversity are observed (Taki et al. 2007, Baldock et al. 2015, Hanuschuk 2021). Understanding how bees are interacting with their environment, in particular the components that make up the landscape, like landscape composition and connectivity metrics, in a changing landscape will help guide conservation efforts and mitigate the impact fragmentation and urbanization that is currently necessary for Manitoba's socio-

economic development (Hendrickx et al. 2007, Brosi et al. 2008a, Fahrig et al. 2011, Rahimi et al. 2021, Priyadarshana et al. 2024). Homogenization of the landscape for agricultural or urbanization purposes decreases pollinator diversity and the potential of the landscape to maintain a diverse pollinator community by removing natural habitat patches, wetland, and forest stands (Rahimi et al. 2021, Priyadarshana et al. 2024).

Examining the current research on landscape heterogeneity's impacts on the bee community is addressed in the Literature Review section of this thesis. Compositional and configurational heterogeneity's impacts on bee abundance and diversity will be examined using ordination statistics, generalized linear mixed effects models, and generalized linear models. An indicator species analysis will be completed to understand the impacts the landscape, floral community, and climate variables have on the bee diversity and abundance in Southern Manitoba, using ordination statistics and generalized linear mixed-effects models.

In this study, I determine the influence of compositional and configurational landscape heterogeneity through landscape characteristics in natural, semi-natural, and agricultural ecosystems on the diversity and abundance of pollinator communities in four Manitoba ecoregions. I predict that compositional variables crop type, natural area type, and human-disturbed landscape types will affect pollinator diversity and abundance significantly across Southern Manitoba. To determine configurational heterogeneity's impact on bee abundance and diversity, I predict that the configurational heterogeneity metrics that determine connectedness within the landscape will influence the diversity and abundance of the bee community. In addition, I predict agriculture in Southern Manitoba will negatively impact the bee diversity and abundance across the province.

To determine if there are additional methods of tracking landscape heterogeneity's impacts on the bee community, I compare the use of roadside verges for foraging and provisioning of forage by bee indicator species across Southern Manitoba in natural, semi-natural, and agricultural landscapes. I predict the composition of indicator species will vary depending on the ecoregion, site type, and life history strategies in roadside verges since different landscape types will host different bee communities. The life history information, sociality, feeding strategy (lecty), and nesting strategy will be included to determine if there are primary life history strategies common amongst indicators identified. In addition, I will test how indicator species abundance in the roadside verges is impacted by regional environmental variables since roadside verges could be impacting the community structure. Considering the importance of floral communities to bee diversity and abundance, I predict, floral abundance and diversity in agricultural areas will be primarily introduced species, with low overall abundance and diversity in comparison with natural and semi-natural ecosystems. Overall, the goal is to highlight any key indicator species within Southern Manitoba using roadside verges as collection points for these species to determine local community dynamics related to environmental changes.

LITERATURE REVIEW

Part 1: Natural History of Native Bees in Manitoba

What is a bee?

Worldwide, there are approximately 20,000 described species of bees (Michener 2007). Bees reside in the superfamily Apoidea, which consists of the two groups, the araphyletic Spheciformes and the bee-containing monophyletic Anthophila (Michener 2007). Bees evolved from within the apoid wasps 120 million years ago, with the rise of angiosperm plants (Michener 2007, Cardinal and Danforth 2011). Fossil records show that angiosperm and some gymnosperm plants had heavy, sticky pollen, not conducive to abiotic pollination methods prior to 120 million years ago (Michener 2007). Since 120 million years, bees appear in the fossil record carrying pollen from various angiosperms endemic to Gondwana (Michener 2007). As Spheciformes wasps experienced speciation events, resulting in the creation of Anthophila, coevolutionary relationships were formed between the angiosperms and bees driven by the resources provided by the plants, creating a new community structure built on mutualism (Michener 2007). This new mutualistic relationship between bees and plants drove adaptations in both parties, creating new species, expanding into new territories, and creating new niches (Michener 2007). Members of Apiformes can be distinguished from Spheciformes by i) plumose body hair, ii) a modified basal hind tarsus where pollen is collected on scopa, iii) sometimes a longer glossa, iv) and the use of pollen as a protein source (exception being a few *Trigona* species) (Michener 2007). Bees source their proteins from plant products and pollen, limiting the community structure to only interactions between angiosperms that produce these resources (Michener 2007, Grozinger and Patch 2024). Within Anthophila, there are seven families of bees: Apidae, Andrenidae, Colletidae, Halictidae, Megachilidae, Melittidae, and Stenotritidae (Michener 2007). Six of the seven

families are found in North America, Stenotritidae being the smallest family, found only in Australia. There are approximately >1000 species of bees in Canada (Canada. Environment and Climate Change Canada. 2018a). In Manitoba, the previously recorded 154 species documented in 2015 has increased to 392 species recorded, due to increases in sampling effort and taxonomic work (Gibbs et al. 2023). Considering the overall diversity in Canada is >1000 species, and Manitoba boasts 392 species, the diversity within Manitoba represents 39% of Canadian bee diversity contained within only 6.5% of the landmass in Canada, showing one of the highest levels of bee diversity per unit area in Canada.

Life History Information

Plants have driven the speciation, evolution, and morphological adaptations of bees, leading to an incredibly diverse interrelated community structure between plants and bees that is seen globally (Johnson et al. 2018). Without bees within the environment, the function, complexity, and success of the animal-pollination-dependent flowering plant community would be negatively impacted. The plant-pollinator relationship between 85% of the world's flowering plants has resulted in a dependency of bees upon flowering plants for reproduction, food, and nesting habitat (Ollerton et al. 2011). When an increased pollinator presence is observed in agriculture, 35% of the world's crops requiring animal pollination will show a 75% increase in seed output and fruit production (Klein et al. 2007, Ollerton et al. 2011). Bees can form specialist relationships with specific genera or families of plants, making them oligolectic, or bees may use a wide variety of flower plants, making them polylectic (Michener 2007, Grozinger and Patch 2024). Understanding bees' use of plants informs conservation initiatives on essential relationships for maintaining diversity, highlights the pollinators best suited to agricultural

landscapes, and how to support floral communities to maintain both populations (Potts et al. 2003, 2016a, Michener 2007).

Bees are one of the few groups of insects that exhibit eusocial behaviour, which is the formation of a social, aggregated community that shares in the responsibilities and requirements of rearing young (Michener 2007, Grozinger and Patch 2024). The eusocial strategy began in response to the transition to nearly exclusive floral resource use that began 120 million years ago and in response to haplodiploidy creating an incentive to rear related young (Michener 2007, Johnson et al. 2018). As a result, eusociality is not the only form of nesting behaviour found in bees, since historically the ancestral nesting strategy used by bees was solitary nesting (Michener 2007). There are six categories of sociality, considered a spectrum between solitary and eusocial strategies, with subsocial being the term to describe all strategies in the middle of the spectrum (Gibbs et al. 2023, Grozinger and Patch 2024). Diversity in sociality creates more functional complementarity, providing greater support to pollination-dependent flowering plant species, in comparison to increasing overall diversity of bees (Fründ et al. 2010, 2013). Variety in sociality methods provides access to various habitat niches, reducing bee resource use overlap that causes competition between species, driving a more functional ecosystem with a stable interaction network (Fründ et al. 2010, 2013). With diversity in social strategy of bees increasing functional complementarity, climate change causing phenological advances in floral resources has a reduced impact on the plant-bee community due to the variety of niches available for use (Ostwald et al. 2024a). Many bee species are solitary, preferring to rear their young in single parent nests, or live in communal groups where reproductive solitary bees create a social aggregation, rear young, and defend the burrow or nest without creating a class of individuals whose sole purpose is the rearing and care of young

(Michener 2007, Grozinger and Patch 2024). The nesting behaviour in bees can be dependent on sociality, with a non-social breeding female creating a nest in a stem, burrow, or creating a brood cell using salivary excretions (Grozinger and Patch 2024). Eggs are then laid within specialized incubating structures which are packed by the female bee with provisions such as pollen, nectar, or oils (Michener 2007, Grozinger and Patch 2024). Utilizing eusocial and subsocial life history strategies has been shown to increase the foraging distance capable of the species, increasing the reproductive success of the species due to the increased likelihood of encountering higher quality foraging further from the nest and decreased intra- and interspecific competition (Grüter and Hayes 2022).

Floral Use

Understanding nutritional requirements for adult or developing bees is key to understanding how to best ensure provisioning for a rich and diverse bee population within their natural ecosystems (Fründ et al. 2010, Blüthgen and Klein 2011, Schmack and Egerer 2023). Without sufficient floral diversity within the habitat, a lack of nutritional diversity results in the loss of pollinator diversity, abundance, and quality (Biesmeijer et al. 2006, Baldock et al. 2015, Potts et al. 2016a). Decreases in floral resources have negatively impacted body size of bees, suggesting that the decrease in nutritional availability decreases the fitness of the current and next generation of bees (Anderson et al. 2024, Arnold et al. 2024). Land use changes that decrease the body size of the bee community within the modified area can be characterized as fragmentation, disturbance, or agricultural conversion, which can alter the floral community, reducing the quality and abundance of nutrition sources (Anderson et al. 2024).

Morphological variation of bees determines the preferred nutritional source collected. Bees can be classified as short-tongue or long-tongued bees based on the use of their glossa,

tongue structure, which will affect the types of flowers the bees prefer (Michener 2007). The main protein source used by bees is pollen, the reproductive gamete of male flowers (Michener 2007). Scopal hair positioning directly influences the size and type of pollen that can be collected by the bees (Thorp 1979). Limitations to what the bees can collect due to their scopal structures can limit floral resources used, while creating evolutionary pressure between the bees' foraging behaviour and the flowering plant resources (Thorp 1979, Dorchin et al. 2021). When plant visitation occurs, pollen is deposited on the body surface of the bee or by active collection of the pollen by the bees using their scopa, providing an opportunity for pollen dispersal between flowering plants to occur (Patiny 2012). Pollen is then used in the provisioning of the brood and for ovarian development of the female bees (Michener 2007, Lan et al. 2021, Grozinger and Patch 2024). Nectar is primarily composed of glucose, fructose, and sucrose, produced by flowering plants solely to attract pollinators (Gill and Walters 2023). This nectar is stored within nectaries, which can be reached using a glossa or tongue structure (Michener 2007). Accessing nectaries drives morphological changes in bees, contributing to niche partitioning by limiting the species capable of accessing the nectaries, producing conditions that can cause speciation to accommodate the flowering plant structure, which contributes to the diversity, abundance, and quality of the bee community (Miller-Struttmann et al. 2015, Gill and Walters 2023). Oil is produced by some plants as a reward for oligolectic or polylectic bees (Michener 2007, Correia Da Rocha-Filho et al. 2018). These oils are rich in lipids that will be used to provision the young and create a vapour barrier in the nest to regulate the humidity in the brood cells (Michener 2007). Novel foraging strategies like the use of plant oils, introduces additional components for further niche partitioning and functional complementarity, reducing competition between bee

species by encouraging specialization on specific plant components (Pauw et al. 2017, Anderson et al. 2024).

Habitat Necessities of Bees

Habitat necessities of bees are difficult to determine due to variable use of landscapes for nesting, foraging, the impacts of environmental conditions, and land use practices limiting or enhancing the functioning of the community (Torne-Noguera et al. 2014, Hopfenmüller et al. 2014, Wenzel et al. 2020). The morphological traits of bees, like body size, and the life history traits, lecty, sociality, and nesting strategy, can influence the use of the landscape and the impact the landscape has on each species (Hopfenmüller et al. 2014). Urbanization impacts the bee community due to low environmental permeability, limiting the amount of nesting area and forage resources, which are key habitat necessities of bees (Torne-Noguera et al. 2014, Wenzel et al. 2020). The habitat amount hypothesis combines habitat patch size and connectivity into one area-based metric, relating the habitat area to non-habitat area to the species richness in both habitat types (Fahrig 2013). When examining an unaltered natural landscape, the habitat amount hypothesis would apply by reaching the maximum amount of available rewarding landscape for a diverse and abundant bee community, emphasizing both nesting and foraging sources available in abundance (Fahrig 2013). There is still unexplained variation in pollinator communities, meaning there are additional aspects within the environment determining the diversity and abundance of pollinators besides having a large proportion of resource-rich landscape (Fahrig 2013, Torne-Noguera et al. 2014, Hopfenmüller et al. 2014). Heterogeneity at the ecosystem type level creates diverse landscape types such as semi-natural areas or natural area remnants. In areas where agriculture is the primary landscape component, maintaining nesting habitat, diverse forage and corridors for movement within the landscape is key to a diverse and abundant

bee community (Tews et al. 2004). The functional landscape heterogeneity hypothesis suggests diversity at all trophic levels is increased by landscape complexity, creating novel niche partitions and functional complementarity (Tews et al. 2004, Hopfenmüller et al. 2014). Corridors like hedgerows and flowering strips are shown to improve the movement and diversity of bee communities by connecting remnant natural landscapes within human-modified ecosystems and are often considered semi-natural components within a landscape that maintain essential resources for bees (Kremen et al. 2018, Killewald et al. 2023). Island biogeography theory states that when the ecosystems contain large amounts of inhospitable land, there needs to be mechanisms to facilitate and incentivize movement between patches of habitable land otherwise, no movement will occur, isolating populations within island-like structures (Kremen et al. 2018, Ponisio et al. 2019, Killewald et al. 2023). Applying the principles of habitat amount, functional heterogeneity, and island biogeography, the intermediate landscape-complexity hypothesis helps us understand the relationships seen in the pollinator-plant systems based on the complexity of the surrounding landscape. The intermediate landscape-complexity hypothesis highlights that complex landscapes are not as affected by agricultural practices due to the increased availability of corridors and gradients of supporting natural habitats, which in turn provide pathways and refuge from simple resource-poor landscapes such as conventional farming areas (Tscharntke et al. 2012a).

Environmental conditions like temperature and wind speed influence bees, with increased temperatures, the metabolism and development of bees are negatively impacted, and the ability for movement decreases with increasing wind speeds (Heinrich 2004, Hamblin et al. 2018). In urban environments, where temperatures tend to be significantly higher than in natural environments, bees experience changes in their metabolism and development patterns (Hamblin

et al. 2018). Ensuring there are enough green spaces within urban areas that offer cooler, sheltered areas for bees is critical for maintaining a healthy population of pollinators in a human-modified landscape (Hamblin et al. 2018).

Predicting the ranges and preferred habitats of each species of bee is incredibly difficult (Marshall et al. 2015). Many factors need to be considered when predicting the ranges of bees due to the complexity of the relationship between the habitat necessities and the preferred use of the landscape components by the bees (Marshall et al. 2015). Polylectic and oligolectic bees will interact with the ecosystem differently; polylectic bees are typically capable of traveling further due to large body sizes with no clear distinction in habitat use (Greenleaf et al. 2007, Marshall et al. 2015). Oligolectic bees typically have a smaller body size, limiting travel, and remain within an area where their preferred habitat or floral resource is predominant (Greenleaf et al. 2007, Marshall et al. 2015). Larger-bodied bees can fly further distances than small-bodied bees, resulting in variable use of habitat patches depending on the dispersal ability of the bees, which can effectively alter the species ranges and habitat use due to the body size-dependent movement limitations (Torne-Noguera et al. 2014, Marshall et al. 2015). Large-bodied bees will travel further in a more linear pattern through landscapes up to 3000 m from the nest, utilizing corridors and fragmented landscapes (Heinrich 2004, Torne-Noguera et al. 2014, Marshall et al. 2015). Small-bodied bees travel around a single point in a circular pattern, very rarely venturing further than 1000 m from a centroid, preferring to remain near their nest, floral resources, or preferred habitat type (Torne-Noguera et al. 2014).

Bee Declines

There are only 88 species of invertebrates listed as Special Concern to be Extirpated, with only two *Bombus* species and one cuckoo bee on the list. Bees in Canada have not been broadly

assessed for conservation status, only 1% of the >1000 species of bees have had their status assessed, 3% of bee species at risk have not been assessed by Environment and Climate Change Canada, and 68% of Canada's species lack sufficient knowledge to begin assessing their status (Independent Auditor's Report 2024).

Loss of local diversity or extirpation of species requires a clear picture of population trends (Winfree et al. 2011). According to the recent 2016 IPBES report, pollinators have shown losses in diversity, abundance, and distribution across North America (Potts et al. 2016b). The changes that are seen in the diversity, abundance, and distribution of bees are not limited to managed populations but also to wild populations (Potts et al. 2016b). The changing climate and continued habitat loss from agricultural intensification have created a need for rapid modification of behaviours by pollinators to accommodate the changing environment across North America (Bartomeus et al. 2011, Potts et al. 2016b). Unfortunately, land-use change and fragmentation stressors faced by wild bees are not as well studied in comparison to environmental climate, pesticide, and pest stressors due to a lack of knowledge on bee population dynamics, life history, and diversity (Mitchell et al. 2013, Potts et al. 2016b).

Short-term studies of bee populations have dominated research, with very few studies doing long-term population dynamic studies of bees (Winfree et al. 2011). This leaves a gap where the declines and increases in the overall populations of pollinators are monitored, rather than examining specific species trends and responses to environmental changes, leading to misunderstandings of decreases or increases in key species populations year over year (Winfree et al. 2011). Along with population dynamics being understudied, the life cycles, including the nesting behaviour, mating patterns, developmental timing, and mortality rates, are not thoroughly documented for every species (Potts et al. 2010, Winfree et al. 2011). Stressors that are observed

in wild bee populations are climate change pressure, introduced bee diseases from managed stock, and the loss of natural habitat areas (Fahrig 2003, Bartomeus et al. 2011, Hadley and Betts 2012, Potts et al. 2016a, Potts et al. 2016b).

Range shifts of foraging resources due to climate change have been documented in North America, with bees adjusting their flight, development, and reproductive times to adjust to ~300 km of northward climatic range shifts in their southern distributions (Bartomeus et al. 2011, Kerr et al. 2015). Northern distributions of bumble bees have remained steady between 1975-2010, although the southern distribution of the bumble bee ranges has shifted northward, effectively decreasing the distributions of bumble bees (Kerr et al. 2015). Range shifts of forage can also be seen, resulting in a decrease in forage availability within current bumble bee ranges (Bartomeus et al. 2011). Phenological mismatch between bee flight periods and flowering periods, could be driving populations of bees into unsuitable areas due to land-use intensification rendering flowering plants scarce or resulting in a shift of host species range or loss of key resources, at a pace bees cannot readily adapt to (Kerr et al. 2015).

The ability of bees to adapt to these continued climate change-related changes is uncertain, especially with additional pressures of the new ranges potentially increasing exposure to pesticides, pathogens, and pests (Bartomeus et al. 2011, Goulson et al. 2015, Kerr et al. 2015). Some of the risks faced by wild bees when they enter agricultural areas are pesticides, and pests and pathogens from managed honeybee colonies (Goulson et al. 2015). Pesticides have been shown to affect pollinators due to persistence within the environment, overspray into non-target areas and spray drift, putting stress on their development, reducing their ability to resist disease, or killing them due to exposure (Brittain et al. 2010, Goulson et al. 2015, Basu et al. 2024). Exposure to pesticides during foraging is not the only risk, but the risk of exposure to diseases

and parasites also increases in agricultural areas, especially where managed bees are present (Goulson et al. 2015, Koch et al. 2017).

Flowers visited by honeybees that are within the area where wild bees are foraging are where wild bees contract diseases and parasites (Koch et al. 2017). This has led to a shift in the floral resource use of wild bees, favoring resources not frequented by honeybees that may be less rewarding, changing the functional complementarity of the ecosystem, and impairing the wild bees' fitness by requiring increased foraging for sufficient nutrition (Koch et al. 2017). Native bees are encountering managed pollinators more frequently since natural areas surrounding agricultural areas are reducing in size every year, resulting in diseases entering and persisting within wild populations (Dolezal et al. 2016, Koch et al. 2017). Further habitat loss will only continue to exacerbate the transmission of these diseases to wild populations by limiting the range area available to wild bees to escape interactions with pathogens.

In Canada, the density of human habitation is 10–30 people per square kilometre in the Southern region, in comparison to Northern Canada which supports ~0.1 people per square kilometre (Natural Resources Canada 2024). Since agriculture and human populations are concentrated in the Southern areas of the country, the Southern area is most impacted by habitat loss due to habitat conversion. Across Canada, approximately 5.6–7.5% of the habitat has been converted to cropland (Coristine and Kerr, 2011). Further habitat degradation has occurred because of the shift to agricultural practices, causing habitat isolation, fragmentation, and changes to the fluvial systems, preventing or reducing movements of key species, nutrients, and water between natural habitat patches (Dobson et al. 2006, Tylanakis et al. 2007, Koper et al. 2010, Hung et al. 2021).

Drought in Canada and North America puts more pressure on native bees in expanses of homogeneous agricultural land rather than fragmented landscapes, though this distinction is not clear since the fragmentation of the landscape may be working against the bees along with drought preventing a clear picture of how the community is impacted (Schindler and Donahue 2006, Hung et al. 2021). Seed dispersal in fragmented landscapes is negatively impacted whether seed movement is abiotic or biotic, preventing colonization or maintenance of populations in isolated patches, gradually decreasing the diversity of floral resources available (Warneke et al. 2022, Fedriani et al. 2023). Maintenance of floral communities that require pollination services are impacted by fragmentation via reductions in bee movements between patches due to a lack of contiguous landscape between patches facilitating bee movement (Krewenka et al. 2011). Bees require patches of semi-natural or natural habitat in human-modified landscapes to maintain diversity in species assemblage, by using semi-natural or natural habitat for nesting, refuge, and resource acquisition, along with providing niches that increase the opportunity for species diversity (Tews et al. 2004, Tscharntke et al. 2012a, Fahrig 2013). Abundance is not as influenced by landscape composition since agricultural landscapes tend to favour medium to large-bodied bees, drawing and maintaining an abundant functionally redundant bee community with behavioural patterns like polylecty and large foraging areas (Grüter and Hayes 2022). Abundance is more impacted by the configuration of the landscape, where isolated populations will not support as abundant a population in comparison to connected landscape inhabitants (Brosi et al. 2008b, Rands 2014, Everaars et al. 2018). Research is still needed to develop a clear relationship between the composition and configuration of the landscape's effects on all community assemblies of bees, including functional diversity, species diversity, abundance dynamics, and body size impacts in both the polylectic and oligolectic categories of resource use

(Winfree et al. 2011, Hadley and Betts 2012, Fahrig 2017, Potts et al. 2016b, Rahimi et al. 2021, Vasiliev and Greenwood 2023).

Part 2: Landscape Heterogeneity in Manitoba

Coevolution and Mutualism

Bees likely began their relationship with plants as oligolectic solitary species, leading to an eventual radiation into polylecty, subsocial, and eusocial nesting strategies (Danforth et al. 2006, Michez et al. 2011). Coevolution is the result of interactions between individuals residing within the same area or community, leading to a clear ecological relationship between community members supported by interactions and functional complementarity (Ehrlich and Raven 1964, Langerhans 2008). The bee-plant coevolutionary relationship is best demonstrated by plant adaptations shaping bee behaviour, morphology, and diversity to optimize fitness (Thorp 2000, Renner and Schaefer 2010). Selection pressure between bees and plants is related to the selection of specific plants or plant traits by visiting pollinators based on signals produced by the plants' morphological attributes, driving long-term changes in bees to suit the anatomy of their florescence (Pauw et al. 2017, Koski 2020). Mutualistic coevolution has shaped the relationship between bees and plants the most, demonstrating a clear benefit to both plants and bees based on their interactions within the landscape (Kiestler et al. 1984). The mutualistic relationship between bees and plants is such, the plants provide nutritional resources to the bees, who then carry the pollen granules from one plant to another, assisting fertilization (Kearns et al. 1998). Mutualistic coevolution occurs during this bee-plant arms race, shaping the plants to better suit the bees and their needs, while the bees adapt to best suit the needs of the plant (Kiestler et al. 1984). The coevolutionary dynamics between bees and plants can lead to changes within a species so profound that speciation occurs (Kiestler et al. 1984, Baguette et al. 2020).

Current issues in the field of evolutionary ecology are related to disturbances in the landscape in response to fragmentation, climate change, or agricultural intensification (Tschamntke et al. 2005, Kerr et al. 2015, Miller-Struttman et al. 2015, Ghisbain et al. 2020, Cristóbal-Pérez et al. 2021, Ostwald et al. 2024b). Habitat fragmentation has caused genetic bottlenecks in the populations of flowering plants due to limitations in pollinator visitation frequency, reducing the transfer of genetic material between populations due to limited connectivity within the landscape (Cristóbal-Pérez et al. 2021). Climate change and habitat fragmentation have been linked to range shifts of bumble bee species across Europe and North America, with climate driving the need for range shifts and habitat fragmentation limiting the movement of bees into new ranges (Bartomeus et al. 2011, Kerr et al. 2015). Heat tolerance of bumble bees has also been linked to limited range shifts when climate change occurs, creating scenarios where bees are forced to adapt to changing climatic conditions (Feuerborn et al. 2023). Heat tolerance has also been shown to have different effects on castes, with bumble bee queens showing the lowest heat tolerance, suggesting that there is social complexity limiting the adaptability of bees (Feuerborn et al. 2023, Ostwald et al. 2024). Morphological adaptations have also been observed in long-tongued bees when there is a decline in native plants within their pollinator network in agricultural areas, resulting in reductions in glossa length (Miller-Struttman and Galen 2014, Miller-Struttman et al. 2015). This morphological adaptation could result in shifts in the plant-pollinator community assembly over time (Miller-Struttman and Galen 2014).

Plant-Pollinator Community Assembly

Pollinator community assembly is affected by inter- and intraspecific relationships with community members, abiotic factors, biotic factors, niche partitioning, dispersal dynamics, and

the evolutionary relationships between pollinators and their floral partners (Goulson 2003, Tilman 2004, Brittain et al. 2010, Winfree et al. 2011, Bartomeus et al. 2013, Kremen et al. 2018). Competition between native and managed bee stock shows that competition is occurring on native and agricultural flowering plants, with overlap in foraging ranges decreasing the available resources for native bees more significantly in comparison to managed bees (Goulson 2003, Goulson et al. 2015, Page and Williams 2023). Introduction of exotic bee species can disrupt niche partitioning, especially when exotic species have become established in native bee foraging ranges, disrupting the specialized relationships between native bees and native floral resources, causing a decrease in the reproduction of the flowering plants (Tilman 2004, Dohzono et al. 2008, Inoue et al. 2008). Habitat fragmentation of natural areas has decreased the dispersal potential within the landscape, preventing the movement of bees between habitat patches and decreasing the potential for colonization and diversity maintenance of flowering plants (Krewenka et al. 2011, Warneke et al. 2022, Fedriani et al. 2023). Increasing connectivity and fragmentation of agricultural areas by introducing patches of naturalized ecosystems, like hedgerows or flowering strips, can have positive effects on both the native bee community as well as the flowering plant community (Kütt et al. 2016, Kremen et al. 2018, Nakamura and Kudo 2019). In Table 1, abiotic and biotic factors that affect the plant-pollinator community assembly are explored, highlighting the negative, positive, or situation-dependent impacts on bees and the floral resources in the landscape.

Abiotic factors like climate variables, cloud cover and wind speed show a general negative impact on both pollinators and plants, with the optimal temperature for both bees and plants being ~26 °C, decreasing suitability at lower and higher temperatures (Heinrich 2004, Tilman 2004, Bartomeus et al. 2011). Looking at the positive impacts of habitat structure on

plant-bee communities, natural, semi-natural, and connected landscapes have positive effects on both the pollinator and plant communities by increasing dispersal abilities, niche availability increasing functional diversity, and refugia for nesting and overwintering (Tylianakis et al. 2007, Bartomeus et al. 2013, Kremen et al. 2018, Kammerer et al. 2021, Vasiliev and Greenwood 2023). Agricultural landscapes, agricultural intensification, and fragmentation of natural ecosystems tend to have a negative affect on diversity of the plant-pollinator community assembly by reducing the amount of nesting and provisioning resources available, limiting seed and bee movement, high levels of disturbance in the landscape, increasing exposure to pathogens, pests, and pesticides, and competition with managed stock or non-native species (Tylianakis et al. 2007, Winfree et al. 2011, Potts et al. 2016b, 2016a, Kremen et al. 2018, Kammerer et al. 2021, Priyadarshana et al. 2021).

Biotic factors such as competition and mutualism rely on the interactions between species. For example, competition between honeybees and native bees has shown a reduction in provision for native bees when honeybees are present (Page and Williams 2023). Competition between plant species will drastically change the community assembly, reducing the diversity in the area by outcompeting their neighbours, decreasing the availability for functional complementarity in the bee community (Tilman 2004). Mutualistic interactions are required between bees and plants, positively increasing the abundance and diversity of both bees and flowering plants by increasing the movement of pollen from one plant to another increasing seed output and supporting the growth and development of bee communities surrounding the flowering plant resources (Potts et al. 2003, Ollerton et al. 2011, Kremen et al. 2018). Predation and parasitism show a negative impact on bees and plants, resulting in decreased fitness, colony collapse, or extinction (Romero et al. 2011, Gamboa et al. 2015, Dolezal et al. 2016, Koch et al.

2017, Manley et al. 2019, Liang et al. 2022, Wei et al. 2022). Niche partitioning, in particular resource, temporal, spatial, and functional trait partitioning, has a positive effect on pollinator diversity and abundance, creating more distinct species that specialize on specific floral resources (Fründ et al. 2010, Blüthgen and Klein 2011, Potts et al. 2016a). Specialization of pollinators on plant species can increase the diversity of pollinators in a landscape through speciation or niche partitioning (Fründ et al. 2010). Specialization on specific plant species or other forms of specialization can lead to increased risk of extinction when host populations change (Biesmeijer et al. 2006). Without understanding and accounting for the abiotic and biotic variables that impact the pollinator-bee community, there is a risk of insufficient conservation efforts to mitigate the changes being seen in the communities.

Table 1: Tabulated abiotic and biotic variables' impact on floral and pollinator community diversity and abundance.

Variables that affect pollinator community assembly in Manitoba				
Type	Abiotic	Biotic	Impact on Pollinator Diversity and Abundance	Impacts on Plant Diversity and Abundance
Climate	x			
Temperature	x		+/-	+/-
Cloud Cover	x			-
Wind Speed	x		-	-
Habitat Structure	x			
Natural landscape availability	x		+	+
Agricultural landscape availability	x		-	-
Semi-natural landscape availability	x		+	+
Connectivity	x		+	+
Fragmentation	x		-	-
Competition		x	-	-
Mutualism		x	+	+
Predation and Parasitism		x	-	-
Niche Partitioning		x	+	+
Dispersal		x	+	+
Source/Sink Dynamics		x	+/-	+
Adaptation		x	+	+

Floral Resources	x		
Density and Diversity	x	+	+
Phenology	x	+/-	+/-
Specialization	x	+/-	+/-

Indicators of community quality

Wild bees have been a topic of concern with the declines in abundance and diversity due to agricultural intensification being recognized globally, along with climate change-related ecosystem changes (Potts et al. 2010, Bartomeus et al. 2011). Habitat fragmentation removes access to the three main components required for a bee's success in the landscape: nesting, food resources, and refugia, with the removal of just one of the components resulting in decreases in bee diversity and abundance (Torne-Noguera et al. 2014, Marshall et al. 2015, Naeem et al. 2020, Escobedo-Kenefic et al. 2020, Chowdhury et al. 2023). Declines in bee diversity and abundance due to human intensification in areas inhabited by bees and their hosts pose risks to conservation efforts and agricultural practices globally (Potts et al. 2010, Winfree et al. 2011, Williams and Winfree 2013, Goulson et al. 2015, Wenzel et al. 2020). This trend has been demonstrated in Manitoba by the rapid decline of Megachilidae bee abundance when there were disturbances to their nesting sites due to the removal of natural habitat to make room for crops, negatively impacting the pollination services provided by the bees (Kevan 1999). Conservation efforts in Canada have focused on broad landscape conservation efforts, identifying bee species at risk for extinction, monitoring of current bee populations, agroecological changes to increase pollinator friendly ecosystems, and public engagement and education (Hanuschuk 2021, Environment and Climate Change Canada 2022, Killewald et al. 2023). Long-term population monitoring data is difficult to acquire and is lacking in the literature with regards to the current and historical bee population dynamics (Schindler et al. 2013). An additional challenge in using bees as indicators

is that the population dynamics, shifts across seasons or from year to year, are not well understood or defined for every area, potentially masking change in the population of bees (Winfree et al. 2011, Albertazzi et al. 2021, Chowdhury et al. 2023). Identifying key bee indicator species despite the challenges faced in monitoring their populations could still provide insight into the impact of habitat structure, based on the impact of agricultural intensification, fragmentation, and increases or decreases in floral diversity in human modified landscapes, could inform conservation initiatives of changes in the bee community related to habitat conditions based on the abundance of the indicator species (Schindler et al. 2013, Chowdhury et al. 2023).

Arthropods can be indicators of the quality of the community and landscape due to their diversity, short life cycles, essential functions in the environment, how they are represented across different trophic levels, and their sensitivity to abiotic and biotic factors (Chowdhury et al. 2023). These characteristics are key for an indicator since the ideal indicator will occupy many landscapes, interact with most components of the landscape, and will be impacted immediately if there are any changes to the landscape (Kremen et al. 1993). The ideal bee candidate would interact across many habitat patches to broadly assess habitat health, have a polylectic feeding strategy to ensure representation of floral diversity and abundance use in the landscape, has a clear relationship with a key component of a landscape, require a keystone plant or nesting habitat to reproduce or rear young, and have a medium-large body size for ease of identification (Kremen et al. 1993). Bees can be used as indicators to show the impact of pollutants, diseases, competition between introduced and native species, landscape composition, and landscape configuration due to their use of floral resources in agricultural and natural ecosystems (Kremen et al. 1993, Kevan 1999, Celli and Maccagnani 2003, Quigley et al. 2019, Chowdhury et al. 2023) (Figure 1). The wide breadth of components the bees interact with is tied to their roles in

Considering globally there are approximately 20,000 species of bees, with >1000 species in Canada, and 392 species recorded for Manitoba, this diversity presents lots of opportunity for niche representation within bees, providing diversity in the life history strategies and interactions with the landscape of potential bee indicator species (Kevan 1999, Michener 2007, Canada. Environment and Climate Change Canada. 2018b, Gibbs et al. 2023). A bee indicator species would be a member of a group that interacts with a wide variety of pollination niches with diversity in nesting and dietary specializations or uses a wide variety of resources across an array of ecosystem components (Chowdhury et al. 2023). Another benefit to using bees as an indicator species is the short life cycles and the number of generations that occur in a short period (univoltine or bivoltine) (Kevan 1999, Chowdhury et al. 2023). Impacts of changes in the landscape can be seen year over year, or throughout the year, with multigenerational species making monitoring efforts quick and easily executed during the bees' flight periods (Kevan 1999, Quigley et al. 2019, Chowdhury et al. 2023). Quigley et al. (2019) put forth the honeybee as a potential representative of social bees in agricultural ecosystems, monitoring the effects of agricultural practices within an area, in particular, environmental stressors' impact on colony performance, physiology, and pesticide accumulation, creating a metric of the environmental quality based on the measurable parameters gathered from the hive. To monitor additional life strategies, such as solitary bees, or wild bees in general, standardized areal netting and pan trap methods of sampling have been proposed for their effectiveness for capturing and monitoring the diversity and abundance of wild bees over a wide area and year to year sampling efforts (Sepp et al. 2004, Schindler et al. 2013).

Scientific methods of quantifying indicator species require sampling of species, identification of species, and a clear understanding of the species' life history requirements

(Kevan 1999, Chowdhury et al. 2023). To sample bees, there are a wide variety of collection methods, with both passive and active sampling methods available, each offering a different perspective on the community (Droege et al. 2010, Hanuschuk 2021, Miller 2021, Martini 2022). This variability in sampling methods makes collection easier and more accessible for long-term or short-term studies (Schindler et al. 2013, Chowdhury et al. 2023). Multiple methods of collecting bees ensures the diversity of bee species is captured, since certain be genera show preferences for trap types, such as pan trap colour or blue vane traps, while aerial netting captures the most diversity but is a time-intesive costly sampling method (Droege et al. 2010, Schindler et al. 2013, Popic et al. 2013, Hall 2018). Identification of bees can be made easier using online resources such as Discover Life or iNaturalist, which can consistently identify species to genus or provide a large selection of dichotomous keys and taxonomic work (Michener 2007, Discover Life 2024, “iNaturalist” 2024). In addition to using these online resources to identify bees, you can also read information about the life history or life strategies of the species, such as sociality, nesting, lecty, and speciality type on Discover Life or taxonomic papers for the area study (Michener 2007, Gibbs et al. 2023).

Currently, research has been focused on the use of honeybees, for monitoring environment “health” directly related to the impacts of pesticides, heavy metals, pathogens, and competition between species to monitor the impact of agricultural practices on the bee community (Kevan 1999, Celli and Maccagnani 2003, Rojas et al. 2022, Gascon et al. 2023, Catalano et al. 2024). The addition of pollutants to natural, semi-natural, and agricultural systems decreases the abundance of bee indicator species significantly by compromising the bees, leading to higher mortality rates and by decreasing the quality due to toxin build up in the honey, pollen, and larvae (Celli and Maccagnani 2003, Rojas et al. 2022, Catalano et al. 2024). Deviations from

the honeybee indicator model shows bumble bees and orchid bees as the indicators of conservation efforts in agricultural and forested areas where pollutants may be impacting the ecosystem due to the bees prevalence, ease of identification, and importance in the pollination networks of the crops (Sepp et al. 2004, Kerr et al. 2015, Naeem et al. 2020, Rojas et al. 2022, Breidenbach et al. 2023).

Bumble bees have also been used for broader landscape monitoring in agri-environmental regions; they were found to be impacted by the distance from the nearest natural habitat characteristics, potentially using corridors within the landscape for movement (Sepp et al. 2004). Examining corridor and broader landscape variable impacts on overall bee diversity and abundance have been completed for many natural, semi-natural and agricultural landscapes, with variations in conclusions (Tschardt et al. 2005, Biesmeijer et al. 2006, Hegland and Boeke 2006, Winfree et al. 2007, 2009, Steffan-Dewenter and Schiele 2008, Ricketts et al. 2008, Quintero et al. 2010, Potts et al. 2010, Garibaldi et al. 2011, Torne-Noguera et al. 2014, Hopfenmüller et al. 2014, Marshall et al. 2015, Rodríguez and Kouki 2017, Senapathi et al. 2017a, Hamblin et al. 2018, Wenzel et al. 2020, Escobedo-Kenefic et al. 2020). Initially, agricultural areas need to take into consideration the level of disturbance present within the landscape, identifying where impacts are highest and developing strategies to reduce damages (Tschardt et al. 2005, Winfree et al. 2007, Quintero et al. 2010). Reductions are seen in the bee and plant community from reduced natural habitat, herbicides, or competition leading to decreases in the pollinator community (Biesmeijer et al. 2006, Hegland and Boeke 2006, Winfree et al. 2009, Potts et al. 2010, Garibaldi et al. 2011).

Fragmentation in natural or semi-natural areas can negatively impact bee communities, although increasing fragmentation of agricultural areas can positively impact bee communities

(Steffan-Dewenter and Schiele 2008, Ricketts et al. 2008, Garibaldi et al. 2011, Torne-Noguera et al. 2014). The configuration of the landscape, with fragments being connected or a general connection between all the landscape connections, can increase the bee community diversity and abundance based on specific bee traits like foraging distance, body size, and lecty (Garibaldi et al. 2011, Hopfenmüller et al. 2014, Marshall et al. 2015, Rodríguez and Kouki 2017, Senapathi et al. 2017b, Wenzel et al. 2020). Agricultural intensification, climate change, habitat loss, and fragmentation impacts are increasing, requiring bioindicators of the health of our ecosystems to highlight the impacts of these environmental changes without major sampling effort across large areas (Escobedo-Kenefic et al. 2020, Albertazzi et al. 2021, Chowdhury et al. 2023). Clear impacts of corridors and edge effects within Southern Manitoba, including the potential bee indicator species of the corridor health, would be useful for identifying any changes to the community due to disturbance, pollution, or disease.

Drivers of Community Diversity

Community diversity of pollinator-plant community is essential for agricultural and natural ecosystems, due to the variations in the abiotic and biotic factors that make up both system types, creating many niches available for speciation (Potts et al. 2016a, Ollerton 2017). In a pollinator-plant community, floral richness and diversity can increase the abundance and diversity of pollinators (Ollerton 2017). In areas where floral resources are decreased in abundance and diversity, like agricultural settings, pollinator richness is also reduced (Winfree et al. 2009). Manitoba is known predominantly for producing rapeseed, wheat, sunflower seed, white beans, soybeans, oats, and potatoes (Pierre and McComb 2022). Considering wheat, oats and potatoes do not require any animal pollination, rapeseed, sunflower, white beans, and soybeans are typically pollinated by managed honey bee stock, there are extensive areas in

Manitoba that could be lacking any resources for wild bees as a result, increasing competition for resources, or leading to an increased risk of acquiring diseases (Garibaldi et al. 2011). Pollinators will have to travel farther and longer to source from the pollinator-dependent crops, especially when less rewarding floral diversity exists within the area designated agricultural land, which will reduce the amount of pollinator services available for the crops that are dependent upon pollinators since sourcing resources will take more time (Klein et al. 2007, Garibaldi et al. 2011). Connecting these rewarding crops via rights-of-way habitats, flowering plant strips, or through natural landscape islands with resource containing floral species has been shown to increase pollinator services to the pollinator dependent crops by increasing the heterogeneity of the landscape, providing greater opportunity for floral resources and bees to colonize and use the landscape (Cranmer et al. 2012, Schmack and Egerer 2023). The natural areas and additional floral resources increase pollination service potential by facilitating pollinator movement which can increase the diversity and abundance of pollinators (Garibaldi et al. 2011, Potts et al. 2016a, Schmack and Egerer 2023). Decreasing the disturbance of remnant natural areas in predominantly agricultural areas by supporting native plant growth in rights-of-way could support and enhance the diversity of pollinators within the area creating heterogenous elements that increase the floral diversity within the area by providing low or no disturbance areas (Winfrey et al. 2007, Hanuschuk 2021, Martini 2022, Meinzen et al. 2024).

Disturbance at the landscape level is the removal or alteration of the area's original community, either naturally or artificially (Sousa 1984). In a pollinator-plant community, disturbance can result in species-dependent positive or negative outcomes. Disturbance in forest ecosystems creates more heterogeneity, potentially increasing diversity and abundance in floral and pollinator communities, resulting in a positive impact when appropriate disturbance regimes

for the area are followed (Fettig et al. 2022). Small-scale disturbances in most natural areas result in increased availability of diverse floral resources, providing more diverse food and nesting habitat (Winfree et al. 2007, Fettig et al. 2022). Disturbance of pollinator-plant communities in other ecosystems, like agricultural areas, has a negative impact on the community, resulting in the loss of richness in both pollinator and floral communities (Ricketts et al. 2008, Winfree et al. 2009, Potts et al. 2010). When disturbance is broad-scale with large areas that are not connected, the negative impact is much greater than if there were some original lands left, resulting in a greater loss of diversity (Fahrig 2020). Leaving fragmented or semi-connected original areas is key to supporting as much richness as possible within the floral and bee communities (Fahrig 2003, 2017, Potts et al. 2016a).

Research in the Canadian prairies is increasingly demonstrating the impact that disturbance from habitat conversion in the Prairie provinces has on native bee community dynamics (Hanuschuk 2021, Miller 2021, Olynyk et al. 2021, Morrice 2021, Martini 2022). Hanuschuk (2021) explores how disturbance within an ecosystem impacts plant-pollinator community assembly, emphasizing the need to thoroughly examine the bee community to track the impacts of habitat conversion and disturbance in Manitoba. Examining the rare and disturbance-reliant Tall Grass Prairie and Mixed Grass Prairie, areas that were disturbed by cattle grazing and natural areas reduced due to habitat conversion, showed negative impacts on pollinator diversity and abundance (Miller 2021, Olynyk et al. 2021). In comparison to agricultural areas, natural areas and semi-natural areas support more bee diversity and abundance, with edge effects in agricultural systems helping to mitigate agricultural impacts on the pollinator community by providing “spill-over” into disturbed areas (Morrice 2021). Martini (2022) continued with the idea of edge habitats supporting bee diversity and abundance, showing

maintained early successional areas like powerline easements or roadside verges as potential sources and refugia for pollinator diversity and abundance. A common theme in these studies was the continued unexplained variation seen year over year in the pollinator communities, with shifts of significant variables varying year over year. Despite the phenomenon of year-over-year irregularity, one of the key variables associated with disturbance in these studies was the impact of fragmentation on the pollinator community.

Fragmentation due to disturbances within ecosystems can have various impacts depending on the scale. Some studies suggest that at smaller scales, greater amounts of fragmentation lead to more species richness; however, fragmentation at larger scales shows a negative impact on biodiversity (Fahrig 2013, 2017, Hanski 2015; Haddad et al. 2015, Haddad et al. 2017). In forested ecosystems, some fragmentation can temporarily increase the diversity and richness of plants and pollinators within the disturbed area (Steffan-Dewenter and Schiele 2008, Andrieu et al. 2018, Fetting et al. 2022). Generally, habitat fragmentation will create habitat isolation, which for species like bees makes it difficult for resource acquisition, nesting, and dispersal (Fahrig 2003, 2017, Hanski 2005, Hadley and Betts 2012, Moreira et al. 2015, Potts et al. 2016a, Escobedo-Kenefic et al. 2020). Fragmentation of landscapes has been shown to create homogenization in the pollinator community by reducing the amount of habitat available, limiting movement, and isolating populations (Hadley and Betts 2012, Rands 2014, Xiao et al. 2016, Everaars et al. 2018, Hung et al. 2021). If populations are unable to share species through corridors of fragmented land, it becomes very difficult for populations to recover from disturbances that reduce the pollinator-plant diversity and abundance (Gilbert et al. 1998, Van Geert et al. 2010).

Corridors in the landscape can present movement, nesting, provisioning, gene flow, and refuge opportunities to bees (Hendry et al. 2011). A corridor within an ecosystem is a series of small, connected patches of semi-natural or natural habitats within a fragmented landscape connecting larger patches of semi-natural or natural habitat (Gilbert et al. 1998). Corridors increase the complexity and connectivity within the landscape. This is demonstrated by the ability to assist pollinators in their movements from natural or semi-natural landscapes to agricultural sites when present in the surrounding matrix (Kremen et al. 2018, Ponisio et al. 2019). They also play a role in increasing matrix permeability, reducing the amount of unusable landscape to pollinators (Ricketts 2001, Kremen et al. 2018, Ponisio et al. 2019). Corridors also present an opportunity for native plants as refuge in agricultural monoculture areas (Martini 2022). This would increase provisioning and nesting resources for bees in floral-deficient agricultural systems (Martini 2022).

As bees are known to use corridors for moving through the landscape, the use of roadside verges, which are linear semi-natural elements in the landscape, as a means of dispersal and provisioning (Hopwood 2008, Baxter-Gilbert et al. 2015, Phillips et al. 2020, Deák et al. 2021, Martini 2022, Vasiliev and Greenwood 2023). However, roads present a potential barrier in the matrix, preventing the safe dispersal of bees across the landscape since the risk of collision, pollution, and management practices may increase the risk of mortality (Baxter-Gilbert et al. 2015, Phillips et al. 2020). Further research has shown that the benefits of supporting diverse plant communities in roadside verges far outweigh the risks to pollinators (Phillips et al. 2020).

What is landscape heterogeneity?

The components that create heterogeneity within the landscape are fragmentation, disturbance, and corridors. At the basis of all these concepts is the idea that each form of

landscape change creates patches within the landscape (Pickett and Cadenasso 1995, Turner and Gardner 2015, Deák et al. 2021). Landscape heterogeneity is dependent on the species composition of the region, the locations of patches, and the connectivity of patches within the landscape at the broader ecosystem or regional level or at the more specific patch level (Pickett and Cadenasso 1995). Patches will consist of communities distinct from the surrounding matrix, creating a mosaic of various landscape types within an area (Pickett and Cadenasso 1995, Turner and Gardner 2015). There are many ways these patches can form, either abiotic or biotic disturbance, such as fire or foraging animals, or due to human intervention within the landscape (Pickett and Cadenasso 1995). As such, patches are not consistent year over year, due to shifts in the ecosystems from environmental changes or disturbance in the ecosystem driving changes at the patch level (Pickett and Cadenasso 1995). Creation and maintenance of patches present an opportunity for different landscape metrics to impact the species composition at all trophic levels within the ecosystem (Pickett and Cadenasso 1995, Turner and Gardner 2015). In Manitoba, the impacts of heterogeneity in the environment are not easily studied due to the large changes in landscape from current and historical agricultural land conversion. Very few remnants of purely natural ecosystems remain in the Southern Manitoba range.

Landscape heterogeneity and its metrics can be divided into two classes, compositional heterogeneity and configurational heterogeneity (Fahrig 2003). Compositional heterogeneity is defined by the amount of different cover types present in the landscape (Fahrig et al. 2011, Priyadarshana et al. 2024). Configurational heterogeneity is defined by the frequency, size, and arrangement of patches in the ecosystem (Fahrig et al. 2011, Vasiliev and Greenwood 2023, Priyadarshana et al. 2024). Compositional heterogeneity has been shown to affect wild bee populations, positively and negatively, depending on the landscape context. Adding

compositional heterogeneity to agricultural areas has been shown to significantly increase diversity, whereas in natural landscapes, increased fragmentation, which can increase compositional and configurational heterogeneity, decreases diversity (Tscharntke et al. 2005). Configurational heterogeneity has been shown to have a positive effect on the pollinator diversity and abundance in already disturbed areas (Fahrig et al. 2011).

Heterogeneity's effects on pollinators are variable with changes in landscape composition and configuration leading to changes in ecosystem services and provisioning across the landscape (Mitchell et al. 2013). The direct links between compositional and configurational landscape heterogeneity on pollinators are understudied, with the scale at which the impact is studied being the most difficult to standardize (Quintero et al. 2010, Potts et al. 2016a). In addition to the scale being difficult to manage, temporal variation has been rarely studied, highlighting the effects landscape change has had in comparison to historical data (Senapathi et al. 2017). Changes in ecosystems from historical land types are predominantly due to agricultural intensification, which has been a major driver of pollinator declines (Kareiva et al. 2007, Potts et al. 2016a). Most studies have focused on singular ecosystem types, like agricultural, urban, or forested areas, with little comparison between land use types in North America (Ricketts et al. 2008, Winfree et al. 2009, Quintero et al. 2010, Senapathi et al. 2017a, Kremen et al. 2018, Schmack and Egerer 2023). When there is focus on singular habitat types, the temporal or seasonality of the surrounding matrix, containing floral resources essential for pollinators in otherwise inhospitable habitats, can be lost, missing a large component essential to supporting a healthy pollinator community (Potts et al. 2016a, Senapathi et al. 2017, Killewald et al. 2023). Along with the loss of heterogeneity from agricultural intensification, there is also an increase in urbanization, removing large portions of the landscape from the original pollinator-plant ranges

(Senapathi et al. 2017, Schmack and Egerer 2023). There are possible solutions for increasing the compositional heterogeneity of the urban landscape by creating pollinator-native flower-focused gardens, though their impact is not thoroughly tested (Baldock et al. 2015, Schmack and Egerer 2023). Urbanization, fragmentation, and heterogenization of agricultural landscapes create edges within the landscape (Andrieu et al. 2018). Edges create heterogeneity, which has been shown to increase the diversity of a community, plant, and pollinator alike, by creating various habitat types harbouring variable host plants and nesting habitats throughout the ecosystem (Rand et al. 2006, Andrieu et al. 2018, Olynyk et al. 2021). Other forms of edge creators are roadside verges or rights-of-way. These generally linear managed early successional land types create compositional and configurational heterogeneity through the landscape, increasing the diversity of the landscape types and increasing connectivity between habitat patches (Kremen et al. 2018, Martini 2022). Roadside verges have the potential to provide refuge, migratory services, and floral resources to pollinators, though their impact and support of the community is understudied (Kremen et al. 2018, Martini 2022).

Agricultural, Semi-Natural, and Natural Landscapes in Manitoba

Delineating landscape types creates an opportunity for boundaries selection to influence the results of analyses (Turner 2005). This can lead to a dominant driver in the ecosystem being missed in the analysis or exacerbating the driver's role within an arbitrary boundary with no ecological meaning (Turner 2005). Delineating boundaries without considering the movement, resource use, and functional community structure of the plant-bee relationship would reduce the ecological relevance of any results, increase the statistical noise in the data set, and produce an inconsistent comparability between studies (Turner 2005, Fahrig 2013). To prevent issues related to the grouping of the data into nominal categories based on landscape types, relating the

nominal categories to clear ecological patterns seen within species or landscape type distributions, be mindful of autocorrelation and correlation between habitat types, ensure the groupings are relevant to the research question, and ensure the scale of analysis is representative of the system of study (Turner 2005, Frazier and Kedron 2017a). Most landscape heterogeneity-based studies have focused on a habitat type, country (European), simulated landscape, or region with distinctions between human-modified sites and non-human-modified sites (Papanikolaou et al. 2017, Hammill et al. 2018, Londe et al. 2020, Rahimi et al. 2021). In Manitoba, the focus of landscape heterogeneity research has been on specific ecoregions, distinctions between site types like agriculture, semi-natural, and natural site types, and with a focus on either Northern, mid, or Southern Manitoba regions (Dunn et al. 2009, Koper et al. 2010, Hanuschuk 2021, Olynyk et al. 2021, Martini 2022, Umbanhowar et al. 2024).

Agricultural landscapes are not designed with pollinators in mind (Morandin and Watson 2003). With the thought that natural areas are sources of weedy plant species and crop pests, in North America and Europe, there has been an extirpation of natural landscapes in and around agricultural areas, leading to vast landscapes with very little floral diversity (Nicholls and Altieri 2013). In Manitoba, there has been a shift in ecosystem composition toward agriculture with approximately 47% of the landscape below the 51st parallel devoted to agricultural practices (Agriculture and Agri-Food Canada 2025). When examining the agricultural lands, there was an average of 809 acres per farm, with 606 acres devoted to crops per farm in 2021 (Statistics Canada 2024). The crop types typically grown on these farms are cereals, grains, pulses, oil seeds, various fruits, and nursery stock. Cereals, grains, and nursery stock do not require pollinators, creating vast landscapes with little to no floral diversity or abundance. This lack of floral diversity places pressure on oligolectic and polylectic bees alike since they must search

further for resources (Nichols and Altieri 2013). Along with putting pressure on pollinators, the lack of natural landscapes means that no new native plants can move into the area unless dispersed by alternative methods, essentially trapping any new landscape in its successional stage (Kremen et al. n.d., Cramer et al. 2008). With the remnant landscape in mind, the vast agricultural areas can create patchworks or remnant semi-natural ecosystems.

Semi-natural landscapes are characterized as an ecosystem that has been modified in the past for agricultural purposes by humans, though it still functions with some of the original natural processes (Miriam-Webster 2024). Semi-natural ecosystems are a complex matrix of native, fallow, and agricultural lands, which may increase overall diversity in an area due to their high edge density, increased patch density, and diverse habitat types. In ecosystems with high quantities of agricultural land, semi-natural landscapes have a source-sink dynamic, with semi-natural sites providing more diverse pollinator communities to agricultural areas when they are in proximity (Vasiliev and Greenwood 2023). Semi-natural ecosystems also create refuge for overwintering bees, since agricultural sites rarely have undisturbed protected areas for stem, cavity, or ground nesting bees (Steffan-Dewenter and Schiele 2008, Sheffield et al. 2008). The composition and configuration of semi-natural landscapes within agricultural areas support or increase the diversity of beneficial insects, providing many services to the semi-natural and agricultural areas. These semi-natural areas that support native floral resources are shown to increase the survival of honeybees through improved body physiology (Alaux et al. 2017). This trend is observed in native pollinators such as the large-bodied bumble bees improved colony survival and queen production due to an increase in semi-natural habitat in urban or agricultural settings (Crone and Williams, 2016, Goulson et al. 2022, Williams et al. 2012).

Natural ecosystems in Manitoba are areas that are not significantly disturbed by human activities over an extended period, maintaining a relatively complete network of endemic species, and are set aside as ecological reserves to preserve the original integrity of the ecosystem type (Government of Manitoba 2008). For Manitoba, four ecoregions were selected for testing: Assiniboine Delta, Precambrian Boreal, Tall Grass Prairie, and Lake of the Woods (Thorpe 2014). Precambrian Boreal and the Lake of the Woods ecoregions are sometimes considered to be synonyms, though there are distinctions seen in Manitoba, with Precambrian Boreal area showing more exposed granite shield in comparison to the sandy Southern Lake of the Woods area (Thorpe 2013, 2014). The differences are seen in the ecodistricts of the Lake of the Woods area. Precambrian Boreal also includes the Stead, Pinawa, and Kenora ecodistricts, whereas the Southern section of Lake of the Woods is predominantly the Whitemouth and Piney ecodistricts (Smith 2001). The Tall Grass Prairie ecoregion is commonly known as the Interlake Plain Ecoregion, with the Steinbach Ecodistrict being the primary area of focus. The name change was in reflection of the predominant area of study being within the Tall Grass Prairie Preserve. Tall Grass Prairie ecosystems once made up a large portion of Southern Manitoba, with their own unique and diverse communities; now, less than 1% remains of Tall Grass Prairie (Koper et al. 2010, Prokopanko 2017, Olynyk et al. 2021). This distinction between the soil types and plant communities could show differences in pollinator communities across the same ecoregion, leading to the distinction between the areas. Natural areas within these ecoregions include Aspen Parkland, Boreal Parkland, Tall Grass Prairie, Mixed Grass Prairie, and Mixed Forest.

Current Issues in Landscape Heterogeneity related to Pollinator-Plant Communities

Research on landscape heterogeneity's impacts on pollinator-plant communities focuses on urbanization, agricultural land use management, the complexity or level of fragmentation found within the landscape, and the connectivity between habitat patches (Figuerola et al. 2020, Huang et al. 2021, Martínez-Núñez et al. 2022, Cork et al. 2024, Zanini et al. 2024, Ulrich and Sargent 2025, Sexton et al. 2025). Urbanization has increased globally, driven by increasing human populations, requiring monitoring of the impact resource-poor urban areas have on the plant-bee community (Ulrich and Sargent 2025, Sexton et al. 2025). In urban areas in North America, Asia, and Europe, increasing the amount of floral resources, nesting habitat, and refugia available within metropolitan park areas or in community gardens, significantly increased the richness and abundance of bee species (Baldock et al. 2015, Nakamura and Kudo 2019, Ulrich and Sargent 2025, Sexton et al. 2025). The effects of landscape heterogeneity on urban bee diversity and abundance are mixed (Williams and Winfree 2013, Harrison et al. 2018, Nakamura and Kudo 2019, Sexton et al. 2025). Instances in Europe found that landscape context influenced the bee community at the local level where the urban community garden was present, with no significant impact on the bee community at the broader urban landscape scale (Baldock et al. 2015, Schmack and Egerer 2023, Sexton et al. 2025). In North America and Asia, results showed that the landscape context does have an impact on the bee community, in particular in areas where highly rewarding floral resources are available, either drawing bees away from native flowering plant species or simply increasing the diversity and abundance of bees within the urban areas (Williams and Winfree 2013, Harrison et al. 2018, Nakamura and Kudo 2019, Ulrich and Sargent 2025). Negative impacts of urbanization and agriculture are seen in some systems in North America, in forested areas where fragmentation has occurred for agriculture or

urbanization intensification, forest bees are replaced by alternative native bee species with phenologies that shift according to landscape type and life-history traits (Harrison et al. 2018).

Agricultural intensification is an ongoing issue in North America, causing the decline of most of the natural habitats. Manitoba has seen the most changes in the Tall Grass Prairie, Mixed Grass Prairie, and Aspen Parkland regions (Koper et al. 2010). To mitigate the impacts of agricultural intensification in Manitoba, research has been focused on increasing the floral diversity in agricultural areas, determining the impact of disturbance on the bee community, and identifying the species of bees interacting with agricultural, semi-natural, and natural areas (Gibbs et al. 2021, 2023, Hanuschuk 2021, Martini 2022, Killewald et al. 2023). Encouraging producers to include flowering strips adjacent to crops has shown that an increase in heterogeneity in the landscape produces an increase in bee abundance found in floral strips, increasing the pollination potential of the native bee community in agricultural areas (Killewald et al. 2023). More long-term studies in Manitoba are needed to determine if there is an increase in the functional community found surrounding flowering strips in comparison to the community of bees utilizing agricultural areas (Killewald et al. 2023). Conversion to agriculture and subsequent continued disturbance have a negative effect on functional diversity and pollination networks, leading to less functional complementarity in the region surrounding agricultural areas (Hanuschuk 2021). Roadside verges can be sources of continued disturbance in a landscape, although they also present opportunities for floral resource provisioning, refugia, and linear connected corridors for movement between patches (Meinzen et al. 2024). In Manitoba, roadside verges attract and support a diverse pollinator community using native or introduced plants (Martini et al. 2025). Roads increase the configurational and compositional heterogeneity of the landscape, creating opportunity for more functional complementarity in the area (Martini et al.

2025). Considering the effectiveness of the flowering strips, roadside verges, and the extent of the impact disturbance has on the bee community is dependent upon having a clear understanding of the bee diversity in a range of ecological settings, having a clear picture of the diversity of bees in Manitoba is key (Hanuschuk 2021, Gibbs et al. 2023). More work is needed to determine the population dynamics of the bee community over an extended period due to the continued disturbances in the landscape, the increase in heterogeneity created by natural habitat patch creation, and the bee community's use of roadside verges (Hanuschuk 2021, Killewald et al. 2023, Martini et al. 2025).

Along with agricultural disturbances and urbanization, forests and other natural ecosystems across North America are being subject to fragmentation (Miller 2021, Ulyshen et al. 2023, Rahimi and Jung 2023, Traylor et al. 2024). Fragmentation in a natural habitat type decreases the diversity and richness of floral resources by disrupting the pollination, species distribution, and niche partitioning within the landscape (Gillespie et al. 2024). These floral resource community adjustments in response to fragmentation modify the relationship between bees and the floral resources, leading to more polylectic species being favoured in comparison to oligolectic species relationships, since the functional specialized relationships are lost in the shift of floral community (Gomez-Martinez et al. 2022, Rahimi and Jung 2023, Gillespie et al. 2024). A polylectic feeding strategy is predominant in agricultural areas, where the fragmentation of the natural landscape is the highest, often with natural habitat limited to small patches, showing that bee species in agricultural areas become functionally redundant with no opportunity available for increased functional complementarity with diverse flowering plants (Rahimi and Jung 2023, Gillespie et al. 2024). Increasing the complexity of the landscape in agricultural areas has been shown to mitigate some of the loss in functional diversity in the plant-bee relationship, by

increasing the resiliency of the community to disturbance within the area (Huang et al. 2021).

This relationship is also dependent upon the crop types surrounding the natural areas, with fruit crop increases leading to decreases in the abundance of bees and oilseed rape sites showing increased pollinator diversity and abundance when natural habitat features were maintained surrounding the crop (Bottero et al. 2023, Gillespie et al. 2024).

To mitigate the impact of fragmentation, research has identified increasing the connectivity between intact habitat patches as a solution to the loss of functional complementarity in plant-bee communities, increasing the genetic connectivity between populations, increasing the plant-bee community resiliency to disturbance, and providing more ecological complexity to the area (Bottero et al. 2023, Gillespie et al. 2024, Martini et al. 2025, Schleimer and Frantz 2025). Connectivity in the landscape has shown an impact on the plant-bee community by influencing the distributions of traits in the bee and plant communities, increasing the functional diversity of an area by promoting niche partitioning of the area, selecting for more specialized life history and morphological characteristics in connected landscapes in comparison to fragmented or agricultural landscapes (Bottero et al. 2023, Parreño et al. 2024, Gillespie et al. 2024). Without connections between populations, isolation of species within an area can result in speciation or extinction due to disease, disturbance of the area, or lack of population replenishment from other patches (Abbott et al. 2013, Ghisbain et al. 2020). When connectivity between populations is present, with the support of sufficient resources, the ability of plant-bee communities to adapt and persist under pressure from disturbance increases (Huang et al. 2021, Bottero et al. 2023, Cork et al. 2024). Ensuring refugia, movement, and alternative resource sourcing are available is the key function of connected landscapes, demonstrating the importance of increased ecological and landscape complexity (Huang et al. 2021, Bottero et al. 2023, Cork et

al. 2024, Martini et al. 2025). Understanding the role, types, and amount of connectivity required in a landscape will be essential moving forward in a landscape continually impacted by fragmentation and disturbance (Cork et al. 2024, Gillespie et al. 2024, Ulrich and Sargent 2025, Martini et al. 2025, Schleimer and Frantz 2025).

Conclusion

Wild bee populations need to be monitored due to habitat loss, agricultural intensification, climate change, urbanization, and human-driven disturbances. Understanding how pollinators and their plant hosts are affected by landscape composition and configuration may provide insight when creating conservation plans to support the pollinator-plant community. Examining previously undervalued areas, such as roadside verges, as potential host habitats for pollinator-plant communities may be key to supporting and creating early successional habitat rich in nesting, floral resources, and protected flight area for pollinators.

METHODS AND MATERIALS

Sites:

Sites were selected based on ecoregion, land use, and accessibility. Four ecoregions in Manitoba, Assiniboine Delta, Tall Grass Prairie (TGP), Lake of the Woods, and Precambrian Boreal, were selected as site areas (Figure 2). Blocks of sites categorized as agricultural, semi-natural, and natural in each ecoregion along an approximately 10–16 km transect, with a minimum of 4 km between each site. Sites are classified based on the percentage of agricultural area in land cover data obtained from Google Earth, the Manitoba Land Cover Database, and field observations (Figure 3). Latitude and longitude of the sites are recorded and tabulated in Table S1. For 2021 and 2022, the same 36 sites were sampled (Figure 2). Each site was sampled three times per field season (June-August).

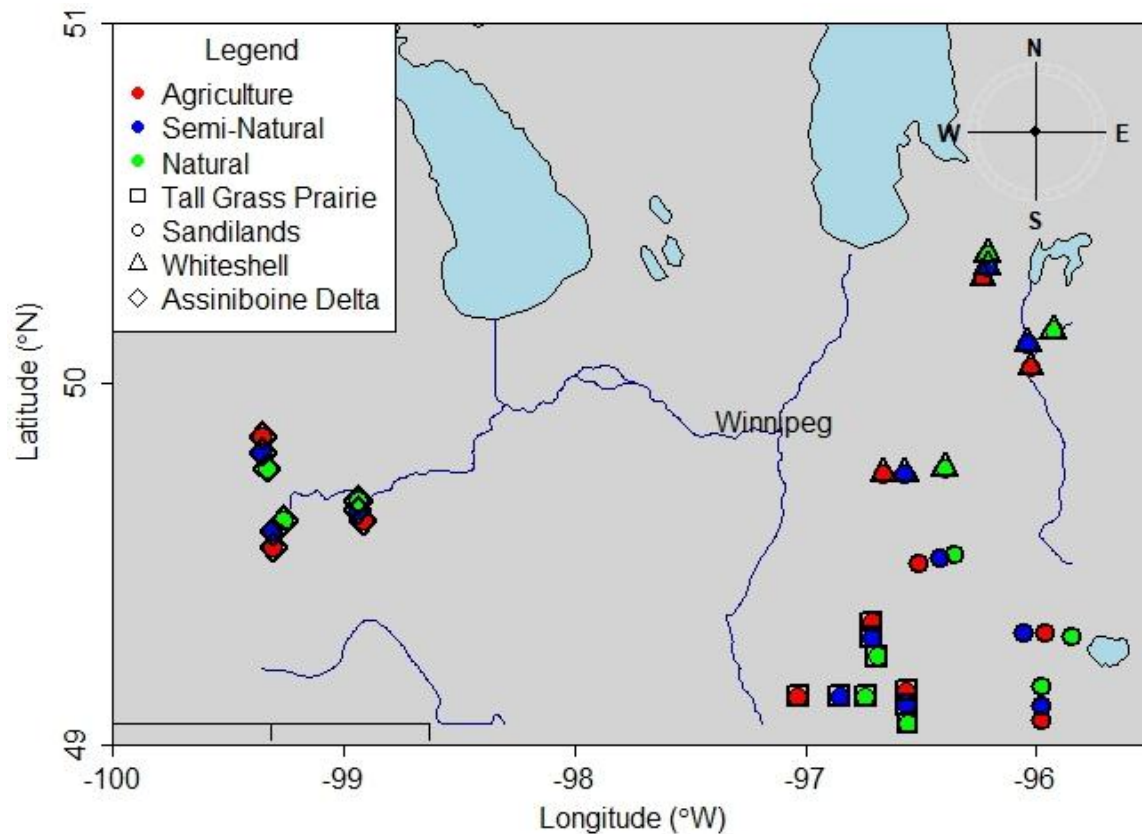


Figure 2: Sample site locations for 2021 and 2022 sample season across Southern Manitoba (n=36).

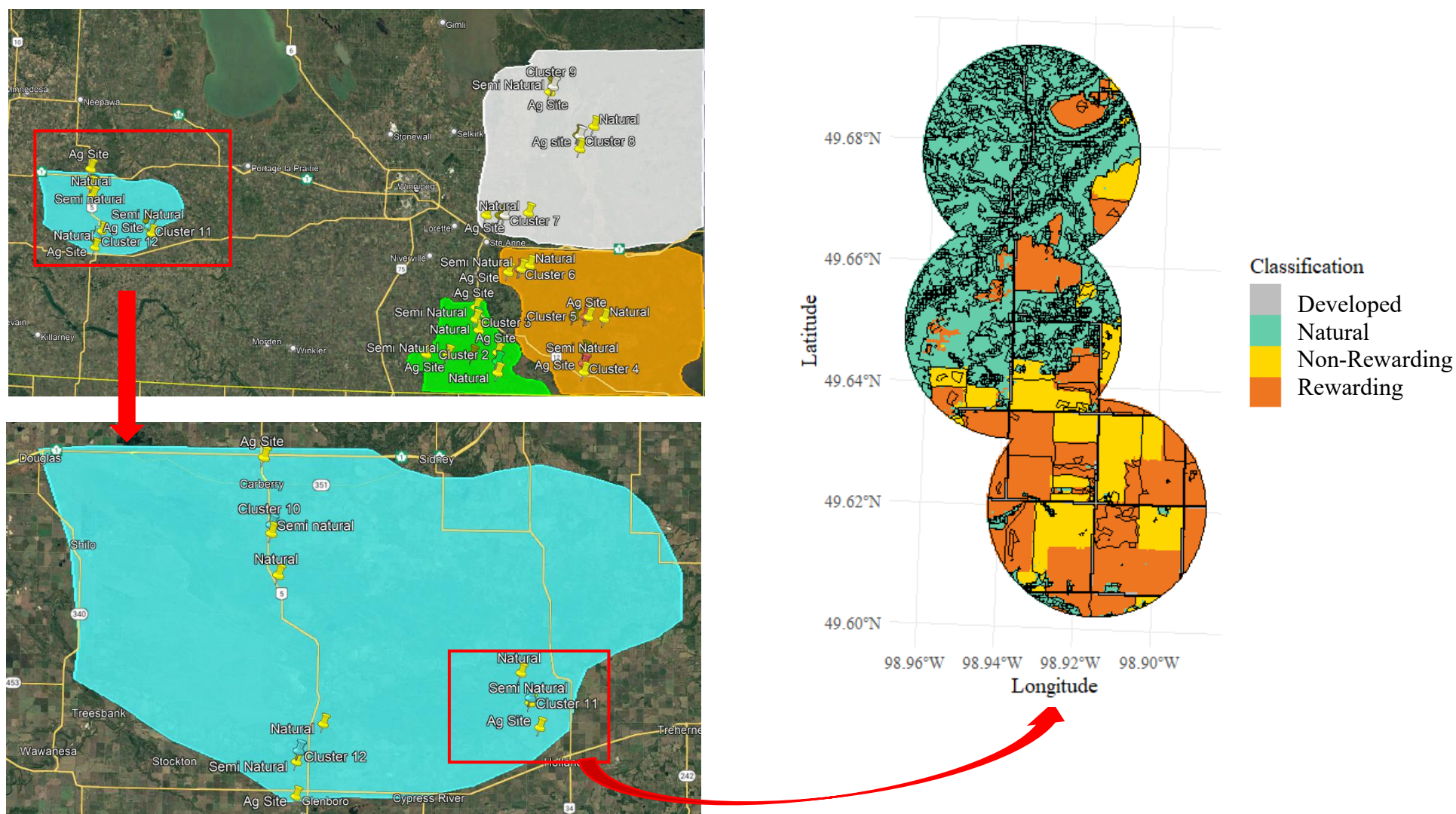


Figure 3: Landscape level breakdown of ecoregion and site distribution across Southern Manitoba, highlighting the clustering of sites within ecoregion, spread across Southern Manitoba, and the classification of landscape classes across natural, semi-natural, and agricultural sites (n=36).

Sampling Methods:

Three sampling methods were used to collect bees: blue vane traps (BVTs), bee bowls (also known as pan traps), and timed, targeted, aerial netting. Multiple methods were used since each approach collects genera in different proportions (Popic et al. 2013, Hall 2018). Sampling did not occur on days where it was raining, the wind speed was on average greater than 15 km/h, or the temperature was less than 18 °C (Heinrich 2004, Tuell and Isaacs 2010). Site, date, temperature, wind speed, and cloud cover were recorded during the vegetation surveys. Temperature and wind speed were recorded using a Kestrel meter with temperature readings taken in the shade and wind speed with the fan perpendicular to the air current. Cloud cover was recorded as none, scattered, partial, and overcast.

BVTs and Bee Bowls:

BVTs and bee bowls were placed in two transects inside roadside verges (Figure 4). Each transect was separated by no less than 5 m and preferably in different directions (N-S and E-W). Setting up each transect, soapy water (one teaspoon Dawn dish soap to 4 L of water) was used to fill the BVT 1/3 of the way full, with the BVT placed at the head of the transect (at the north end of the N-S transect and east end of the E-W transect). Five metres from the blue vane trap, I placed 12 alternating blue, yellow, and white bee bowls, each 5 m apart, halfway filled with soapy water (Figure 4) (Droege et al. 2010). Any vegetation that may cover or block the pollinators' entrance to the traps was removed, flattened, or pruned. Each transect, trap type, and bowl colour collection was stored separately. Any traps that were damaged, disturbed, dried out, or had no specimens were recorded. BVTs and bee bowls were used to assess pollinator communities at each site.

Aerial Netting:

Three, 10-minute, targeted net collections were completed at each site along a 50 m transect (Figure 4). Each transect was completed following a different direction and/or roadside verge. Along a 50 m transect within the roadside verge, targeted netting was done on the flowering plants present. Pollinators were caught and euthanized in cyanide jars, separated by the plant species the pollinator was caught visiting. The timer was stopped when handling collected individuals, to only run during active sampling. Aerial netting was used to assess the pollinator community, with samples providing community data to compare to landscape heterogeneity analysis and pollen for future analysis, since pollen samples rarely survive in BVT and bee bowl specimens.



Figure 4: Sampling scheme for vegetation surveys, aerial netting, bee bowls, and blue vane traps.

Vegetation Surveys:

Vegetation surveys were completed at each site in the aerial net transects (Figure 4). The survey examined the floral community and structure of the roadside verges. Ten quadrats were blindly tossed along a 50 m transect, overlapping with the aerial netting area (Figure 4). In each quadrat, percent cover per species of the forbs in bloom and overall cover of grasses, sedges, shrubs, and bare ground were recorded. Percent cover was estimated visually using the percent cover diagram from Moore et al. (2009). Litter depth in centimetres, estimated using a ruler, and dominant species within the quadrat were included.

Species Identification:

Bees were identified using available taxonomic keys and reference material in the J.B. Wallis/ R.E. Roughley Museum of Entomology at the University of Manitoba (LaBerge 1956, LaBerge 1956, 1961, 1967, 1969, 1971, 1973, 1977, 1980, 1985, 1987, 1989, LaBerge and Bouseman 1970, LaBerge and Ribble 1972, 1975, Baker 1975, Bouseman and LaBerge 1978a, 1978b, Laverty and Harder 1988, Romankova 2003, Coelho 2004, Arduser 2009a, 2009b, 2009c, 2009d, 2019, Droege S. and Brady 2010, Gibbs 2010a, 2010b, 2011a, 2011b, Rightmyer et al. 2010, Rehan and Sheffield 2011, Dumesh and Sheffield 2012, Gonzalez and Griswold 2013, Gibbs et al. 2013, 2023; Williams and Colla 2014, Andrus and Droege 2016, Droege 2016). Genera that were difficult to identify, for example, *Nomada*, were given approximate identifications based on keys and reference material. Additional assistance for troublesome or difficult to identify specimens, in particular Halictidae, Colletidae, Andrenidae, and *Nomada* species, was provided by Dr. Jason Gibbs.

Analysis:

Landscape Data:

Landscape data were extracted from Agriculture and Agri-Food Canada Inventory GEOTIFF files for 2021 and 2022, using the R landscapemetrics and the retired rgdal packages (Agriculture and Agri-Food Canada 2021, 2022). For this analysis, six metrics were extracted (Table S4): Edge Density, Shannon Diversity Index, Aggregation Index, Cohesion Index, Mean of Patch Area, and Mean Shape Index to quantify the landscape heterogeneity in the landscape surrounding the sites (Figure 5-7). The metrics extracted are tabulated in Table S4, showing the metric, equation, and description from Maximilian & Hesselbarth (2024). Metrics were extracted at 1500 m based on maximum foraging distance limitations of most bees (Osborne et al. 2008, Zurbuchen et al. 2010). The metrics measure the size, variability, and location of polygons demarcating the area of different landscape types in the GEOTIFF file. The habitat was visualized using polygons of each habitat type, created using ArcGIS Pro 3.3.1 by converting the GEOTIFF file from Agriculture and Agri-Food Canada to polygons using the Raster to Polygon tool (Figure 5-7).

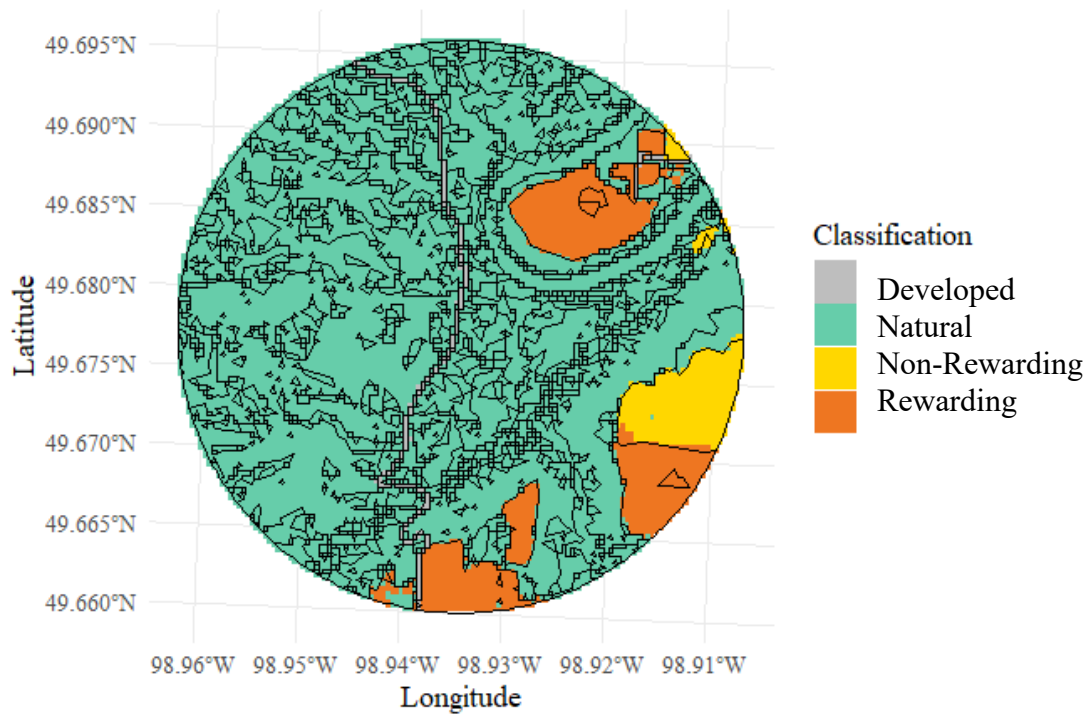


Figure 5: Raster image of landscape metrics for a natural site highlighting how the metrics are interpreted from the image.

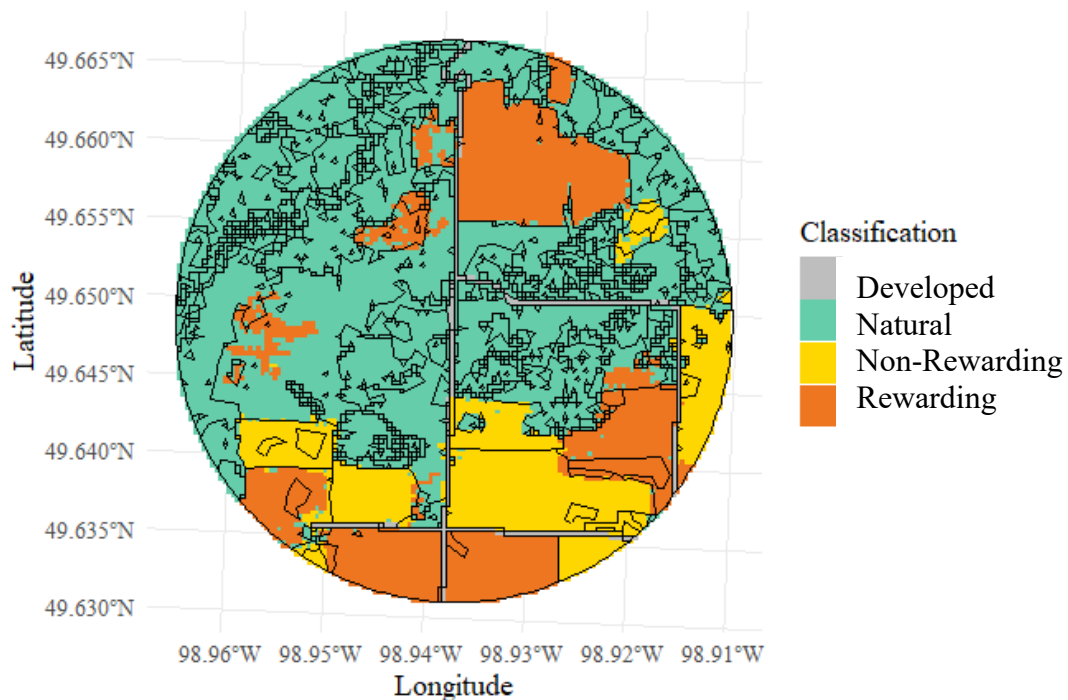


Figure 6: Raster image of landscape metrics for a semi-natural site highlighting how the metrics are interpreted from the image.

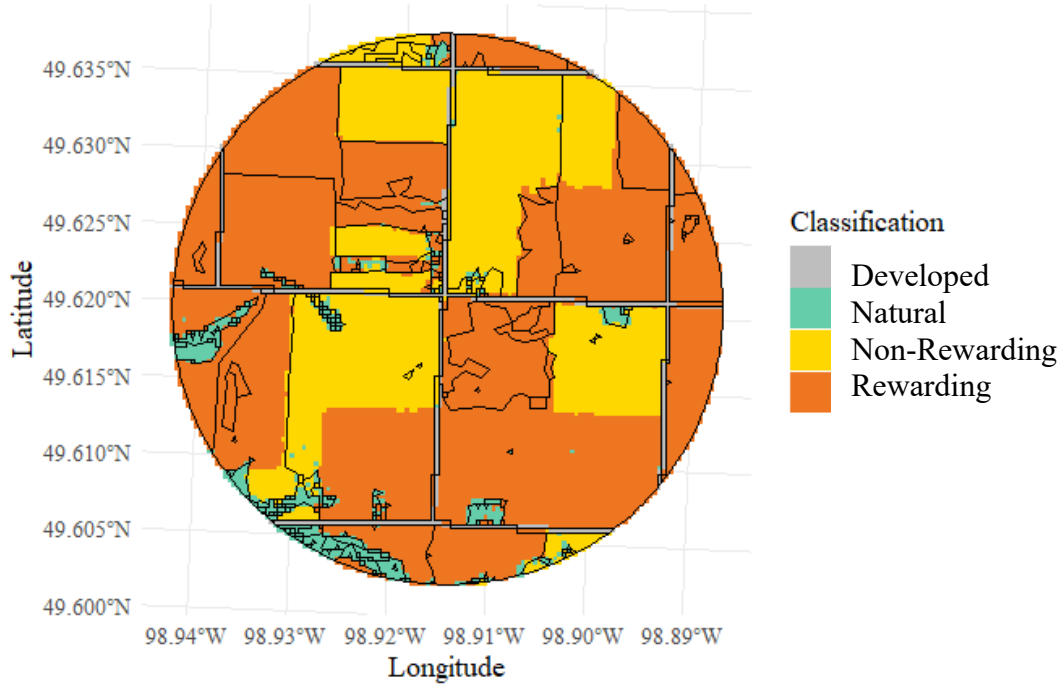


Figure 7: Raster image of landscape metrics for an agricultural site, highlighting how the metrics are interpreted from the image.

Generalized Linear Mixed-Effect Models:

Negative binomial generalized linear mixed-effect models were used for testing the hypotheses of this study. Landscape effects on bee abundance and diversity were examined by creating GLMM models for each year with configurational and compositional landscape metrics as fixed effects. Random effects for compositional and configurational models was the site variables. All compositional and configurational variables were scaled before testing to ensure comparability between variables.

Global model used for configurational heterogeneity analysis:

Bee Abundance or Diversity $\sim \beta_0 + \beta_1$ (Shannon Diversity Index) + β_2 (Edge Density) + β_3 (Mean Patch Area) + β_4 (Aggregation Index) + β_5 (Cohesion Index) + β_6 (Mean Shape Index) + β_7 (Julian Day) + γ (Site) + ε

Global model for compositional heterogeneity analysis:

Bee Abundance or Diversity $\sim \beta_0 + \beta_1$ (Water) + β_2 (Barren Land) + β_3 (Urban Land) + β_4 (Shrubland) + β_5 (Wetland) + β_6 (Grassland) + β_7 (Pasture) + β_8 (Oats) + β_9 (Wheat) + β_{10} (Corn) + β_{11} (Canola) + β_{12} (Soybeans) + β_{13} (Coniferous Forest) + β_{14} (Broadleaf Forest) + β_{15} (Mixedwood Forest) + β_{16} (Julian Day) + γ (Site) + ε

Configurational heterogeneity's impact on dependent variable bee abundance and diversity was tested using, Shannon Hill Landscape Diversity, Edge Density, Mean Patch Area, Aggregation Index, Cohesion Index, and Mean Shape Index, all at the 1500 m to account for flight distances of bees, as the independent variables (Osborne et al. 2008, Zurbuchen et al. 2010). Julian Day was included in the model to account for phenological variation in the bee community throughout the sample period (Duchenne et al. 2020). Model fitting and comparisons to a simplified model were completed using the GLMM and GLM methods to test the importance of the random effects in the model. If random effects did not improve the model, the GLM method was used. Multicollinearity checks were leveraged to remove highly correlated variables from the model, prioritizing the maintenance of ecologically significant attributes. A Bonferroni p-value correction was used to mitigate any risks of a Type I error. A Likelihood Ratio Test was used to determine if the random effects benefited the model. Random effects were further tested for their importance in the model using the variance and Intraclass Correlation Coefficient test. The residuals were assessed for normality by using a Q-Q plot, with an overdispersion check testing for any dispersion anomalies, and a check for the homogeneity of variance. Model selection was completed using the Akaike Information Criterion (AIC), with alternative models being fitted based on variables that impact the bees the most, with the best model having the lowest AIC value. A Bonferroni-adjusted p-value was used on the selected model to prevent any errors in the conclusions. The same normality, heterogeneity, and

dispersion tests were performed on the final model in addition to a Pearson Chi-Square statistic for a goodness-of-fit test.

This method was repeated for the compositional heterogeneity independent variables, water, exposed land, developed land, shrubland, wetland, grassland, pasture, oats, spring wheat, corn, canola, soybeans, coniferous forest, broadleaf forest, and mixed wood forest at the 1500m buffer zone. Variables removed before analysis were barley, rye, quinoa, winter wheat, sunflower, peas, beans, potatoes, due to the very small proportion of the landscape they covered near the sample sites or their lack of resource provisioning to the bee communities. If the random effects did not benefit the model based on the Likelihood Ratio Test results, a GLM was used to simplify the model. Correlation between variables was tested, and any highly correlated variables were removed before further testing, ensuring remaining variables had ecological significance to bees. Bonferroni adjusted p-value, variance inflation factors, dispersion testing, Q-Q plots, and heteroscedasticity plots were used to ensure normality, independence of samples, and freedom from errors. The same methods were used to further test the model.

Testing the indicator species, the dependent variable was the abundance of each indicator species collected at each site for the 2021 and 2022 sample season. Independent variables selected were wind speed, temperature, grass cover (%), flowering plant cover (%), bare ground cover (%), and litter depth (cm). Independent variables were collected during the vegetation surveys and scaled during analysis for ease of comparison. Random effects were selected based on Likelihood Ratio Testing, determining significance and comparisons of the model with or without the random effects. The best combination of random effects, having the highest explanation of variance, was site (n=36) nested in ecoregion (n=4). Residual, normality, heteroscedasticity, and overdispersion testing was completed as well. The most parsimonious

model was determined using a dredged Akiakes Information Criterion corrected analysis with delta set to <2.5 . The models selected were determined to be the model with the lowest AICc value and highest weighting with the most parsimonious approach. For 2021, the best model resulted in a simple model with only one explanatory variable, flowering plant cover (%). For 2022, two variables were included in the model, flowering plant cover (%) and grass cover (%), where an Interclass Correlation Coefficient test was completed to ensure no correlation between the two variables. Pearson Chi-Squared Statistic and DHARMA nonparametric dispersion tests were used to determine the goodness of fit of the models, using both to ensure no erroneous conclusions were made. For the GLMM model, the DHARMA nonparametric dispersion test was used for the robustness to non-normal data and issues related to GLMM goodness of fit. The MASS, MuMin, and DHARMA packages were used for the analysis of the GLMM (Venables and Ripley 2002, Barton 2024, Hartig 2024, Posit team 2024).

Indicator Species Analysis:

To extract indicator species from the data set collected, the Indicspecies package for R Studio 4.4.1 was used (Cáceres and Legendre 2009, Posit team 2024). The count data was collected from the roadside verges at 36 sites, 12 each of agricultural, semi-natural, and natural land use types across Southern Manitoba. Groupings of counts and species were done at Ecoregion, Site Type, and Site Cluster (groupings of Agriculture, Semi-Natural, and Natural sites within a 10km radius). Ecoregion was selected to see if any differences across Southern Manitoba were region-specific based on groupings described in the Literature Review. Site type was included to determine if there were variations in indicator species between land use types across Manitoba. 2021 and 2022 data were analysed separately to account for any variation in bee species between the two years. The Multipatt function from the Indicspecies package was

used for comparing the counts of species lists to the various selected groupings. The default IndVal was used as the test statistic for analysis. Any site that did not have any bees was removed from the dataset to allow for analysis. Species life history information, such as sociality, nesting strategy, lecty, and speciality, was extracted from Discover Life (2024) or Gibbs et al. (2023).

Distance-Based Redundancy Analysis:

A distance-based redundancy analysis (dbRDA) using the Bray-Curtis dissimilarity was used on the flowering plant cover data and the bee count data to identify any relationships within the communities' surrounding variations between site types. A matrix was created using the species of flowers or bees as the x-axis and the sites (n=36) as the y-axis, with the proportion of flowering species cover or bee counts as the values in the matrix. Flowering plant cover was collected during the vegetation surveys outlined in this chapter. Bee data were collected using the passive and active sampling in this chapter. The environmental variables were extracted from the landscape data analysed, grouped into non rewarding agriculture (crops with no nectar or pollen reward for pollinators), rewarding agriculture (crops with pollination rewards), developed land (cities, towns, roads, etc), and natural land in acres. Grouping of flowering plant species and bee counts was by site type, either agriculture, semi-natural, or natural sites. Using the vegan package version 2.6-6.1 the plot was created with flowering plant cover and bee counts as the points, grouped by site type, with the environmental variables as vectors. Adonis2, using the pairwiseAdonis package that leverages the vegan permutational analysis of variance (PERMANOVA) function, was used to perform a PERMANOVA on the groupings of site type blocked by cluster with the number of permutations set to 999, to determine if there was significant variation in the plot (Martinez Arbizu 2020). Further PERMANOVA tests completed were examining if there was any variation between ecoregions and if there was any variation in

bee diversity and abundance from the area of nonrewarding and rewarding agricultural landscape covers. A pairwise test was used as a post-hoc test to highlight any site type groupings that may have differences in the plot. Dispersion was tested using betadisper, and differences between the groupings' dispersion were tested using a TukeyHSD test.

RESULTS

From both the active and passive sampling efforts for 2021 and 2022, 8781 bee specimens were collected (Table S2). The 2021 sample season totaled 4105 bees collected, and 2022 had 4676 bees (Table S2). Of the 37 known genera in Manitoba, 33 genera were collected, representing all six families of bees found in Manitoba (Table S2) (Gibbs et al. 2023). 214 out of the possible 392 species of bees in Manitoba were identified from the samples, representing 55% of the total bee community in Manitoba (Gibbs et al. 2023). The most abundant genus was *Lasioglossum*, making up 26.1% of the total individuals captured (Figure S1). The ten species found to make up the 51.6% of the samples were *Melissodes agilis* Cresson 1878 (11.18%), *Halictus confusus* Smith 1853 (8.83%), *Agapostomen texanus* Cresson 1872 (4.92%), *Anthophora terminalis* Cresson 1896 (4.46%), *Melissodes trinodis* Robertson 1901 (4.43%), *Bombus ternarius* Say 1837 (4.10%), *Anthophora occidentalis* Cresson 1896 (3.97%), *Lasioglossum pilosum* (Smith 1853) (3.85%), *Lasioglossum zonulus* (Smith 1848) (3.63%), and *Lasioglossum paraforbesii* McGinley 1986 (2.23%) (Table S2). Tall Grass Prairie ecoregion had the lowest average bee abundance from both combined sample seasons ($\pm$ SD) (3.63 ± 0.88), followed by Lake of the Woods (4.19 ± 2.78), Precambrian Boreal (5.66 ± 2.64), with the highest average bee abundance in Assiniboine Delta (8.65 ± 4.64) (Figure S2, S3). Species accumulation curves show that there was good sampling effort, with a small spread in the confidence intervals, suggesting reliable sampling efforts for both 2021 and 2022 (Figure 8, 9). The vertical lines overlap regularly, suggesting that rarefied species richness is consistent, though the length of the lines show more variability between sites than what should be expected (Figure 8, 9).

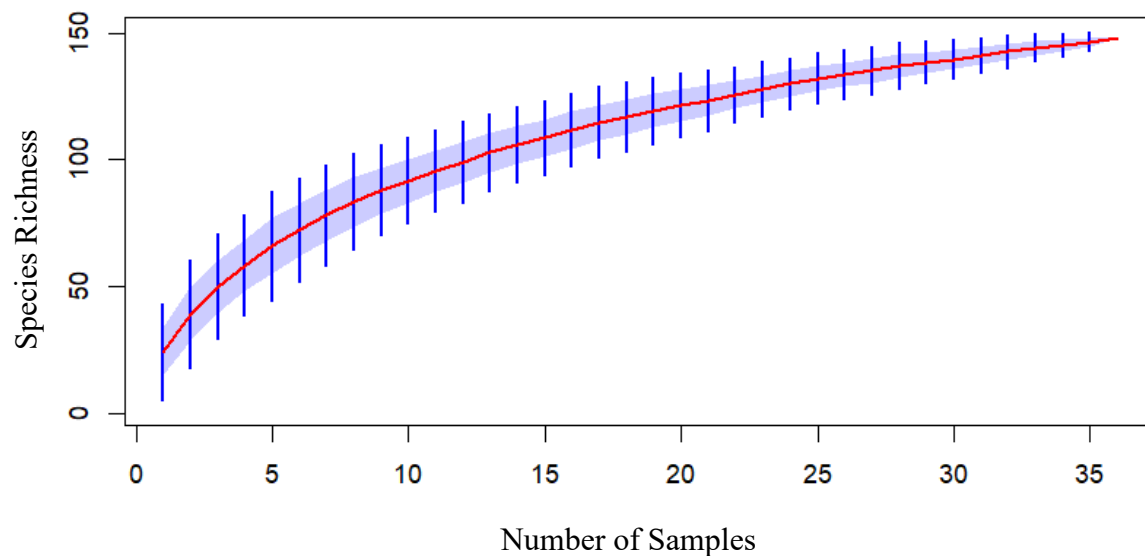


Figure 8: Bee species accumulation curve for sites across Southern Manitoba in 2021 (n=36).

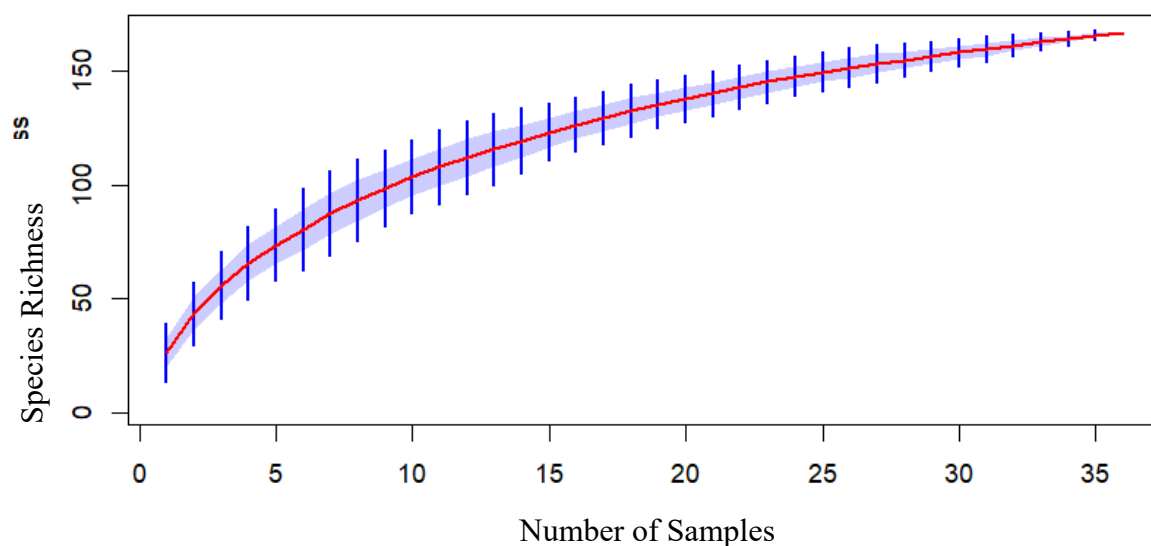


Figure 9: Bee species accumulation curve for sites across Southern Manitoba in 2022 (n=36).

Distance-based redundancy analysis using the Bray-Curtis dissimilarity testing the bee species and counts data matrix demonstrated variation between site types for 2021 and 2022 (2021: $F_{2,33} = 1.3406$, $R^2 = 0.07513$, $p = 0.003$) (2022: $F_{2,33} = 2.1485$, $R^2 = 0.11$, $p = 0.01$) (Figure 10, 11). Examining trends in 2021 showed differences between site types during round 1 of sampling ($F_{2,33} = 1.4461$, $R^2 = 0.08058$, $p = 0.003$), with the variation coming from the agricultural and natural site comparison ($F_{1,x} = 2.1495969$, $R^2 = 0.08901171$, $p\text{-adjusted} = 0.0150$) (Figure S4).

Round 2 and Round 3 of sampling showed no variation between the site types (Round 2: $F_{2,33} = 1.0596$, $R^2 = 0.06034$, $p = 0.114$) (Round 3: $F_{2,33} = 0.7188$, $R^2 = 0.04432$, $p = 0.642$) (Figure S6, S8). Ecoregion groupings also had no effect on the bee data for 2021 ($F_{3,33} = 2.1924$, $R^2 = 0.1705$, $p = 1$). Examining the relationship between the bee community and the hectares of rewarding and nonrewarding agriculture in the surrounding landscape, there was very little variation explained by rewarding agriculture ($R^2 = 0.009$) and nonrewarding agriculture ($R^2 = 0.0214$) for 2021 (Figure 10). Nonrewarding agriculture had no significant impact on community composition ($F = 0.3141$, $p = 0.804$), with rewarding agriculture also showing no significant impact ($F = 0.7456$, $p = 0.526$).

2022 showed similar relationships as 2021. Round 1 had differences between the site types ($F_{2,33} = 1.2878$, $R^2 = 0.0724$, $p = 0.007$) (Figure S5), and Round 2 had no differences between site types ($F_{2,33} = 1.062$, $R^2 = 0.06224$, $p = 0.091$) (Figure S7). The deviation between the two years was shown in Round 3 with differences between site types being seen in 2022 ($F_{2,33} = 1.3591$, $R^2 = 0.0761$, $p = 0.022$) (Figure S9). Only in Round 1 were there any significant groupings of site types, agriculture and natural sites being significantly different ($F_{1,x} = 1.829$, $R^2 = 0.0768$, p -adjusted = 0.024). Round 3 had no significant groupings post False Discovery Rate (FDR) adjustment, although before adjustment the agriculture and natural site types were significantly different ($F_{1,x} = 1.690$, $R^2 = 0.0714$, $p = 0.108$). Ecoregions were significantly different from each other for 2022 ($F_{2,33} = 1.02881$, $R^2 = 0.08797$, $p = 0.001$), though after an FDR p-value adjustment, there are no significant groupings of ecoregions. Exploring the relationship between the bee community and the nonrewarding and rewarding agriculture area showed very little variation being explained by rewarding agriculture ($R^2 = 0.0156$) or nonrewarding agriculture ($R^2 = 0.1009$) (Figure 11). As a result, rewarding agriculture had no significant impact on the bee

community ($F_{1,33} = 0.6274$, $R^2 = 0.01559$, $p = 0.593$), and nonrewarding agriculture also had no significant impact ($F_{1,33} = 4.0606$, $R^2 = 0.10092$, $p = 0.076$).

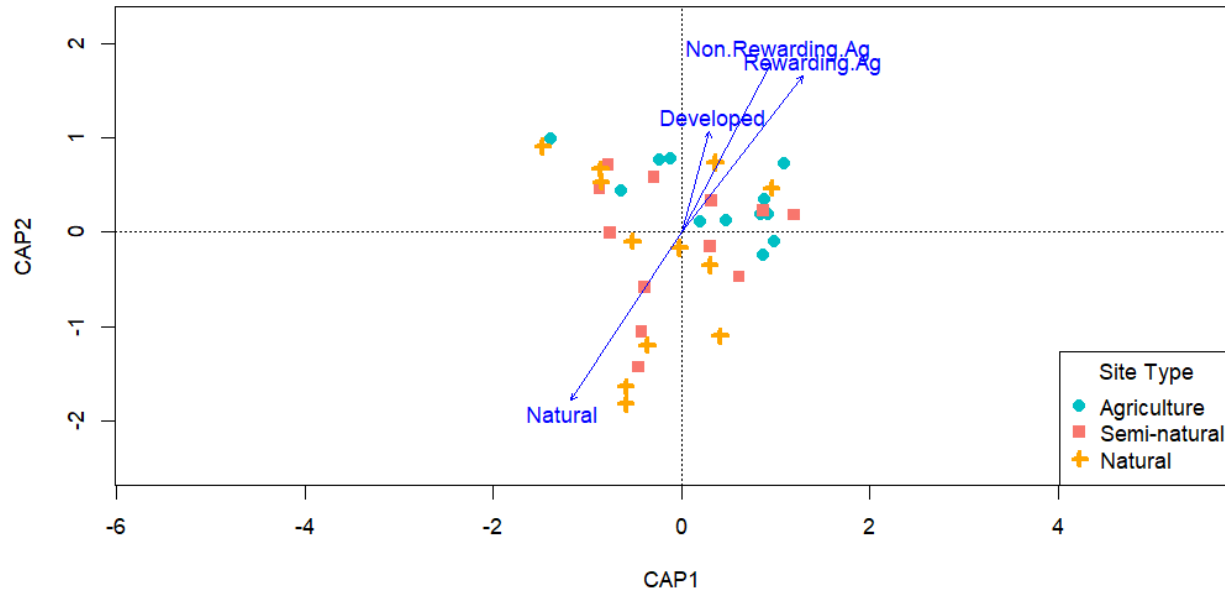


Figure 10: Ordination of bee counts for 2021 using dbRDA analysis across 36 sites grouped by cluster, testing variation across site type. Bee counts by site were also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

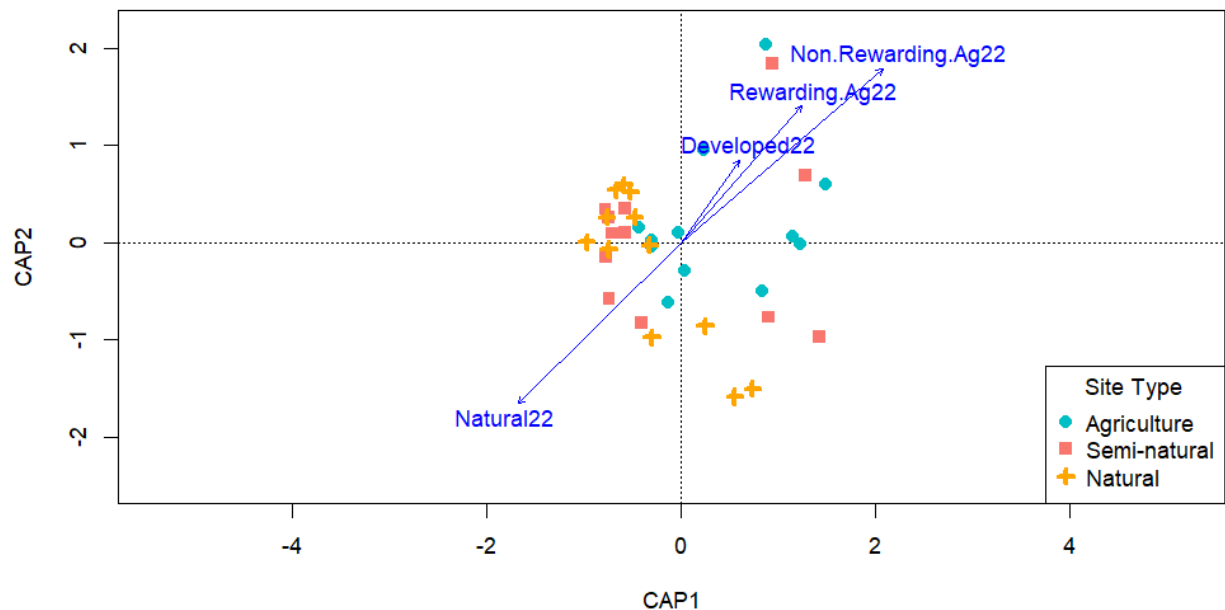


Figure 11: Ordination of bee counts for 2022 using dbRDA analysis across 36 sites grouped by cluster, testing variation across site type and the impacts of landscape components. Bee counts by site were also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

GLMM results:

Variables were selected from a global model based on values that were not highly correlated and significantly impacted the model after Akaike Information Criterion (AIC) on the configurational heterogeneity variables (Table 2, 3). Mean Shape Index did not affect bee abundance (2021: GLM, $\beta=0.15595$, $SE=0.7870$, Bonferroni adjusted p-value =0.095; 2022: GLMM, $\beta=-0.0853$, $SE=0.165$, Bonferroni adjusted p=1) (Table 4; Figure 12, 13). Julian Day did not affect bee abundance in 2021 or 2022 (2021: GLM, $\beta=-0.0854$, $SE=0.0787$, Bonferroni adjusted p-value =0.555; 2022: GLMM, $\beta=-0.0187$, $SE=0.080$, Bonferroni adjusted p-value =1) (Table 4; Figure 12, 13). Patch Area (2021: GLM, $\beta=-0.08296$, $SE=0.04907$, $p=0.273$; 2022: $\beta=-0.1335$, $SE=0.0824$, $p=0.315$), Mean Shape Index (2021: GLM $\beta=0.0679$, $SE=0.0483$, $p=0.4785$; 2022: GLMM, $\beta=-0.00118$, $SE=0.0769$, $p=0.1$), or Julian Day (2021: GLM, $\beta=-0.0915$, $SE=0.04695$, $p=0.154$; 2022: GLMM, $\beta=0.0464$, $SE=0.0438$, $p=0.867$) did not affect bee diversity after a Bonferroni adjustment of significance (Table 5; Figure 14, 15).

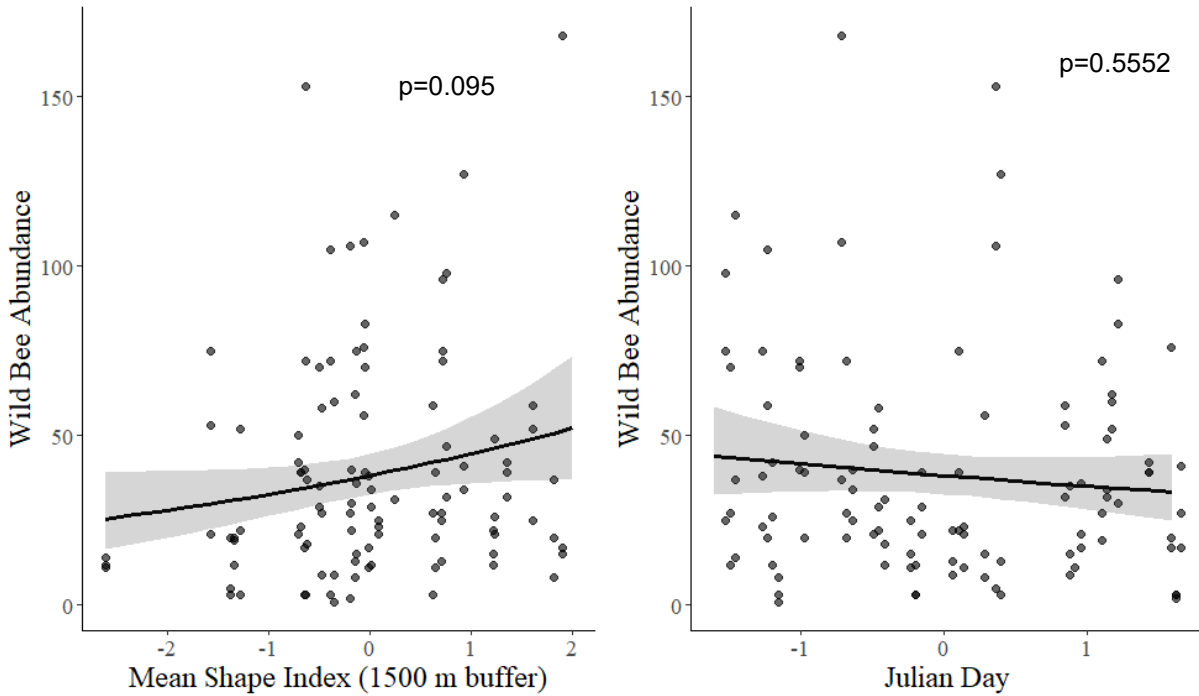


Figure 12: Mean Shape Index, at the 1500m buffer range, and Julian Day effects on the wild bee abundance for 2021. Regression line and shaded area represent the predicted values based on the GLM and the associated 95% confidence intervals.

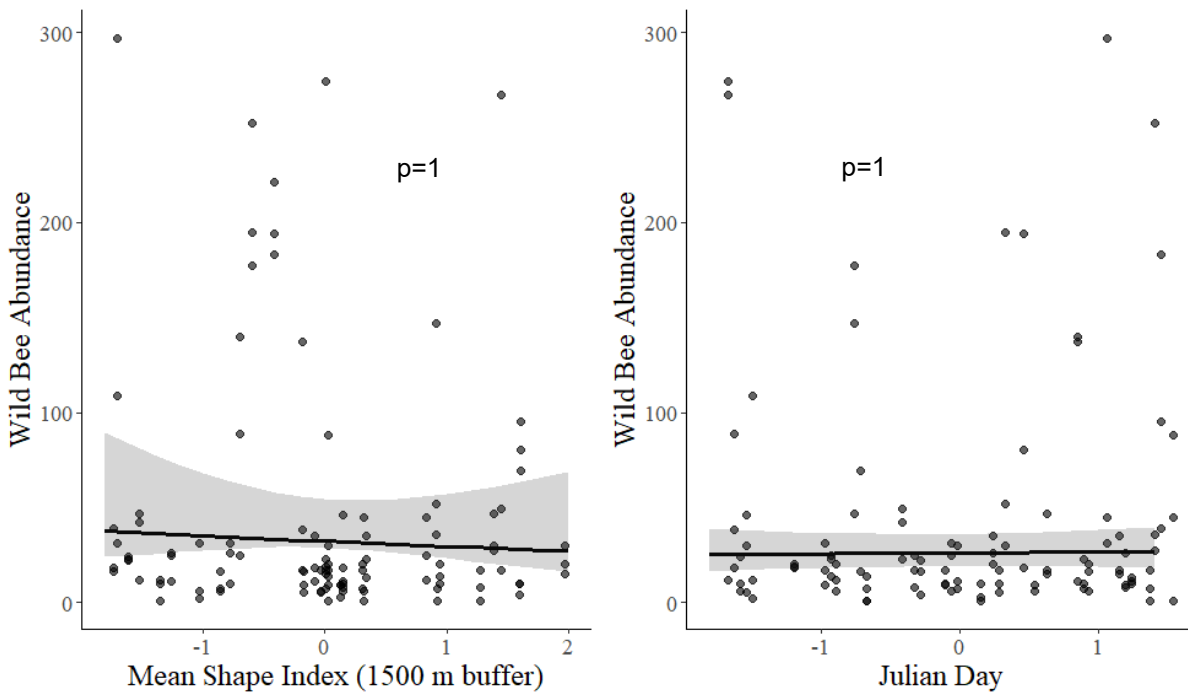


Figure 13 Mean Shape Index, at the 1500m buffer range, and Julian Day effects on the wild bee abundance for 2022. Sample points represent the samples collected in all sample methods. Regression line and shaded area represent the predicted values based on the GLMM and the associated 95% confidence intervals.

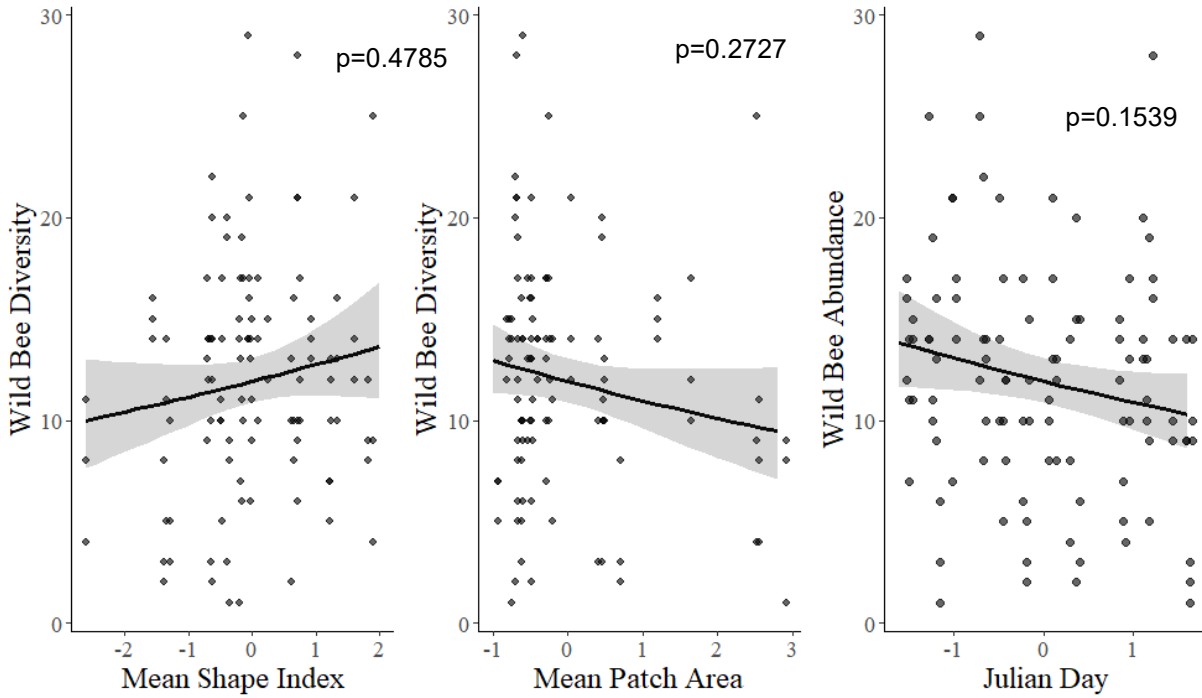


Figure 14: Mean Shape Index, Mean Patch Area and Julian Day, at the 1500m buffer range, effects on the wild bee diversity for 2021. Regression line and shaded area represent the predicted values based on the GLM and the associated 95% confidence intervals.

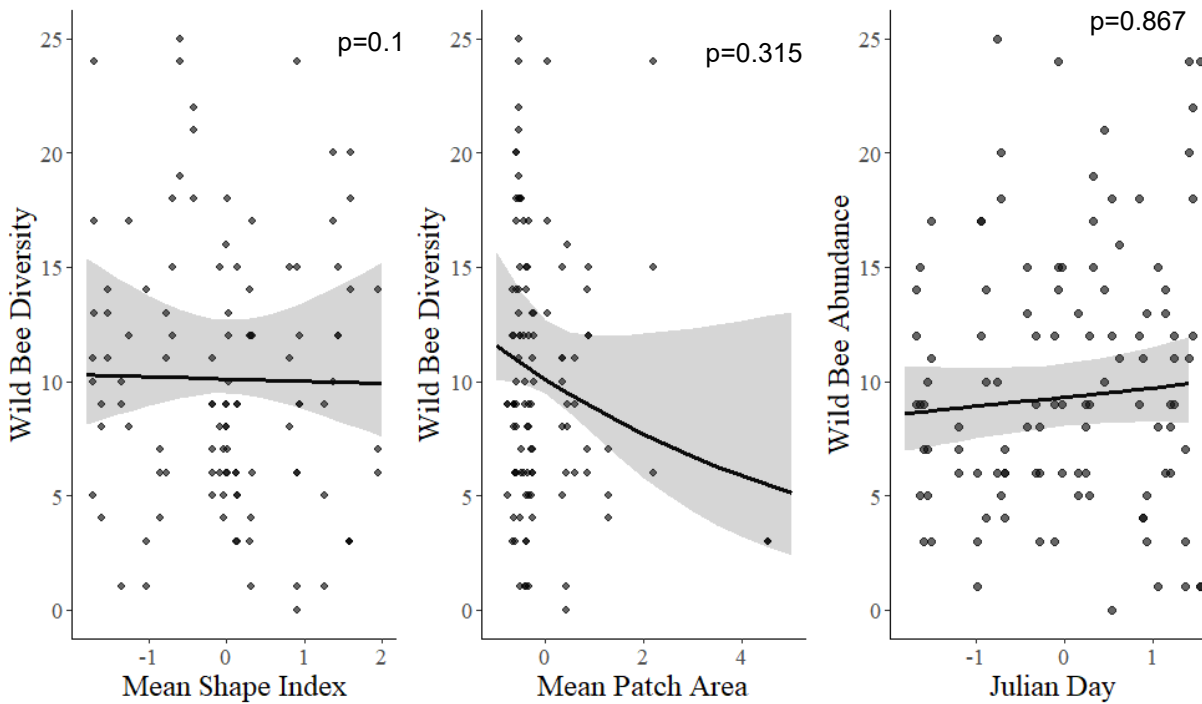


Figure 15: Mean Shape Index, Mean Patch Area, and Julian Day, at the 1500m buffer range, effects on the wild bee diversity for 2022. Regression line and shaded area represent the predicted values based on the GLMM and the associated 95% confidence intervals.

Table 2: AIC model selection for bee abundance and configurational heterogeneity variable impacts at 1500m. Where applicable random effect was site (n=36). All variables were scaled.

	Intercept	Julian Day	Patch Area	Mean Shape Index	Cohesion	df	LogLik	AIC	ΔAIC
Abundance 2021	3.642	-0.0891	-0.0373	0.152	-0.0271	6	-975.31	987.3	3.55
	3.642	-0.0906	-0.048	0.154		5	-975.4	985.4	1.64
	3.643	-0.0854		0.156		4	-975.76	983.8	0
	Intercept	Julian Day	Patch Area	Mean Shape Index	Cohesion	df	LogLik	AIC	ΔAIC
Abundance 2022	3.262	0.0178	-0.0236	-0.0768	0.0267	7	-492.5	998.9	3.98
	3.262	0.0185	-0.0995	-0.0818		6	-492.5	996.9	2
	3.262	0.0187		-0.0853		5	-492.5	994.9	0

Table 3: AIC model selection for bee diversity and configurational heterogeneity variable impacts at 1500m. Where applicable random effect was site (n=36). All variables were scaled.

	Intercept	Julian Day	Patch Area	Mean Shape Index	Cohesion	df	LogLik	AIC	ΔAIC
Diversity 2021	2.4785	-0.0915	-0.0834	0.0679	0.00112	6	-662.64	674.6	2
	2.4785	-0.0915	-0.0829	0.0678		5	-662.64	672.6	0
	2.482			0.0807		4	-665.4	673.4	0.76
	Intercept	Julian Day	Patch Area	Mean Shape Index	Cohesion	df	LogLik	AIC	ΔAIC
Diversity 2022	2.245	0.0473	-0.162	0.00896	-0.0525	7	-323.1	660.1	1.6
	2.245	0.0464	-0.133	-0.0012		6	-323.3	658.5	0
	2.217	0.053		-0.0378		5	-333.6	677.3	18.8

Table 4: Configurational Heterogeneity and Abundance of Pollinators with Bonferroni p-value adjustment.

Fixed Effects					
Year	Predictor	Estimate (β)	Std.Error (SE)	z-value	p-value
2021	(Intercept)	3.64291	0.07821	46.580	<0.001
	Julian Day	-0.0854	0.07866	-1.086	0.5552
	Mean Shape Index	0.15595	0.7870	1.981	0.095
2022	(Intercept)	3.262	0.16514	19.753	<0.001
	Julian Day	0.0187	0.080	0.233	1
	Mean Shape Index	-0.0853	0.165	-0.518	1

Table 5: Configurational Heterogeneity and Diversity of Pollinators with Bonferroni p-value adjustment.

Fixed Effects					
Year	Predictor	Estimate (β)	Std.Error (SE)	z-value	p-value
2021	(Intercept)	2.4118	0.04839	49.839	<0.001
	Julian Day	-0.0915	0.04695	-1.949	0.154
	Mean Patch Area	-0.08296	0.04907	-1.691	0.2727
	Mean Shape Index	0.0679	0.0483	1.407	0.4785
2022	(Intercept)	2.245	0.0727	30.894	<0.001
	Julian Day	0.0464	0.0438	1.061	0.867
	Mean Patch Area	-0.1335	0.0824	-1.620	0.315
	Mean Shape Index	-0.00118	0.0769	-0.015	1

Table 6: Random effects for configurational heterogeneity and abundance of bees.

Random Effects			
Year	Group	Variance	Std.Dev
2021	NA	NA	NA
2022	site	0.7608	0.8723

Table 7: Random effects for configurational heterogeneity and diversity of bees.

Random Effects			
Year	Group	Variance	Std.Dev
2021	NA	NA	NA
2022	site	0.1204	0.347

After modifying the global model to represent the variables that provide bees the most resources, no crop types were included in the compositional heterogeneity model, since they had no significant impact to the bee community or were correlated with other variables. Natural areas like forests and grasslands were not included due to AIC selection not including them in the best model in 2021, though they were included in 2022 (Table 8). Human-disturbed landscapes, pastures, and urban land were impactful on bee diversity and abundance based on the Akaike Criterion and were included in the model for 2021 (Table 9). Compositional heterogeneity's impacts on bee abundance were not significant for 2021, with Urban/Developed land ($\beta=-0.1802$, $SE=0.0804$, $p=0.075$), Pasture/Forage ($\beta=0.1155$, $SE=0.07941$, $p=0.438$), and Julian Day ($\beta=-0.1007$, $SE=0.07808$, $p=0.5859$) not significantly impacting bee abundance (Figure 16). Bee abundance in 2022 was also not significantly impacted by compositional heterogeneity components; Shrubland at the 1500m ($\beta=-0.2536$, $SE=0.1611$, $p=0.23$) and Julian Day did not significantly impact bee abundance ($\beta=0.03356$, $SE=0.05033$, $p=1$) (Figure 17).

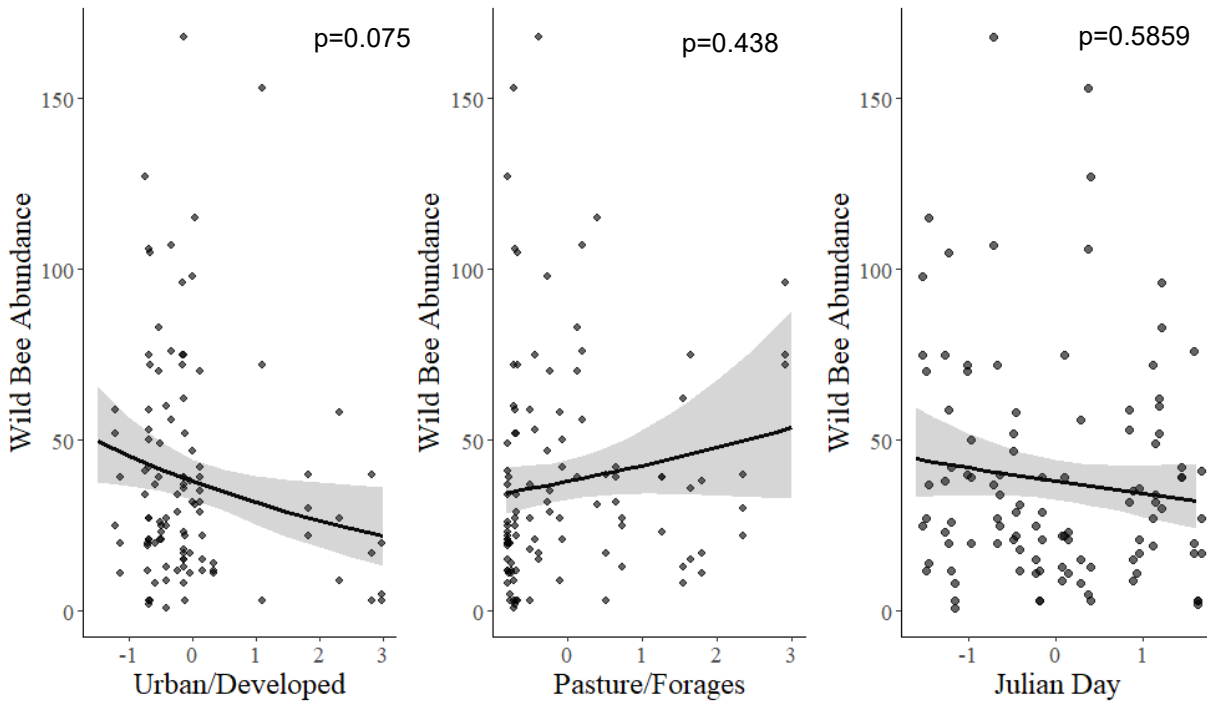


Figure 16: Urban/Developed land, Pasture/Forages and Julian Day, at the 1500m buffer range, effects on the wild bee abundance for 2021. Regression line and shaded area represent the predicted values based on the GLM and the associated 95% confidence intervals.

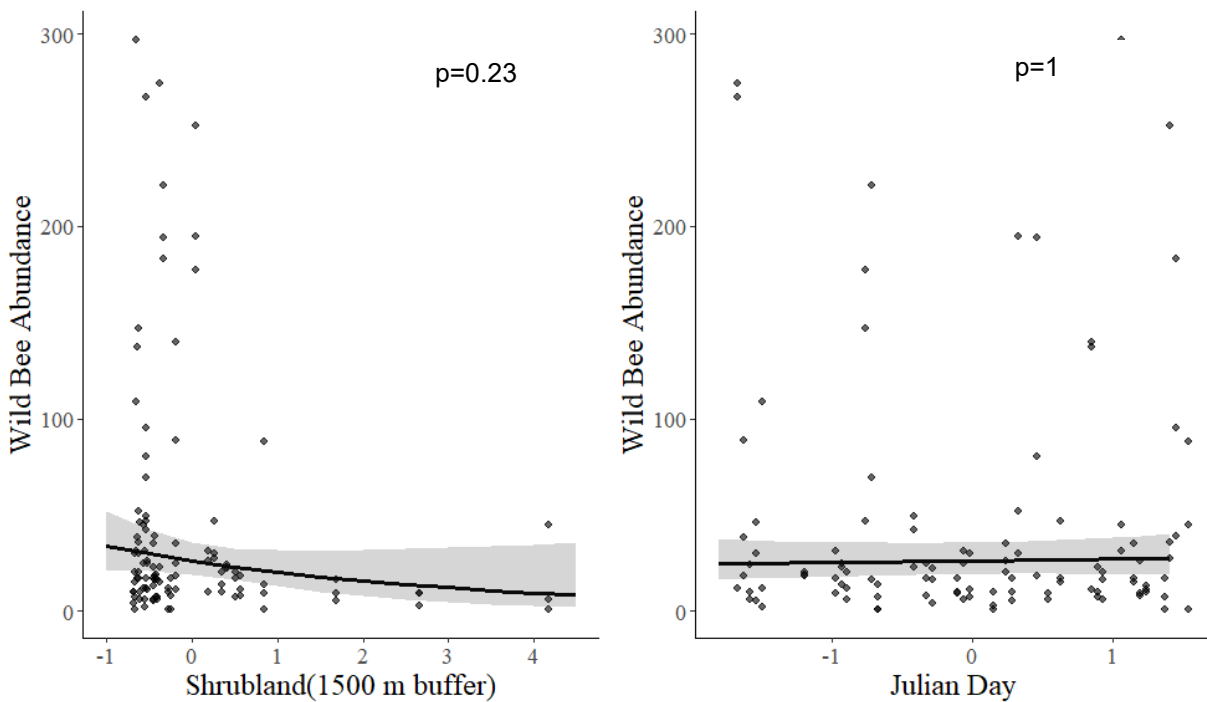


Figure 17: Shrubland, at the 1500m buffer range, and Julian Day effects on the wild bee abundance for 2022. Regression line and shaded area represent the predicted values based on the GLMM and the associated 95% confidence intervals.

Bee diversity for 2021 was significantly negatively impacted by Urban/Developed land (GLM, $\beta=-0.13645$, $SE=0.04962$, $p=0.013908$), Pasture/Forage land showed a significantly positive impact on bee diversity (GLM, $\beta=0.15917$, $SE=0.04553$, $p=0.000946$), and Julian Day had no impact (GLM, $\beta=-0.0925$, $SE=0.04435$, $p=0.11089$) (Table 12; Figure 18). 2022 bee diversity was not significantly impacted by Mixed Wood Forest ($\beta=0.13969$, $SE=0.06635$, $p=0.1059$), Shrubland ($\beta=-0.13567$, $SE=0.071$, $p=0.1680$) or Julian Day ($\beta=0.04835$, $SE=0.13969$, $p=0.8073$) after a Bonferroni adjusted p-value (Table 12; Figure 19). Correlation between variables may have resulted in some key relationships being missed between the bees and the landscape.

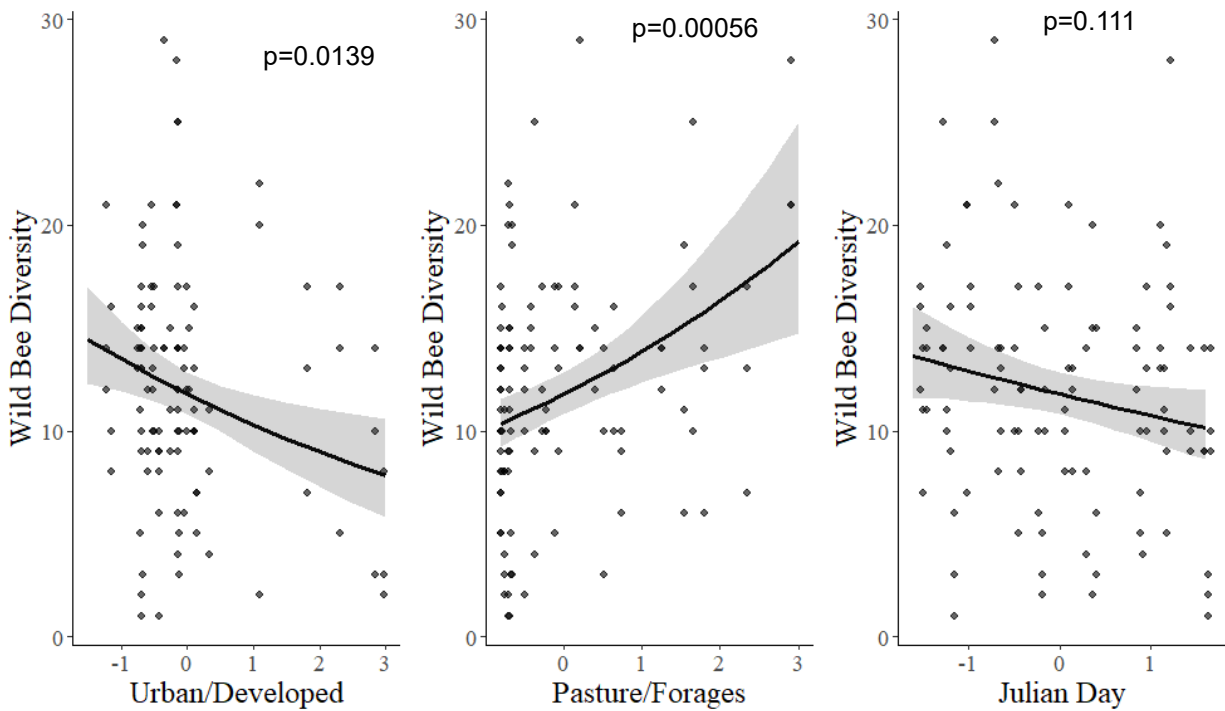


Figure 18: Urban/Developed land, Pasture/Forages and Julian Day, at the 1500m buffer range, effects on the wild bee diversity for 2021. Regression line and shaded area represent the predicted values based on the GLM and the associated 95% confidence intervals.

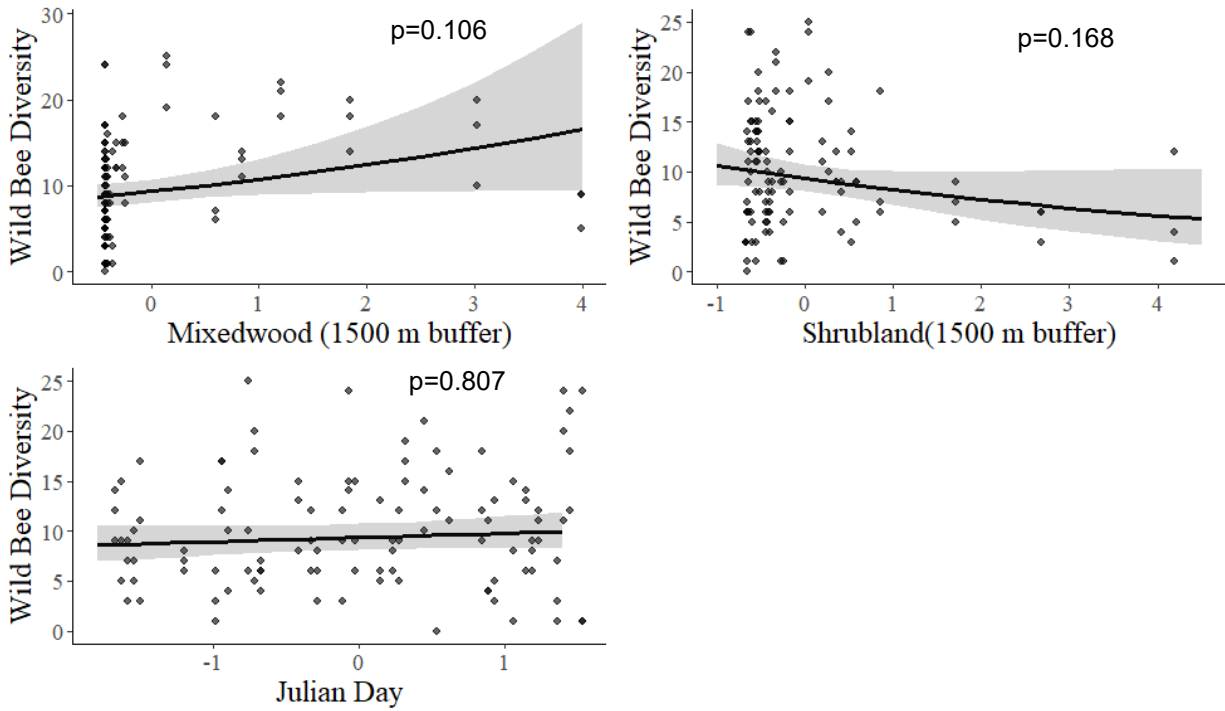


Figure 19: Mixedwood, Shrubland and Julian Day, at the 1500m buffer range, effects on the wild bee diversity for 2022. Regression line and shaded area represent the predicted values based on the GLMM and the associated 95% confidence intervals.

Table 8: AIC model selection for bee abundance and compositional heterogeneity variable impacts at 1500m. Random effects were set as site (n=36) combined with round. All variables were scaled.

	Intercept	Julian Day	Urban/Developed	Shrubland	Wetland	Pasture/Forage	Canola	Mixed-wood	df	LogLik	AIC	Δ AIC
Abundance 2021	3.63425	-0.0991	-0.1889	-0.06633	-0.01055	0.12837	-0.0198	0.04656	9	-972.9	990.92	7.21
	3.63429	-0.0967	-0.18954	-0.07271		0.12908	-0.01720	0.05068	8	-972.93	988.93	5.22
	3.63615	-0.10346	-0.17991			0.127995	-0.000523	0.087454	7	-973.55	987.55	3.84
	3.63615	-0.1034	-0.18010			0.12814		0.03881	6	-973.55	985.55	1.84
	3.63664	-0.10073	-0.18020			0.11551			5	-973.71	983.71	0
	3.64325	-0.09595	-0.15691						4	-975.88	983.88	0.17
	Intercept	Julian Day	Urban/Developed	Shrubland	Wetland	Pasture/Forage	Canola	Mixed-wood	df	LogLik	AIC	Δ AIC
Abundance 2022	3.26985	0.02644	-0.05793	-0.16884	-0.1361	-0.19201	0.07646	0.11482	10	-489.6	999.19	6.34
	3.26807	0.03136	-0.0588	-0.22253		-0.17514	0.10174	0.14062	9	-489.9	997.82	4.97
	3.26767	-0.03012	-0.04317	-0.2413		-0.18751		0.11619	8	-490.1	996.19	3.34
	3.26757	0.02964		-0.23177		-0.19217		0.11853	7	-490.1	994.27	1.42
	3.26379	0.03303		-0.26265				0.17802	6	-490.8	993.61	0.76
	3.26191	0.03356		-0.25361					5	-491.4	992.85	0

Table 9: Generalized Linear Model AIC model selection for bee diversity and compositional heterogeneity variable impacts at 1500m. Random effects were set as site (n=36) combined with round. All variables were scaled.

	Intercept	Julian Day	Urban/Developed	Shrubland	Wetland	Pasture/Forage	Canola	Mixed-wood	df	LogLik	AIC	ΔAIC
Diversity 2021	2.466072	-0.08777	-0.13038	-0.036772	-0.02411	0.15723	-0.02411	0.004239	9	-650.39	668.39	7.44
	2.46619	-0.09086	-0.12859	-0.02325		0.15476	-0.02849	-0.01005	8	-650.53	666.53	5.58
	2.46645	-0.09277	-0.12506			0.15542	-0.02331	-0.01203	7	-650.77	664.77	3.82
	2.466683	-0.09227	-0.13619			0.161239		-0.00531	6	-650.93	662.93	1.98
	2.46670	-0.09253	-0.13599			0.16285			5	-650.95	660.95	0
	2.48025	-0.08228	-0.09795						4	-664.23	672.23	11.28
	Intercept	Julian Day	Urban/Developed	Shrubland	Wetland	Pasture/Forage	Canola	Mixed-wood	df	LogLik	AIC	ΔAIC
Diversity 2022	2.24854	0.04821	-0.03908	-0.12355	-0.06458	0.009258	-0.02479	0.12686	10	-320.8	661.51	6.88
	2.24867	0.04717	-0.04265	-0.12064	-0.05984	0.01320		0.13345	9	-320.8	659.63	5
	2.24879	0.04747	-0.04135	-0.11768	-0.06119			0.12929	8	-320.8	657.66	3.03
	2.24870	0.04635		-0.11005	-0.05925			0.13318	7	-321.0	656.04	1.41
	2.24840	0.04835		-0.13567				0.13969	6	-321.3	654.63	0
	2.24730	0.04516						0.13264	5	-323.0	656.09	1.46

Table 10: Compositional Heterogeneity and Abundance of Pollinators with Bonferroni p-value adjustment.

Fixed Effects					
Year	Predictor	Estimate (β)	Std.Error (SE)	z-value	p-value
2021	(Intercept)	3.63664	0.07758	46.874	<0.001
	Julian Day	-0.10073	0.07808	-1.29	0.5859
	Urban/Developed	-0.18020	0.08040	-2.241	0.075
	Pasture/Forages	0.11551	0.07941	1.455	0.438
2022	(Intercept)	3.26191	0.15999	20.389	<0.001
	Julian Day	0.03356	0.05033	0.418	1
	Shrubland	-0.25361	0.16111	-1.574	0.23

Table 11: Random effects for compositional heterogeneity and abundance of bees.

Random Effects			
Year	Group	Variance	Std.Dev
2021	NA	NA	NA
2022	site	0.6978	0.8354

Table 12: Generalized Linear Model of Compositional Heterogeneity and Diversity of Pollinators with Bonferroni p-value adjustment.

Fixed Effects					
Year	Predictor	Estimate (β)	Std.Error (SE)	z-value	p-value
2021	(Intercept)	2.46670	0.04406	55.985	<0.001
	Julian Day	-0.09253	0.04435	-2.086	0.110889
	Urban/Developed	-0.13645	0.04962	-2.75	0.013908
	Pasture/Forages	0.15917	0.04553	3.496	0.000564
2022	(Intercept)	2.24840	0.06763	33.246	<0.001
	Julian Day	0.04835	0.13969	1.105	0.8073
	Mixedwood	0.13969	0.06635	2.105	0.1059
	Shrubland	-0.13567	0.07100	-1.911	0.1680

Table 13: Random effects for compositional heterogeneity and diversity of bees.

Random Effects			
Year	Group	Variance	Std.Dev
2021	NA	NA	NA
2022	site	0.09465	0.3076

Indicator Species Analysis:

For 2021 and 2022, there were 34 species, out of a possible 392 species of bee, identified as having the potential to be indicator species (Figure 20). Eleven species identified as potential indicators of ecoregion and site type had 25 species. The sociality, lecty, and nesting strategies of the indicators there are a few dominant traits found (Figure 21; Table S5). Of the 34 indicator species identified, 16 species were found in 2021, and 14 species were found in 2022 (Figure 21; Table S5). The dominant sociality strategy was eusociality (17 species), with solitary second (12 species) and two subsocial species last. Most species were polylectic (30 species), with four species being oligolectic. There was diversity in the nesting strategies with predominantly ground nesting species (24 species), four hive-nesting species, three stem nesters, and two wood nesting species.

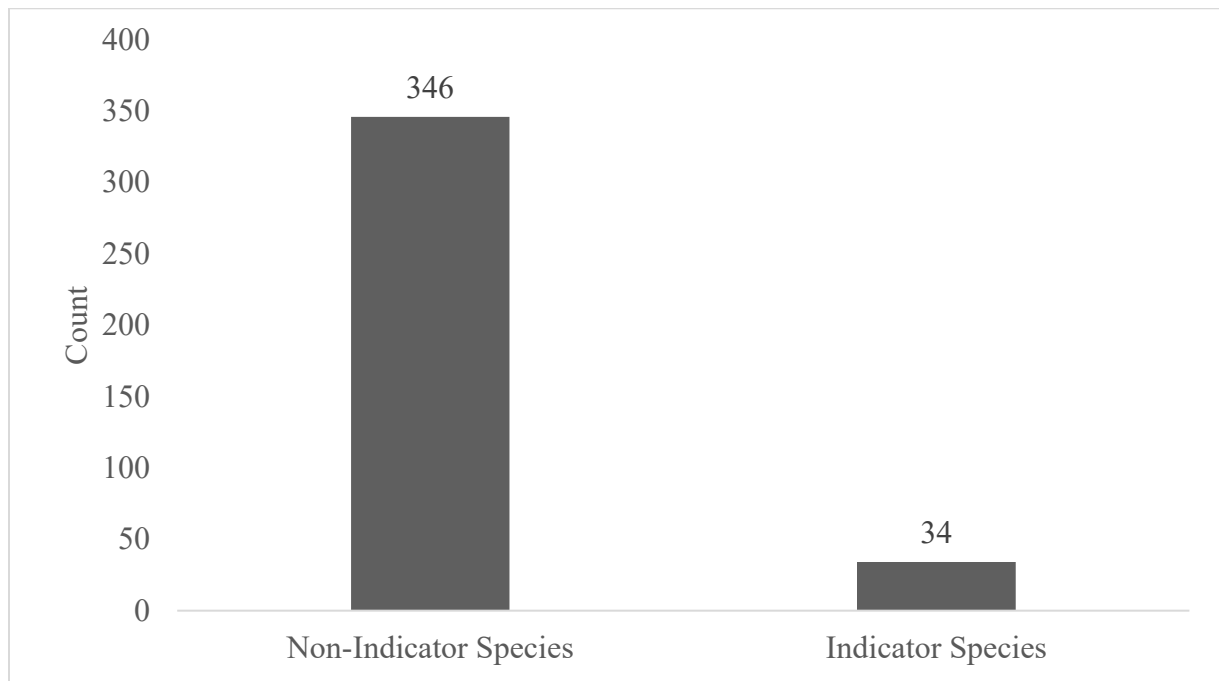


Figure 20: Count comparison of non-indicator species and indicator species determined through indicator species analysis for 2021-2022.

For 2021, there were seven species with strong or moderate associations with ecoregions (*A. cyanophila* Cockerell 1906, *L. subversans* (Mitchell 1960), *H. rubicundus* (Christ 1791), *B.*

griseocollis (DeGeer 1773), *B. vagans* Smith 1854, *C. dupla* Say 1837, *L. novascotiae* (Mitchell 1960)) (Table S5). 2022 had six species with strong to moderate associations between ecoregions, (*H. confusus*, *L. cressonii* (Robertson 1890), *L. leucocomus* (Lovell 1908), *L. semicaeruleum* (Cockerell 1895), *H. rubicundus*, *L. novascotiae*) (Table S5). In 2021, *Bombus vagans* had the highest indicator value (82.2%), suggesting a strong association with the landscape for Assiniboine Delta and Lake of the Woods. Other species of note are *Halictus rubicundus* and *Ceratina dupla* (76.6% and 74.8%), with Precambrian Boreal and Lake of the Woods combined and Precambrian Boreal alone being the areas they are associated with, respectively. *Halictus confusus* in 2022 had a strong association (90.4%) with Precambrian Boreal. *Halictus rubicundus* in 2022 also had a moderate association with Lake of the Woods and Precambrian Boreal (72.9%). All other indicator species had moderate associations, less than 70%, with the landscape (Table S5). When reviewing the life history traits for the indicator species, 2021 had mostly eusocial, ground-nesting, polylectic indicators (Figure 21; Table S5). Assiniboine Delta did not have an indicator for the ecoregion alone, though when grouped with other ecoregions, there were indicator species found. 2022 showed similar indicator species life history traits with eusocial, ground nesting, and polylectic being predominant (Figure 21; Table S5). There were no indicators found in TGP, Lake of the Woods, or Assiniboine Delta without grouping with another ecoregion (Table S5).

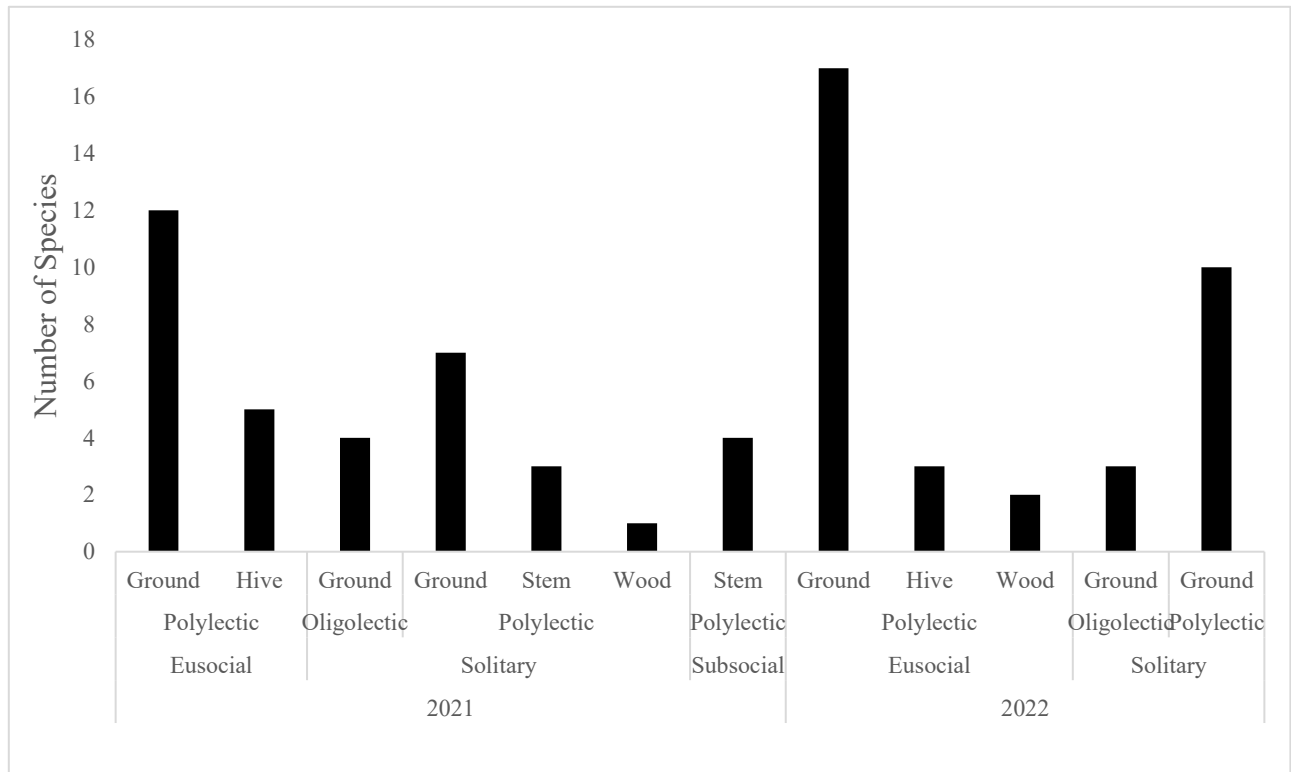


Figure 21: Count of indicator species and their functional traits for 2021, 2022, and the combination of 2021-2022 to highlight overlap between the years.

Grouping at the site type level, agriculture, semi-natural, or natural, showed more species with moderate to strong associations, with 19 species moderately or strongly associated with a site type for 2021 (Table S5). 2022 showed fewer indicator species for site type, with only 15 species moderately to strongly associated with ag, semi-natural, and natural sites (Table S5). *Bombus vagans*, *Halictus rubicundus*, *Melissodes agilis*, *Melissodes trinodis*, *Halictus confusus*, and *Certina mikmaqi* Rehan & Sheffield 2011, had strong associations with natural and semi-natural site types, along with combinations of ag and natural or natural and semi-natural habitat types (80.5%, 79.9%, 88%, 84.8%, 87.8%, 86.2% respectively) for 2021. All other indicator species had moderate associations, less than 77%, with the landscape (Table S5). 2022 showed different relationships. *Halictus confusus* was strongly associated with semi-natural habitat (92.7%), with *Halictus rubicundus* having a strong-moderate association (75.6%), though not as

strong as *Halictus confusus*. *Melissodes trinodis* had a strong association with ag and natural (78%). All other species had moderate associations, less than 70%, with the landscape (Table S5). For 2021, there was more diversity in the life history strategies of the indicator's species, with mostly solitary and eusocial ground nesters as indicator species. There were a few oligolectic species, with the majority being polylectic. Only two specialist species were found to be indicators. In 2022, there were no indicator species found for natural areas without combining with other site types. For life history information, a combination of eusocial and solitary ground-nesting bees was found to be an indicator. Lecty strategy showed mostly polylectic, though some were oligolectic.

Cluster groupings of natural, agricultural, and semi-natural sites within ecoregions shed some light on the specific site locations driving some of the indicator species. Ten species were identified with moderate to strong associations as indicators for clusters of sites in 2021: *L. admirandum*, *L. subversans*, *A. splendens*, *C. dupla*, *M. trinodis*, *H. confusus*, *B. vagans*, *H. pilosifrons*, *A. terminalis*, and *A. texanus* (Table S5). 2022 had fourteen indicator species identified with mostly strong associations: *A. occidentalis*, *L. pilosum*, *A. sericeus*, *L. pictum*, *L. vierecki*, *B. sandersonii*, *H. rubicundus*, *A. texanus*, *L. cressonii*, *L. viridatum*, *A. mellifera*, *H. confusus*, *M. agilis*, *L. zonulum*. For 2021, *Agapostemon texanus* had a very strong association (95.2%) with cluster 2, 3, 4, 5, 6, 8, 9, and 10, which are predominantly sites in the Southeast Region (Table S1, S5). *Anthophora terminalis* had a similar relationship (94.7%) with 2, 3, 4, 5, 6, 7, 9, and 11 (Table S1, S5). *Melissodes trinodis* had a strong association (94.1%) with 1, 3, 5, 6, and 7, all sites close to the Southeast corner (Table S1, S5). *Halictus confusus* had a strong association (93.2%) with mostly Southwestern clusters 5, 9, 10, 11, 12 (Table S1, S5). *Hoplitis pilosifrons* had a strong association with most of Southern Manitoba, 1, 3, 5, 6, 7, 9, 10, 12

(Table S1, S5). *Bombus vagans* was strongly associated (87.5%) with 5, 6, 7, 8, 9, and 12 clusters, like the ecoregion groupings previously described. *Ceratina dupla* had a strong association (85.9%) with 9, 10, 12 (Table S1, S5). All other associations were <82% (Table S5). 2022 had a few different species of indicators, with *Halictus confusus* being the strongest repeat species for both years, having a very strong association (98.9%) with 3,4,5,9,11,12 (Table S5). *Melissodes agilis* also showed a very strong association (99%) with 1,2, 3, 4, 5, 8, 11, 12 (Table S5). *Agapostemon texanus* again had a very strong association in 2022 with 3, 4, 8, a few of the sites it was associated with in 2021 (Table S5). *Lasioglossum zonulum* had a strong association (89.8%) with 1, 3, 4, 5,6, 7, 11, 12 (Table S5). *Anthophora occidentalis* was only associated (88.7%) with cluster 3. For 2021, there were no clusters that had their own individual indicators; all clusters were grouped with another cluster. Indicators found had a combination of life history traits with no clear distinction. There were eusocial, solitary, or subsocial indicators with ground, stem, hive, or wood nesting strategies. The majority are polylectic generalists, similar to the ecoregion and site type groupings (Table S5). 2022 had one cluster (3) showing an indicator species that was a solitary, ground-nesting polylectic. All other indicators were for combinations of clusters. There were solitary and eusocial ground hive or wood nesters. All but one of the species were polylectic (Table S5).

In 2021, flowering plant cover in roadside verges negatively affected the abundance of indicator species (GLMM, $\beta=-0.23891$, $SE=0.04477$, $p\text{-value}<0.001$) (Table 14; Figure 22). Flower cover only was the most parsimonious model, with an AICc value of 2696.236 and a weight of 0.2055. There were some overdispersion issues; overdispersion was 1.7328 and significantly differed ($p<0.05$) between the predicted and observed values, suggesting poor fit of the model. There is evidence of heteroscedasticity within the model as well, although the pattern

observed is typical of count data (Figure S18). 2022 showed a shift in a significant variable; grass cover had a significant positive effect on the abundance of indicator bees ($\beta=0.21508$, $SE=0.09055$, $p\text{-value}=0.0350$) (Table 14; Figure 23). Flower cover in 2022 did not have a significant effect, although the relationship showed a weak negative effect on pollinator abundance ($\beta=-0.09088$, $SE=0.06040$, $p\text{-value}=0.2648$) (Table 14). Flower cover and grass cover were the most parsimonious model, with an AICc value of 2621.516, with a weight of 0.1791. 2022 also had an issue with overdispersion, overdispersion was 5.5371 and significantly differed ($p=0.008$) between the predicted and observed values, suggesting poor fit of the model. There is evidence of heteroscedasticity within the model, although the pattern observed is typical of count data (Figure S19).

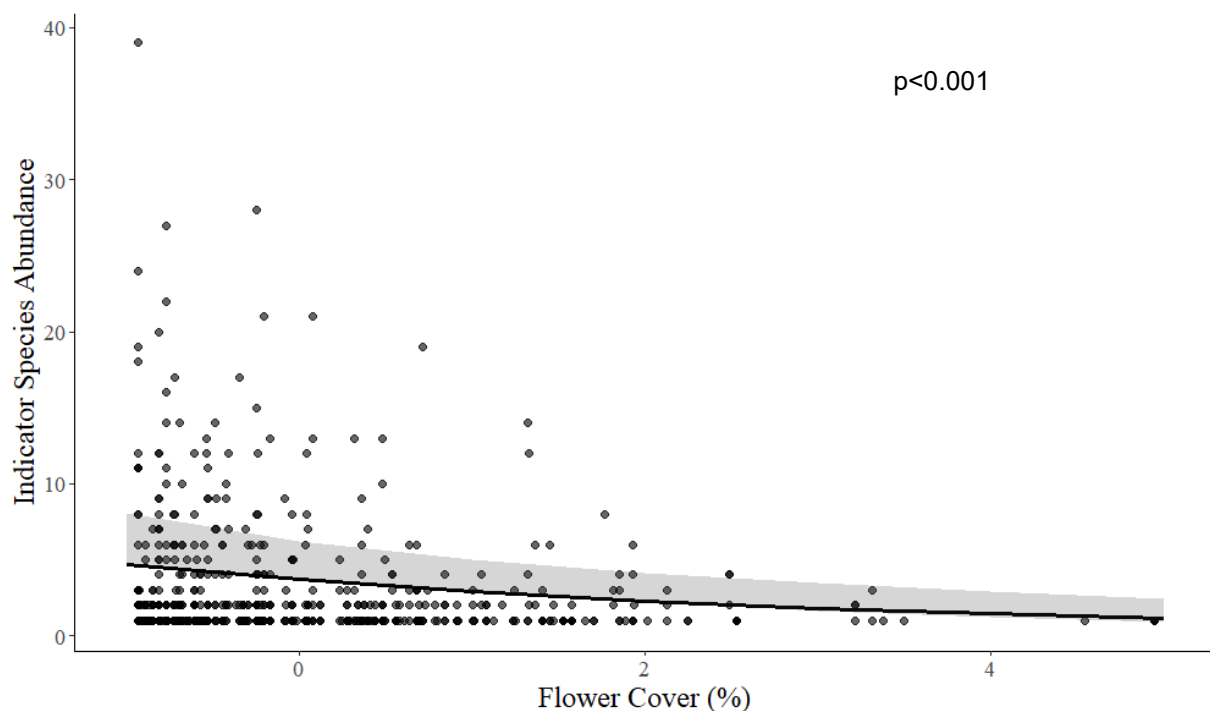


Figure 22: Flowering plant cover in roadside verges effects on the indicator species abundance for 2021. Sample points represent the samples collected via passive and active sampling techniques. Regression line and shaded area represent the predicted values based on the GLMM and the associated 95% confidence intervals.

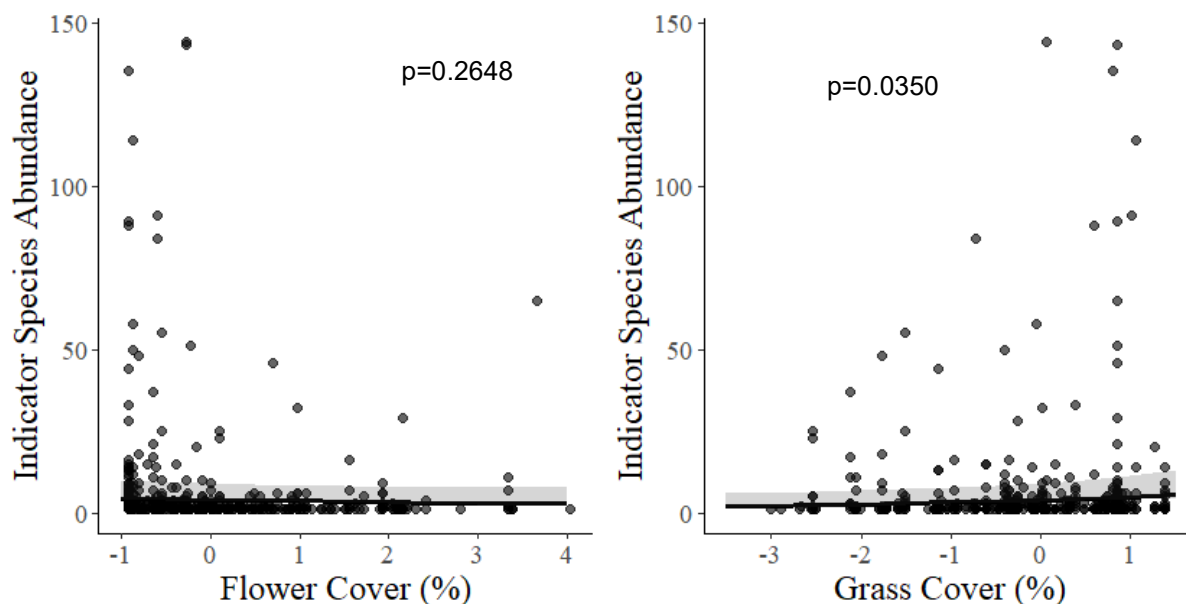


Figure 23: Flowering plant cover and grass cover in roadside verges effects on the indicator species abundance for 2022. Regression line and shaded area represent the predicted values based on the GLMM and the associated 95% confidence intervals.

Table 14: Generalized Linear Mixed Effects Model of Landscape Components impacts on the abundance of indicator species for 2021, 2022, and both years.

Fixed Effects					
Year	Predictor	Estimate (β)	Std.Error (SE)	z-value	p-value
2021	(Intercept)	1.02850	0.12713	8.090	<0.001
	Floral Cover	-0.23891	0.04477	-5.336	<0.001
2022	(Intercept)	1.01474	0.23846	4.255	<0.001
	Floral Cover	-0.09088	0.06040	-1.505	0.2648
	Grass Cover	0.21508	0.09055	2.375	0.0350
Combined	(Intercept)	1.15846	0.1499	7.728	<0.001
	Floral Cover	-0.155	0.038	-4.078	0.000136
	Grass Cover	0.13699	0.05192	2.639	0.02499
	Temperature	0.06506	0.03992	-1.63	0.30954

Table 15: Random effects for indicator species
analysis of key landscape components.

Random Effects			
Year	Group	Variance	Std.Dev
2021	site/ecoregion	0.044	0.2098
	ecoregion	0.0525	0.2291
2022	site/ecoregion	0.4466	0.6683
	ecoregion	0.1494	0.3866
Combined	site	0.1935	0.44
	ecoregion	0.0276	0.166
	year	0.0169	0.13

Combining the two years of indicator species to see any relationships that were consistent showed the addition of temperature as a fixed effect. The most parsimonious model, with a weight of 0.317 and AICc value of 5444.727, included the flowering plant cover, grass cover, and temperature variables with the random effects identified as site, ecoregion, and year (Table 14, 15). Flower cover had a significant negative effect on indicator abundance ($\beta=-0.15500$, $SE=0.03800$, $p\text{-value}=0.00136$) (Table 14; Figure 24). Grass cover had a positive significant impact on indicator abundance ($\beta=0.13699$, $SE=0.05192$, $p\text{-value}=0.0249$) (Table 14; Figure 24). Temperature did not significantly impact indicator abundance ($\beta=-0.06506$, $SE=0.03992$, $p\text{-value}=0.3095$) (Table 14; Figure 24). There were significant amounts of outliers in the data, resulting in significant overdispersion between the observed and expected values. Due to this overdispersion issue, there is potential for a Type I error to have occurred. There was also evidence of heteroscedasticity in the data beyond what is typical for count data (Figure S20).

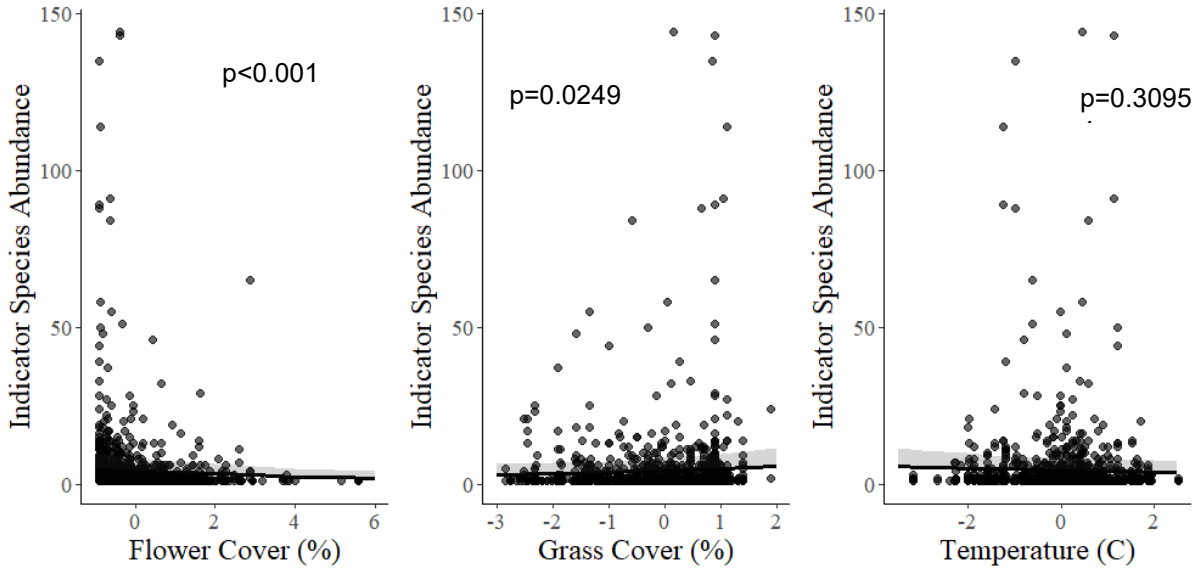


Figure 24: Flowering plant cover, grass cover, and temperature in roadside verges effects on the indicator species abundance for 2021 and 2022. Regression line and shaded area represent the predicted values based on the GLMM and the associated 95% confidence intervals.

Floral resources by site, round, and ecoregion for 2021 and 2022, using distance-based redundancy analysis, showed few trends besides some temporal variation throughout the sample season. 2021 did not have any significant differences between site types using Bray-Curtis dissimilarities of the permutational multivariate analysis of variance (PERMANOVA) ($F_{2,33} = 1.2093$, $R^2 = 0.06829$, $p = 0.075$) (Figure 25). Examining per sample round for 2021, there were no differences in round 1 ($F_{2,33} = 0.8528$, $R^2 = 0.04914$, $p = 0.414$) or round 3 ($F_{2,33} = 1.3217$, $R^2 = 0.07416$, $p = 0.07$) (Figure S10, S14). Round 2 showed differences between sites ($F_{2,33} = 1.2106$, $R^2 = 0.06835$, $p = 0.031$), though the pairing close to significant was a comparison between agricultural and natural sites ($F_{1,x} = 1.76307$, $R^2 = 0.074194$, $p = 0.037$), there were no significant pairings after an FDR p-value adjustment (adjusted $p = 0.111$) (Figure S12). 2022 also did not have any significant differences between site types based on results from the PERMANOVA using the Bray-Curtis dissimilarities method ($F_{2,33} = 0.9687$, $R^2 = 0.05545$, $p = 0.132$) (Figure 26). There was potential for model assumption violations due to outliers within

the data set for 2022, though the permutation test for homogeneity of multivariate dispersions was not significant ($F_{2,33} = 2.9419$, $p = 0.055$). Examining per sample round for 2022 there were no differences in Round 1 ($F_{2,33} = 0.9499$, $R^2 = 0.05443$, $p = 0.16$), Round 2 ($F_{2,33} = 1.1403$, $R^2 = 0.06464$, $p = 0.055$), or Round 3 ($F_{2,33} = 0.9647$, $R^2 = 0.05524$, $p = 0.161$) (Figure S11, S13, S15).

The flowering plant species trends showed that across all sites, introduced species held a greater proportion of flower cover compared to native species. Introduced species constituted 58.71% of the total cover, while native species only contributed 41.29%. The 58.71% total cover was made up of 29 introduced species, in contrast to the 120 native species making up the 41.29% total cover (Figure 27).

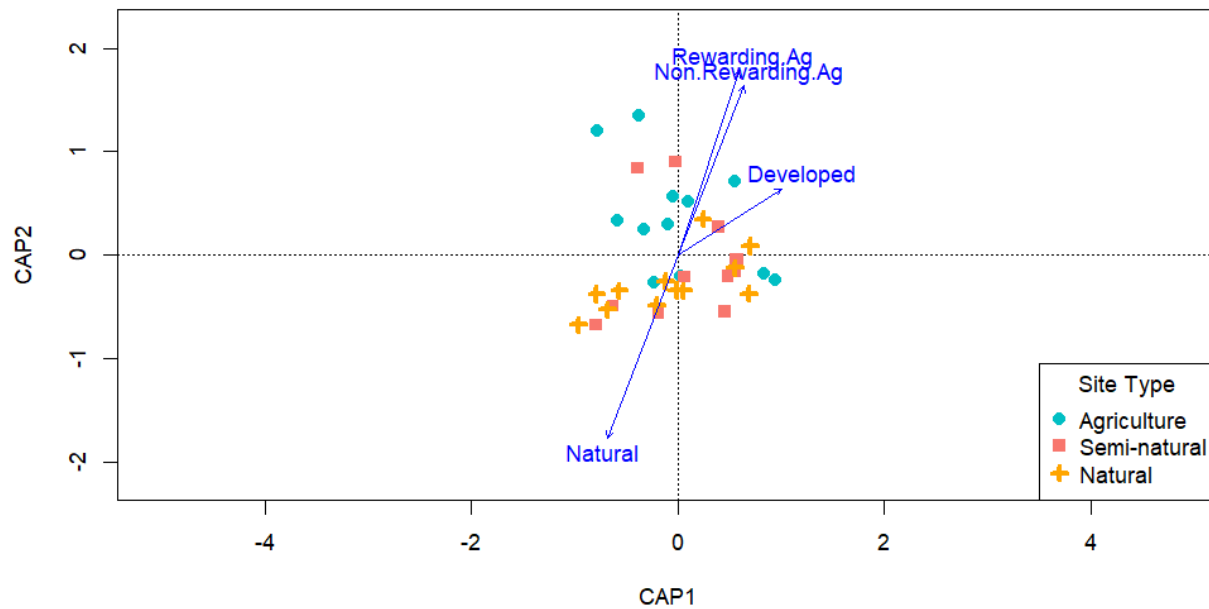


Figure 25: Ordination of floral species cover for 2021 using dbRDA analysis across 36 sites grouped by cluster, testing variation across site type. Flowering plant cover by site was also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

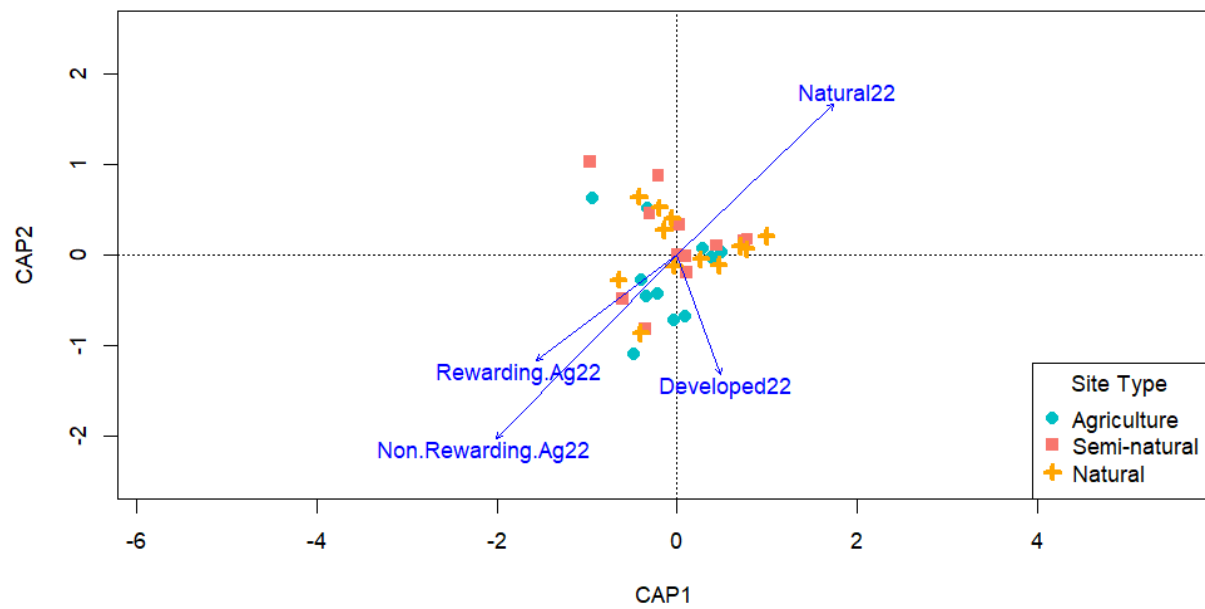


Figure 26: Ordination of floral species cover for 2022 using dbRDA analysis across 36 sites grouped by cluster, testing variation across site type. Flowering plant cover by site was also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

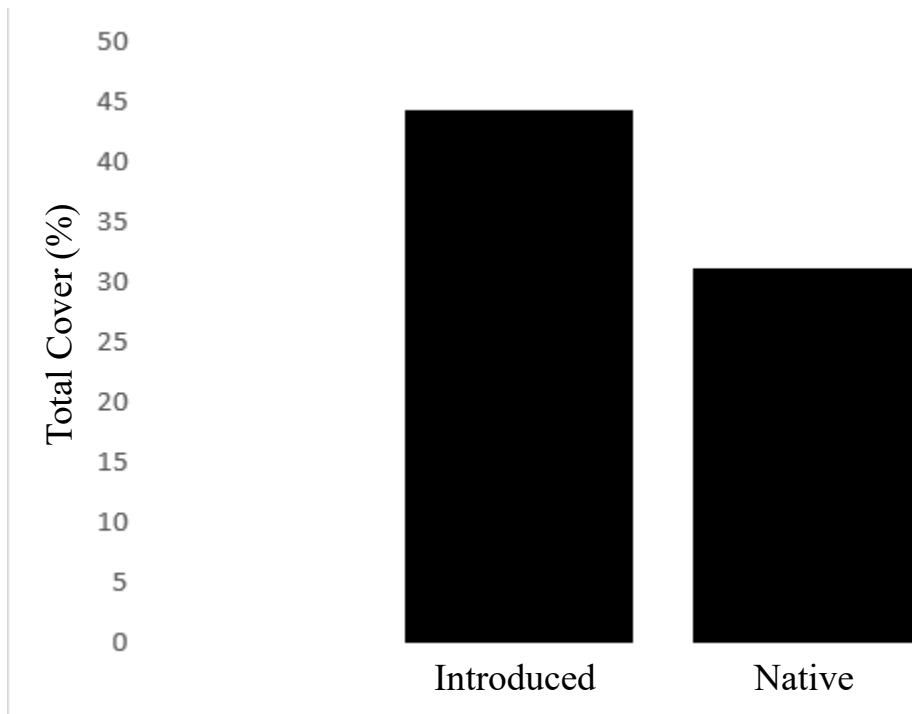


Figure 27: Total flowering plant cover for introduced and native plant species for 2021 and 2022 sample seasons.

DISCUSSION

Compositional and Configurational Heterogeneity:

A large proportion of southern Manitoba is dedicated to agricultural practices, which typically has a negative impact on bee diversity and abundance (Kremen et al. 2002, Tscharnkte et al. 2005). Site type had a significant impact on the bee community for both 2021 and 2022, suggesting variation in the bee community is dependent on the site types (Figure S22).

Agricultural and natural sites had distinct bee communities, shown in the Figure 10 and 11 ordination plots via the agricultural and natural site points maintaining a separate and distinct shape in comparison to each other. Semi-natural sites' bee communities did not differ from either agricultural or natural site types, showing a high level of bee community overlap with both natural and agricultural bee communities (Figure 10, 11). A combined agricultural and natural bee community seen in semi-natural site types has been documented in previous studies, showing species richness is limited by the surrounding landscape community (Hopfenmüller et al. 2014, Killewald et al. 2023). Semi-natural habitat positively affects bee abundance and diversity, suggesting it could be providing resources such as flowering plants, nesting habitat, and refugia lacking in the surrounding area (Hopfenmüller et al. 2014, Killewald et al. 2023) (Figure S21).

The benefit of including semi-natural habitat in an analysis, despite a lack of response from community composition, lies in the ecological relationship with a transitional space like semi-natural habitat (Hopfenmüller et al. 2014, Wu et al. 2019). Semi-natural sites can harbor unique species or spillover bee diversity into surrounding areas, while supporting agriculturally significant bee species such as large-bodied bees, or cleptoparasitic bees (Hopfenmüller et al. 2014, Wu et al. 2019). Additionally, including semi-natural habitat increases scientific rigour by preventing oversimplification of the system, removes biases, and captures more of a gradient of

the community that can inform management practices, while providing additional ecological context to future studies (Senapathi et al. 2017b, Gillespie et al. 2024).

Ecoregion did not affect the bee communities in 2021, suggesting no clear variation in bee community composition across the province using roadside verges (Figure S2). Ecoregion in 2022 was significant, due to 11.8% of samples being *Melissodes agilis* and 8.83% being *Halictus confusus*, skewing the 2022 data within the Assiniboine Delta and Precambrian Boreal ecoregions (Figure S3). Considering the variation in significance seen in the ecoregion data year over year, the creation of additional groupings of ecoregions, like dividing Precambrian Boreal and Lake of the Woods in this study for testing, does not yield any significant relationships, highlighting the need for careful consideration when creating delineations within the landscape (Turner 2005). In Manitoba, ecoregion-specific relationships have been mixed, with the responses of the bee community showing variation in their relationship to landscape heterogeneity metrics dependent on ecoregion context, supporting the original delineations of ecoregions (Hanuschuk 2021, Martini 2022). Although the bee communities between the ecoregions were not significantly different in 2021, maintaining the distinctions between ecoregions, without creating additional delineations, for testing landscape heterogeneity will prove beneficial to fully understand the ecological context (Turner 2005, Hanuschuk 2021).

Sampling round variations in the bee community captured, showed round 1 (late May, early June) to be significant in both 2021 and 2022 (Figure S4, S5). There is a transition of species from spring to summer flight period bees, demonstrating distinct communities of bees depending on the phenology of flowering plant species and climate conditions (Bartomeus et al. 2011, Duchenne et al. 2020, Buckner and Danforth 2022). The inclusion of Julian day in the compositional and configurational heterogeneity models provides phenological context,

accounting for variations in bee community seen throughout the sample season (Bartomeus et al. 2011, Duchenne et al. 2020). Variation in bee species abundance and diversity can be seen in 2021 and 2022 in this study and previous research, and has been attributed to the temporal instability of the bee community due to rotational cropping systems and insect population dynamics (Vankosky et al. 2017). Variability in year-to-year bee community trends is documented in Manitoba, with variability in abundance over time and across research studies being common (Patenaude 2007, Hanuschuk 2021, Miller 2021, Martini 2022). The reason for the population fluctuations year over year, or the drivers of the population dynamics seen, are not clearly understood, but could be highlighting the abiotic and biotic variables' impacts on the bee community dynamics seen in the landscape (Hillary and Bees 2004, Marshall et al. 2024) (Figure 1). The trend of year-over-year variation could also be dependent on sampling regime, sampling effort, and bias, coupled with the natural fluctuations of bee populations in patchy ecosystems, further complicating trend analysis over an extended period (Hillary and Bees 2004). To properly determine the fluctuations being seen, either at the population or the community dynamic level, there needs to be included in this discussion the idea that the use of roadside verges for sampling and resource sources for bees could be creating noise in the sampling regime, influencing the results of the studies using the roadside verges as sample sites (Meinzen et al. 2024, Horstmann et al. 2024, Martini et al. 2025). Roadside verges drawing a bee community more likely to use roadside verges or skewing the abundance in agricultural areas due to the abundance and diversity of floral resources drawing bees from the surrounding landscape has been seen in previous studies (Hanley and Wilkins 2015, Horstmann et al. 2024, Martini et al. 2025). Showing preferential use of roadside verges facing roads in comparison to facing crops, likely in response to the disturbance, pesticides, and proportion of edge habitat found in field margins (Hanley and

Wilkins 2015, Horstmann et al. 2024, Martini et al. 2025). There are additional risks to bees when using roadside verges, as resource presence increases the risk of harm from vehicle collisions, predators, and pesticides, potentially selecting for bee species that are more tolerant of these disturbances (McCormick et al. 2019, Phillips et al. 2020, Fitch and Vaidya 2021, Horstmann et al. 2024). Further research would be required to confirm these observations, provide clear sampling regimes to avoid future biases, and provide insight into how to account for variation during analysis.

The agricultural area had no impact on the bee community at the scale of testing, 1500 m. If the amount of agricultural area is not impacting the bee community, then the composition of the landscape particularly, the crop type, natural area type, and human disturbance intensity could show an impact on the bee diversity and abundance by increasing or decreasing the availability of nesting or provisioning resources within the landscape based on the type of crop, rewarding or non-rewarding to bees, floral abundance in natural areas, and the level of modification the area has experienced (Tscharntke et al. 2005). Compositional heterogeneity had inconsistent impacts on bee diversity and abundance for 2021 and 2022, with shifts in significant variables between sample years likely due to the variability seen in the bee community through the sample seasons (Figure 28). In 2021, urban land cover area, which made up 2.95% of total land cover, negatively impacted bee abundance across Southern Manitoba. Fragmentation, habitat degradation, isolation, pollution, and pesticides are all results of increased human-disturbed land in Southern Manitoba, resulting in resources that are essential for bees being modified or removed entirely (Steffan-Dewenter and Tscharntke 1999, Fahrig 2003, Winfree et al. 2011, Hamblin et al. 2018, Mesquita et al. 2025). Urban land typically does not provide sufficient resources to bees, showing fewer floral resources and nesting habitat (Schmack and

Egerer 2023, Ulrich and Sargent 2025, Sexton et al. 2025). In large, urbanized landscapes that are deficient of flowering resources, pollinator communities are typically limited to polylectic species capitalizing on any floral resource found within the area (Ulrich and Sargent 2025, Sexton et al. 2025). Some instances have found that increased floral resources within urban landscapes can positively impact the bee community, particularly large-bodied polylectic species or managed pollinators (MacIvor et al. 2017, Hamblin et al. 2018, Wenzel et al. 2020, Schmack and Egerer 2023). Negative impacts on the abundance of bees in Southern Manitoba due to urban land cover could demonstrate a lack of sufficient floral and nesting resources in urban areas for the maintenance of abundant bee communities. Urban area warming also impacts the bee community by decreasing the abundance of bees by 41% per increase in C° (Hamblin et al. 2018). Considering in this study urban areas, representing developed rural spaces, are decreasing the abundance and diversity of bees, examining the amount of floral resources, nesting habitat, the impact of microclimate shifts, and the colonization or spillover of species into larger developed areas, will identify how to mitigate the negative impact of urbanization as the rate of urbanization in Manitoba continues to increase with the socio-economic growth Manitoba is experiencing (Hamblin et al. 2018, Ulrich and Sargent 2025, Sexton et al. 2025).

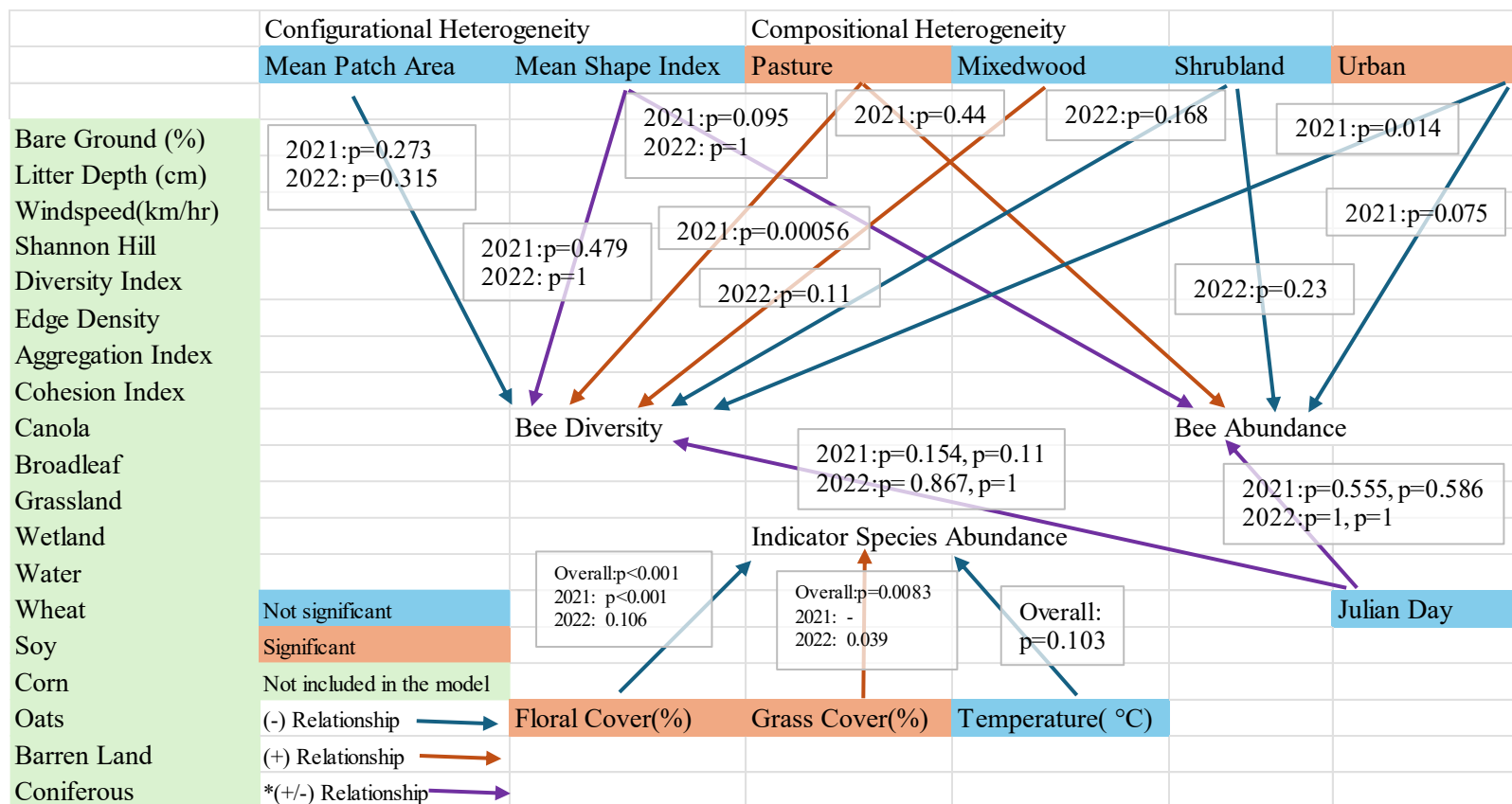


Figure 28: Conceptual diagram of testing results of 2021 and 2022 bee data for landscape heterogeneities effects on bee diversity and abundance and indicator species abundance dynamics related to local abiotic and biotic factors. Analysis was completed using GLMM or GLM (n=36).

* Relationships are positive or negative depending on sample year.

Pasture had a significant positive impact on bee diversity, suggesting that maintaining or increasing the amount of pastureland available in human-disturbed areas may provide essential resources to bees (Figure 28). Pasture fills in the gaps where agricultural landscapes with high soil disturbance, offering refuge from urbanization, agricultural pesticides, and providing essential resources in resource-poor areas dominated by ephemeral resource-rewarding crops (Blitzer et al. 2012, Traveset et al. 2024). Pasture also can increase landscape heterogeneity, improving the diversity and complexity of the landscape by increasing edge density, cover types, refuge habitat, or providing corridors for movement, all of which have shown cases of improving the pollinator community (Kremen et al. 2002, Steffan-Dewenter and Schiele 2008, Zurbuchen et al. 2010, Tschardt et al. 2012a, Van Geert et al. 2014, Torne-Noguera et al. 2014, Delaney et al. 2015). Pastureland, forage, or semi-natural habitat is shown to support bee abundance and diversity in managed ecosystems, creating a bee community that has the potential to provide pollination services to the surrounding crop lands (Sepp et al. 2004, Steffan-Dewenter and Schiele 2008, Blitzer et al. 2012, Frost et al. 2015).

Mixed wood did not significantly impact the diversity of bees in our system in 2022 after a Bonferroni p-value adjustment, though mixed wood habitat has been found to significantly impact bee and arthropod communities in heterogeneous landscapes in Europe, North America, and South America (Sepp et al. 2004, Ulyshen et al. 2024, Mesquita et al. 2025). The amount and the distance from mixed wood forests, particularly the distance between patches, were found to drive the diversity of bumble bee species within the landscape (Sepp et al. 2004). This relationship can be related to the intermediate landscape complexity hypothesis, where the size and complexity of the conserved natural landscape patches typically host a more complex stable

community (Tscharntke et al. 2012b). In this case mixed wood area will positively impact the bee community, with more complexity supporting a more complex bee community (Tscharntke et al. 2012b). Mixed wood offers refuge, nesting habitat, and a diversity of floral resources in landscapes where there are transitions between habitats occurring (Sepp et al. 2004, Ulyshen et al. 2023, 2024). Mixed wood landscapes are also indicative of succession on the prairies, being one of the stages occurring several years after disturbance has occurred (Scott 1996). Succession of communities typically drives the shift in plant and pollinator communities, due to niche partitioning, competition, and mutualism (Scott 1996, Delaney et al. 2015). The presence of mixed wood habitat could be supporting a larger more diverse bee community in comparison to other early successional stages, like shrubland, since the mixed wood area has been undisturbed for an extended period, the bee community could be reflecting a spectrum of previous bee communities in the same area, and there is the potential for more functional complementarity within the area due to a variety of resources (Franzén and Nilsson 2010, Williams and Winfree 2013, Fründ et al. 2013, Delaney et al. 2015, Glenny et al. 2023).

In 2022, shrubland was identified as a variable that could be impacting bee abundance and diversity, though was not significant after a Bonferroni p-value adjustment (Figure 28). Bee diversity was not significantly impacted by shrubland variables, suggesting other variables may be more impactful on the bee diversity for 2022, such as environmental variables or compositional heterogeneity variables like urban land or pastureland. Shrubland negatively impacting the bees' abundance and diversity in 2022 could be due to reduced floral resources by outcompeting other floral resources for space while producing understory shade, reducing availability of ground nesting habitat (McKinney and Goodell 2010, Wu et al. 2019, Glenny et al. 2023, Keele et al. 2023) (Figure 28). Invasive shrubs and shrubs that produce shade have been

shown to outcompete floral resources, decreasing the diversity and abundance of the floral community available to bumble bees (McKinney and Goodell 2010, Keele et al. 2023). In contrast, a study has found that within agriculturally disturbed landscapes, the presence of shrubland can significantly increase the bee assemblage diversity, provide refuge, and be a source of pollinators in the surrounding agriculturally modified landscape (Wu et al. 2019).

Understanding the context of which the shrubland is included in the study is a key factor, where the Wu et al. (2019) paper was studying increasing shrubland in orchards and plantations, areas with considerable agricultural intensification, which are typically monocrops, while the Keele et al. (2023) paper discussed the importance of floral resources in managed shrubland and early successional forest areas, areas that are meant to support more plant diversity separate from the agricultural context. Shrubland has an overall negative impact on the bee community in Manitoba in natural, semi-natural, and agricultural landscapes, suggesting that Shrubland growth should be avoided when possible, so as not to negatively impact the flowering plant community and nesting capabilities of bees (McKinney and Goodell 2010). Including mixed wood and shrubland could represent a mixture of successional habitat types and the subsequent effect those successional stages have on the bee community. Additionally, successional habitats could show patch dynamics between agricultural, semi-natural, and natural landscapes, demonstrating a time-dependent shift in the bee community as related to the composition and configuration of the landscape and the impacts shifts in the resource availability have on the functional network over time (Tscharntke et al. 2012a).

Compositional heterogeneity variables impacting the bee community do not explain the entirety of the impacts being seen on bees in Manitoba and globally, since bees are not limited to one area, they move through the environment using a variety of habitat types, requiring the

addition of configurational heterogeneity components to effectively determine if the landscape is influencing the bee community (Hopfenmüller et al. 2014, Hass et al. 2018, Bottero et al. 2023). Mean shape index was found to positively influence bee abundance for 2021 before a Bonferroni p-value adjustment, showed no impact in 2022, and had no impact on bee diversity for either year (Figure 28). 2021 mean shape index at 1500m not having a significant positive impact on bee abundance after a bonferroni p-value adjustment, could be masking how the complexity of the landscape, such as the number of patches and the adjacency of those patch types, could be driving positive relationship with the number of bees being supported in the landscape (Marja et al. 2022) (Figure 28). Patch diversity, created by including a variety of landscape types in an area, the connectivity between patches, and the amount of beneficial resource-rich habitat the bee community has access to, has been shown to drive the population dynamics of bees (Franzén and Nilsson 2010, Prokopanko 2017, Boscolo et al. 2017, Fahrig 2020). More irregularity in patch density and shape in the landscape might be increasing the amount of edge habitat that supports increased amounts of floral resources, drawing more bees but not necessarily increasing the number of species in the area (Andrieu et al. 2018, Hamblin et al. 2018). Considering larger-bodied bees can traverse more area using corridors or edge habitats than smaller-bodied species, large-bodied bees would be able to exploit complex landscapes with irregular-shaped corridors or patches (Hamblin et al. 2018, Grüter and Hayes 2022). Shape index represents a suite of complex patch characteristics; rather than representing the irregularity of shapes, it may be quantifying the development of transitory habitat types in a small area, showing the development of a gradient habitat type surrounding irregularly shaped patches (Frazier and Kedron 2017a, Maximilian and Hesselbarth 2024). This initially would drive an increase in abundance by early colonizer bee species, large-bodied or bees able to move between patches easily. Bees that can

transition to these areas more readily, interacting with the early colonizer plant species, increasing the potential seed output of the plants, will further support niche partitioning within these small areas, creating space ready for diversity but lacking the species diversity source area limiting the diversity of bees in the patches (Hamblin et al. 2018, Schirmel et al. 2018, Marja et al. 2022).

The 2021 and 2022 mean shape index and patch area variables at the 1500m buffer zone, were not significantly impacting bee diversity (Figure 28). Bee diversity showing no significant impact from mean shape index or patch area could be because of impacts from environmental (abiotic) and ecological (biotic) filters reducing the use or limiting the colonization of complex patches in the landscape (Franzén and Nilsson 2010). The abiotic and biotic filters could be limiting the number of species able to colonize a newly disturbed area by limiting the number of species supported, resource poor area cover percentage deterring colonization, and flight distances limiting travel (Osborne et al. 2008, McKinney and Goodell 2010, Zurbuchen et al. 2010, Hamblin et al. 2018, Grüter and Hayes 2022, Mesquita et al. 2025). The landscape could also be incapable of hosting a more diverse bee population due to fragmentation reducing the diversity of the bee community in the region, along with a generalization of the floral and bee communities preventing the creation of specialized relationships within the fragmented patches (Hadley and Betts 2012, Xiao et al. 2016, Fijen et al. 2019, Yuan et al. 2024) (Table 1). High concentrations of agricultural areas increase the complexity of the landscape, which increases species richness, but typically will not affect the abundance of pollinators, supporting the mean shape index's positive effect on bee diversity seen in the results of this study (Marja et al. 2022).

In addition, a relationship that can be seen in agricultural areas is that large-bodied polylectic bee species with increased foraging ranges in source habitats, would move into newly

disturbed or natural area patches in the landscape for nesting, overwintering, and foraging opportunities when crops are no longer flowering (Schirmel et al. 2018, Fijen et al. 2019, Marja et al. 2022). The movement of species in agricultural spaces could skew how the community is being represented in the data since bee movement into patch habitats, as it relates to specialist, small-bodied, or solitary bees, can be delayed in comparison to the large-bodied polylectics with a larger foraging range (Zurbuchen et al. 2010). Since travel and establishment of bee species is limited by landscape connectivity, resources, foraging distance, and nesting requirements, bee communities' plasticity to adapt to a variety patch communities across the region would be limited by the bees' physical traits, not solely by the configuration of the landscape (Zurbuchen et al. 2010, Fijen et al. 2019). Considering a significant difference between agricultural and natural bee communities was seen in this study, along with semi-natural sites having considerable community overlap with both agricultural and natural site types, a colonization delay is likely, requiring movement from natural or semi-natural sites into agricultural sites with no incentive for the bees to colonize agricultural sites, especially in fragmented or patchy landscapes like Southern Manitoba (Franzén and Nilsson 2010, Cranmer et al. 2012, Rands 2014).

Patch area having a negative impact on the bee community could be related to large agricultural components being considered patches within the metrics calculation or the patches showing isolation from other patches in the landscape, as well as the number of patches showing a negative impact on bee communities (Senapathi et al. 2017b, McCormick et al. 2019, Lázaro et al. 2020) (Figure 28). A perspective beginning to be represented in the literature is the natural landscape perspective and associated bee community interactions with the complexity of the landscape (Marja et al. 2022, Ulyshen et al. 2024). Often, fragmentation and the edge effects are

considered in natural landscapes, but the bee communities' use of naturally occurring patches and their complexity in natural ecosystems, rather than in already human-modified landscapes, is not as discussed in the literature (Mitchell et al. 2013, Marja et al. 2022, Ulyshen et al. 2023, Priyadarshana et al. 2024).

Sampling efforts need to incorporate the combination of landscape complexity, habitat amount, and availability of resources within the fragmented landscape and the potential impacts on the species present in isolated patches (Mitchell et al. 2013, Marja et al. 2022). If isolation due to fragmentation occurs, where no replenishment or addition of community members occurs, it could elicit a response from the bee community, either showing behaviour or physical modifications, simply could be encouraging a polylectic bee community with a lack of functional complementarity, or have no impact on the bee community (Rahimi and Jung 2023, Gillespie et al. 2024). Spillover of bees into agricultural areas is well documented, showing a clear relationship between the abundance of bees in semi-natural sites and the increased heterogeneity of semi-natural areas in and around agricultural areas (Martínez-Núñez et al. 2022, Traveset et al. 2024). The movement of species from agricultural areas into natural or semi-natural areas from the native pollinator perspective is not well documented, creating a gap in the knowledge as it pertains to bee movements across the landscape and throughout the year (Blitzer et al. 2012). Understanding the dynamics of bee movements, pinpointing which resources are used when and how, will emphasize which aspects of the landscape are essential to support bee abundance and diversity (Blitzer et al. 2012). Increased non-agricultural habitat area provides nesting habitat within a landscape which significantly increases the number of brood cells produced by social bees (Steffan-Dewenter and Schiele 2008). In Manitoba, a typical 30-60 day rotation is used for pasturelands, allowing rest periods when pastures are supporting livestock, allowing the

grassland recovery periods (Elsinger and Thornton 2017, Carnochan et al. 2018). Rotational grazing regimes have increased the diversity and abundance of flower-visiting insects, providing access to nesting and provisioning resources (Ravetto Enri et al. 2017). Emphasizing the importance of pastureland, fallow land, or semi-natural area within an agricultural context as a conservation measure for bee diversity and abundance would provide support for the bee community in an area subject to agricultural intensification, while increasing the complexity of the landscape (Fijen et al. 2019, Marja et al. 2022).

Since correlation between variables is difficult to overcome, some variables could have been removed without full consideration of the overall impact they may be having within the landscape. There may be variables that were missed entirely during sampling, like the proportion of nesting habitat, floral diversity, etc. The sample size and the sample only being drawn from roadside verges could be making it difficult to draw appropriate conclusions.

Bees as Indicator Species:

Bees identified as indicator species can be used to assess the health, quality, and productivity of the landscapes they are functionally associated with, within Southern Manitoba (Chowdhury et al. 2023). Based on analysis, bee species associating with specific ecoregions or site types in favour of others, could be providing information on the quality of the resources in the area or the overall availability of resources in comparison to the less strongly associated areas (Schindler et al. 2013, Chowdhury et al. 2023). Additionally, bees showing associations with site types provide some context on how bees are associating with the various landcover types, highlighting key landscape types required throughout the season (Schindler et al. 2013, Chowdhury et al. 2023). Areas that are not supporting abundant populations of the indicator species have the potential to be showing negative impacts from fragmentation, agricultural

intensification, disturbance, or a lack of connectivity between habitat patches (Escobedo-Kenefic et al. 2020, Albertazzi et al. 2021, Chowdhury et al. 2023). To better understand the variation in responses in a bee indicator species analysis, consideration of life history traits that could provide additional context in determining an indicator needs to be identified.

Bees identified as indicator species in this study were primarily polylectic, ground nesting, and eusocial, which is a common life history strategy in Manitoba (Table S5) (Gibbs et al. 2023). Solitary species were also found to be indicator species, showing relationships more clearly with site types or clusters of sites (Table S5). Very few specialists were found to be indicator species, suggesting they are not the ideal life history strategy for broader landscape composition and configuration indicator species relationship analysis in Southern Manitoba (Naeem et al. 2020). Flowering plant species found in the roadside verges were predominantly native plants, though the percentage of flower cover was dominated by introduced species, showing non-native plant species to be a dominant source of floral resources for the bee community in roadside verges (Figure 26). Non-native plants in roadside verges are attractive resources for bee species, in the absence of native flowering plant species, though they have been known to attract polylectic species disproportionately in comparison to other landscape areas (Martini et al. 2025). Applying this roadside verge flowering plant data to the broader landscape, the roadside verges may prove a good example of the surrounding landscape for the use of monitoring the seasonality of non-native and native flowering plants in Manitoban ecosystems and the associated bee community utilizing the plant species. Roadside verges are subject to a high amount of disturbance, which may be homogenizing the plant communities within them, favouring species that are more tolerant of disturbance, and favouring polylectic species that can adapt and thrive in high disturbance areas (Meinzen et al. 2024, Horstmann et al. 2024). The

roadside verge flowering community composition and the associated landscape dynamics could confound indicator species analysis results, especially when the roadside verge community does not closely emulate the broader ecological community (Hopwood 2008, Martini et al. 2025).

Utilizing roadside verges as a model of the surrounding flowering plant community, roadside verges could be used as a way of monitoring phenological advances in the flowering plant community due to climate change (Gonsamo et al. 2013). Flowering plant phenological changes impact the interactions found between bees and the plants, potentially leading to a mismatch between flight periods and flowering times (Bartomeus et al. 2011, Gonsamo et al. 2013). Roadside verges could also be more consistent, human-managed features in the landscape in comparison to the surrounding landscape that is subject to unmanaged or agricultural practice-dependent patch dynamics (Fahrig 2020, Horstmann et al. 2024). Utilizing bee species as indicators of habitat quality and roadside verge flowering plants as proxies, or examples of the surrounding area, could be an early warning system to the impacts of ecological, agricultural, or climatic changes in the landscape (Meinzen et al. 2024). Wild bees that are sensitive to the availability of flowering resources and high levels of disturbance have also been identified as potential indicators of the habitat quality in agricultural settings (Schindler et al. 2013, Naeem et al. 2020). Utilizing wild bee indicator species as a means of monitoring species relationships to disturbance and landscape changes in natural and agricultural systems has focused on cleptoparasitic bees, built on the idea that the cleptoparasitism strategy is the pinnacle of the trophic system, which is the first to experience the effects of disturbance (Sheffield et al. 2013). Since cleptoparasites are closely tied to their hosts, the host population would need to be pervasive in the landscape, not limited to one area or habitat type, to truly encompass any disturbance effects seen throughout the landscape (Sheffield et al. 2013). I propose that the bee

indicator species for Southern Manitoba should cover a broad range of habitat types and life history strategies, tailored as representatives of the broader bee community in the regions from which they are endemic. The lack of granularity in population monitoring clouds the impact changes in the environment have on the broader bee community, potentially missing pivotal conservation intervention points (Sheffield et al. 2013, Chowdhury et al. 2023). Exploring the entire bee community for indicators for the state of the landscape or surrounding habitat could inform conservation policy makers of key species to monitor for the maintenance of ecologically functional habitats (Chowdhury et al. 2023). Additionally, the indicator species could be used as proxy for additional hard to detect bee diversity, utilizing a more common or prevalent species of bee as an indicator of potential shifts of the environment on a rarer species, the potential for the presence of rarer species, or highlight any losses that are being missed in more specific monitoring methods (Sheffield et al. 2013, Chowdhury et al. 2023).

An issue identified in prior analysis in this study and in the indicator species analysis was the presence of outliers, particularly *Melissodes agilis* and *Halictus confusus* (Table S5). *Melissodes agilis* and *H. confusus* do make appearances in the indicator species analysis, though there are comparatively rarer species in the data set that show significant potential as indicator species (Table S5). *Halictus rubicundus*, *Bombus vagans*, *Ceratina dupla*, and *Lasioglossum novascotiae* were the only species identified to be indicators at the ecoregion, site type, and site cluster groupings for either 2021 or 2022 (Table S5). The indicator species identified as consistent across all grouping types were not the most abundant, suggesting the results are not an artifact of the species dominating the samples (Urban et al. 2012). More indicators were found for site type in comparison to ecoregion, most likely due to the variation between the site types and their associated bee community discussed in previous analysis (Figure 24, 25), which would

follow the trend of distinct communities between agricultural and natural site types rather than seeing significantly distinct communities between ecoregions. Considering the complexity of the landscape, the significant differences in bee community in the site types, and the impacts of landscape composition found to be significant in the heterogeneity analysis of this study, not including groupings focused on specific habitat traits may exclude potential indicators of habitat components and the impacts they have on the community as a whole, especially when attempting to determine indicator species for agricultural areas as well as natural areas (Naeem et al. 2020, Chowdhury et al. 2023).

Ecoregion indicator species were found in the *Andrena*, *Lasioglossum*, *Halictus*, *Bombus*, and *Ceratina* genera for 2021 and 2022. Most of the species associated with these genera in this study, at the ecoregion grouping, were eusocial and polylectic, with some diversity in the nesting strategies (Table S5). *Bombus vagans* had the strongest association with the Lake of the Woods ecoregion in 2021, suggesting that *B. vagans* could be indicating floral resource availability, the habitat quality, connectivity, or environmental factors within the region (Naeem et al. 2020). Considering bumble bees are frequently used as a representative of the pollination potential of native bees, this result supports the continued use of bumble bees as indicators (Sepp et al. 2004, Schindler et al. 2013, Naeem et al. 2020). The habitat structure and connectivity are shown to be potentially influencing the bee community in Manitoba, considering the mean shape index, pastureland, and urbanization were significant factors in determining the abundance of the bees. *B. vagans* may be a candidate for consideration as an indicator species for the overall functionality of the Lake of the Woods ecoregion landscape components. Further testing would need to be done to substantiate this result, focusing on a broader spectrum of landscape type

sampling, beyond sampling within roadside verges, to account for imperfect detection issues within roadside verges (Urban et al. 2012).

Ecoregion groupings for 2022 showed a shift in the indicator species community, *H. confusus* being the strongest candidate as an indicator for Precambrian Boreal (Table S5). Considering this species is highly associated with Precambrian Boreal for 2022, 8.83% of my samples being *H. confusus*, with the majority found in the Precambrian Boreal, the strong indicator species association is not reliable (Urban et al. 2012, Naeem et al. 2020). The next strongest candidate for indicator species in 2022, which happened to be a strong candidate for 2021 as well, was *Halictus rubicundus*, also associated with Lake of the Woods and Precambrian Boreal. *H. confusus* and *rubicundus* are both eusocial, polylectic, ground nesters within the same genus, supporting a strong association of the *Halictus* genus and their life history strategies to Precambrian Boreal and Lake of the Woods. *H. rubicundus* is a species found throughout the Holarctic, with preferences in soft sandy soils as ground nesting sites, matching the sandy soils found in the Precambrian and Lake of the Woods ecoregions (Potts and Willmer 1997, Smith 2001). Abiotic and biotic factors affecting the nesting habitat of *H. rubicundus* has found that when disturbance or extirpation of essential nesting habitat occurs, the *H. rubicundus* species is negatively affected, suggesting that *H. rubicundus* could be an indicator of the type of soil, amount of soil disturbance, soil moisture, and the temperature of the nesting substrate (Potts and Willmer 1997).

The *Lasioglossum*, *Ceratina*, and *Andrena* species were not as strongly associated with a grouping of ecoregions as the previously discussed species. *Lasioglossum* species tend to skew results in studies exploring the effects of landscape heterogeneity, often with a response opposite to the expected result or demonstrating a strong affinity with sampling methods (Miljanic et al.

2019, Hung et al. 2021). Considering the complexity of the *Lasioglossum* genus, rendering identification difficult, and the broad association with many landscape components, using *Lasioglossum* as an indicator species is difficult (Urban et al. 2012, Hettiarachchi and Gibbs 2024). Considering indicator value analysis is easily swayed by high numbers of individuals from one species found at specific sites, *Lasioglossum*'s affinity for specific sampling methods, like pan traps, further analysis should not be done, including the *Lasioglossum* genus, without more robust analysis and sampling techniques (Urban et al. 2012, Miljanic et al. 2019). *Ceratina* had a strong association with Precambrian Boreal and Lake of the Woods, considering these ecoregions were divided in two (originally Lake of the Woods Ecoregion) for this analysis to emphasize landscape variation, the result of several indicators being identified for the combined grouping suggests that maintaining the Lake of the Woods Ecoregion distinction would be the best course of action to prevent arbitrary groupings impacting analysis (Turner 2005) (Table S5). *Andrena* are typically early to late spring oligolectic species, which limits their representation of the landscape effects on the community throughout the season (Davis Jr and LaBerge 1975, Herrera et al. 2023). Considering their prominence in the early spring, they could be early detectors of floral phenology shifts within an ecoregion, based on their abundance and diversity related to their specific plant species abundance and key flight periods (Wray and Elle 2015, Martins et al. 2021, Herrera et al. 2023). Further analysis would need to be completed to determine if *Andrena* have applications as indicators in other contexts, beyond simple ecoregion and site type groupings, potentially indicating the success of other life history traits, overwintering success, spring emergence conditions, or other unexplored variables (Table S5).

Tall Grass Prairie and Assiniboine Delta ecoregions did not have definable relationships with indicator species, suggesting that there may be other factors coming into play in these

ecoregions, like primary pollinator for the flowering plant species or the disproportionate use of roadside verges in comparison to the surrounding landscape's floral use. Tall Grass Prairie typically shows greater reliance on Syrphid flies or Lepidopterans for the pollination of the flowering plant species (Borkowsky 2006, Semmler 2015, Miller 2021, Martini 2022). Assiniboine Delta could be following alternative patterns of bee and plant community dynamics since it is mostly Mixed-Grass Prairie, not Aspen Parkland, Boreal, or Tall Grass Prairie, which can shift the plant-bee community dynamics seen (Patenaude 2007).

The bee indicators for site type shift in comparison to the ecoregion groupings based on the site types they are associated with, keeping with the previous analysis showing overall bee community variations in agricultural and natural ecosystem types (Table S5). *B. vagans* appears again to be a strong candidate for natural site types in 2021, most likely driven by the relationship to the landscape found in the Lake of the Woods ecoregion level grouping. The combination of the two results would indicate that *B. vagans* would be an indicator species of the quality of the natural habitats found within the Lake of the Woods ecoregion in Southeast Manitoba for 2021 (Naeem et al. 2020). This significant relationship could be due to *B. vagans* body size, allowing travel between habitat patches, the composition of the flowering community in natural sites being favourable for *B. vagans*, or the lack of disturbance within the Lake of the Woods area (Greenleaf et al. 2007, Torne-Noguera et al. 2014). *Bombus griseocollis* is highlighted as a potential indicator species at the site type level, in particular, the agricultural and natural site groupings for 2021, and the 2022 agricultural sites. Considering *B. griseocollis* is not strongly associated with either of these site groupings, based on the indicator value, and does not appear in the ecoregion grouping analysis, utilizing them as an indicator species would not be an appropriate approach based on concerns related to the validity of the data requiring a more

conservative interpretation of the indicator value and significance (Urban et al. 2012). Additional genera that appeared to show significant promise as indicator species in the site type analysis were *Agapostemon*, *Lasioglossum*, *Andrena*, *Anthophora*, *Ceratina*, *Halictus*, *Hoplitis*, *Augochlorella*, and *Melissodes*.

Agapostemon and *Melissodes* species are highly associated with agricultural areas, and combinations of agricultural and natural site types, respectively, in this analysis and additional research (Kennedy et al. 2013, Discover Life 2024). The *Agapostemon* species native to Manitoba are polylectic ground nesting species with either eusocial, communal, or solitary nesting strategies, who can frequently be found in agricultural areas due to their ability to travel long distances due to their medium body size, feed off many plant species, and nest in disturbed soil areas (Greenleaf et al. 2007, Kennedy et al. 2013, Gibbs et al. 2023, Discover Life 2024). Considering their appearance in the agricultural site types of this analysis, their strong association with agroecosystems across North America, *Agapostemon* species would be a good candidate for estimating the amount and impact of agricultural landscape within an area due to their strong association with agricultural areas in North America (Kennedy et al. 2013, Chowdhury et al. 2023). Further analysis of this relationship would need to be completed to ensure this is not an artifact of the sampling technique and analysis method (Urban et al. 2012). *Melissodes* species can be highly associated with agricultural areas due to their specialization on *Helianthus* and Asteraceae plant species (Discover Life 2024). Considering the specialization on *Helianthus* species and the association with natural and agricultural sites seen for 2021 and 2022, this suggests that there was a large proportion of *Helianthus* or Asteraceae present in the landscape in agricultural and natural site types (Cilla et al. 2012, Mallinger et al. 2019). *Melissodes* sp. have the potential to be excellent indicators of the abundance of *Helianthus* and

Asteraceae species within the landscape in North America and South America (Cilla et al. 2012, Mallinger et al. 2019). However, *Melissodes* species make up 15.61% of the total abundance of my samples, which presented as outliers in my analysis. Considering the impact *H. confusus* had on my analysis, further use of *Melissodes* species for this study is not advised based on the outlier issue present in the data (Urban et al. 2012).

Anthophora was only a significant indicator species for 2022, with only one species showing a significant relationship with agricultural areas. Considering the lack of continuity between the sampling years, the association of this species with the more unreliable of the sampling years, and the weaker association with agricultural site types suggests that this genus was only related to the analysis issues highlighted previously (Urban et al. 2012). *Hoplitis* and *Augochlorella* were found to be potential indicators of natural and semi-natural sites for 2021 (Table S5). The *Hoplitis* genus is Boreal specific, preferring cooler areas in comparison to most bee species (Wilson and Messinger Carril 2015). Examining the relationship that *Hoplitis* has with cooler landscapes, natural and semi-natural sites are shown to have cooler microclimates due to increased vegetation, decreased bare ground, and less urbanization, potentially forming ideal conditions for *Hoplitis* in heterogeneous landscapes (Londe et al. 2020). The dependence on specific climatic conditions for the success and maintenance of *Hoplitis* suggests that changes in the *Hoplitis* species community will be indicators of the impact of the changing climate in natural and semi-natural landscapes (Wilson and Messinger Carril 2015, Chowdhury et al. 2023). The nesting strategy of *Augochlorella aurata*, being primitively eusocial with a founding female laying while her daughters take over foraging duties, returning to the original ground nest for the season, would suggest that a level of low ground disturbance would be necessary for the success of these bees (Wilson and Messinger Carril 2015). Natural and semi-natural sites tend to be

lower disturbance areas, with a very low chance of ground disturbance in comparison to agricultural areas, suggesting this species could also be an indicator of the level of disturbance in natural and semi-natural areas (Sousa 1984, Winfree et al. 2007, 2009, Rodríguez and Kouki 2017).

Cluster showed similar groupings of indicators to ecoregion. In the cluster analysis, only the addition of the *Apis* genus was seen (Table S5). Considering *Apis mellifera* Linnaeus 1758 species were avoided during sampling, to only capture the wild bee data, including them in this analysis as a significant indicator species for consideration is unreliable due to sampling bias (Urban et al. 2012). The use of *A. mellifera* as indicators of the impacts of pesticides, pollutants, and pests as managed pollinators is well documented, with clear decreases in population size and fitness, with an increase of pesticides, pollutants, and pests in agricultural areas (Celli and Maccagnani 2003, Quigley et al. 2019, Catalano et al. 2024). Since *A. mellifera* are not endemic to Manitoba and are managed colonies limited to agricultural areas, utilizing their population dynamics as indicators of landscape complexity and configuration beyond agricultural areas would provide no insight into the wild bee populations in the surrounding natural landscape (Urban et al. 2012, Chowdhury et al. 2023). Cluster is the most unreliable method due to its subjective grouping types that hold no real ecological weighting but provide some insight into which locations may be driving the relationship in the ecoregions (Urban et al. 2012, Chowdhury et al. 2023). Further analysis utilizing a cluster would not be advisable since the arbitrary groupings with no clear ecological context or comparability render the results subjective (Kevan 1999, Turner 2005, Urban et al. 2012). Exploring other factors that could be influencing the indicator species beyond what is known of the ecoregions, site types, and clusters, such as abiotic

and biotic components within the landscape, would determine what is driving the variations in the community seen.

The relationship rewarding flowering resources in agricultural, natural, and semi-natural landscapes have with the bee community in each landscape type, would be essential to describing any connections between indicator species and the landscape based on the resources seen in the roadside verges (Chowdhury et al. 2023). Emphasizing whether agricultural sites support different floral communities in comparison to semi-natural and natural sites, provides additional context to why certain bee species may be more prevalent in an area, which resources drive this relationship, and predict the effects on the bee community when resources are removed (Chowdhury et al. 2023). Analysis showed that there were very few significant differences between the site types for 2021 and 2022, suggesting very little variation in plant species composition between site types, suggesting the presence of a consistent flowering plant community found in roadside verges across Southern Manitoba agricultural, natural, and semi-natural sites (Figure 24, 25). The significant points were seen at the most diverse periods during a Manitoba Summer, showing many spring, summer, and fall species with converging flowering periods around July (Dunnell and Travers 2011, Mulder et al. 2017). Examining the flowering seasonal variability in Canada and across North America, demonstrating flowering periods shifting over the summer, the marginal differences between rounds of sampling during the sample season could be attributed to this known flowering plant seasonality trend (Gonsamo et al. 2013, Martins et al. 2021). Marginally significant differences around Round 2 of sampling (end of June to July) were seen, highlighting a transition from spring to summer plant species (Figure S12). Agricultural and semi-natural sites show a lot of overlap in their community, especially in the rewarding and non-rewarding agricultural landscapes, with developed land

occasionally supporting the agricultural and semi-natural flowering plant community similarities (Figure 24, 25). Considering developed/urban land had a negative impact on the bee community in the previous analysis, this result supports the premise that disturbance changes the plant community with knock on effects to the bee community by showing a connection to the changes in the floral community in agricultural and semi-natural sites (Hegland and Boeke 2006, Kremen et al. 2018). Roadside verges may be homogenizing the plant community found based on their disturbance regimes, the colonizability of the area, and the plant species suited to these conditions (Meinzen et al. 2024). Considering there were no significant differences found in roadside verge floral communities, only marginal trends across the sample season, there was evidence of a potential trend with differences seen in comparison to agricultural, semi-natural, and natural site types (Meinzen et al. 2024). Natural landscape features showed potential in shifting the natural site plant communities away from the agricultural and semi-natural sites, suggesting in the future, more in-depth sampling and analysis would find a distinction between natural site plant communities and agricultural and semi-natural site types.

Environmental variables impact the overall bee community and the trends seen in the floral communities in roadside verges, requiring some consideration of the abiotic and biotic environmental factors driving the relationships bee communities have with the roadside verges and broader landscape. Determining if the indicator species were significantly impacted by flower cover, grass cover, temperature, wind-speed, litter depth, and ground cover could determine which factors should be considered when completing sampling in roadside verges. Local level landscape community compositions continuously shift due to year-to-year variation, disturbance, and ephemeral resources, with broader landscape perspectives remaining relatively consistent in comparison (Hendrickx et al. 2007, McCormick et al. 2019, Fahrig 2020). Flower

cover was the only significant variable for 2021, which negatively impacted indicator bee abundance (Figure 28). This is likely due to the flowering plant abundance outside of the roadside verges drawing the bees from the flowering plants within the roadside verges, showing a negative impact on pollinators using roadside verge resources as the surrounding landscape floral diversity and abundance increases (Hanley and Wilkins 2015). Typically, roadside verges can support a diverse and dense flowering plant community that can support bee diversity and abundance by providing nesting habitat, floral resources, and movement facilitating corridors (Hopwood 2008, Fitch and Vaidya 2021, Horstmann et al. 2024). Notably increasing floral diversity, incorporating more native plant species, and allowing for full season growth free from mowing, bee species richness and abundance increased (Hopwood 2008, Horstmann et al. 2024). Fitch and Vaidya (2021) theorized that increasing habitat quality, in particular, increases in floral richness and semi-natural habitats in rural areas, would increase the pollination potential and bee community abundance and diversity within the roadside verges. The negative response from the indicator species collected in the rural roadside verges in this study appears to be opposite to the broader bee community observed by Fitch and Vaidya (2021), suggesting that the 2021 indicator species were being influenced by other factors in the landscape. Additional factors that could be impacting the indicator species analysis are the variation in the amount of species captured by the sampling techniques (Droege et al. 2010). Disparity can be seen in the number of bees captured by trap type, potentially influencing the community representation in the data set (Figure S21).

Flower cover continued to show the same negative relationship to the bee indicator species abundance in 2022, as seen in 2021, although the relationship was not significant with the addition of grass cover (Figure 28). In 2022, grass cover had a significant positive effect on

bee indicator abundance. Grass cover is related to the amount of disturbance seen within an area, particularly the amount of mowing in roadside verges, with more disturbed areas having reduced grass cover (Hopwood 2008, Meinzen et al. 2024, Horstmann et al. 2024) (Figure 28). The accepted reasoning for roadside verge mowing in Manitoba is meant to increase the safety of drivers, prevent debris from encroaching on the roads or the spread of weeds, and allow for easy movements of water during the spring snow melt (Government of Manitoba 1988). Excessive mowing has been linked to decreases in pollinator diversity and abundance, reduced nesting habitat availability, increased mortality of pollinators, and reduced nectar sources (Meinzen et al. 2024). Utilizing the amount of grass cover found as a diagnostic of the amount of disturbance found within an area would highlight areas that would benefit the most from restorative practices or decreased mowing (Hopwood 2008, Jakobsson et al. 2018). Restoration of grassland-like habitats that provide floral resources and nesting habitat in roadside verges has shown significant increases in pollinator diversity and abundance (Hopwood 2008). The most promising method to aid in the restoration and diversification of roadside verges has been delayed mowing, providing ample opportunity for grasses and flowering species to produce seeds and establish themselves throughout the key flight periods of pollinators (Hopwood 2008, Meinzen et al. 2024). Ensuring phenological matchup between the bee species and essential resources, by delaying mowing that could disrupt the growth and production of inflorescence, would continue to demonstrate this positive grass cover relationship to indicator species abundance seen in 2022 (Hopwood 2008, Bartomeus et al. 2011, Meinzen et al. 2024, Horstmann et al. 2024). Combining the two sample years for analysis, flower cover and grass cover continued to be significant factors in the abundance of the indicator species, emphasizing the importance of each of these components on the abundance of the indicator species in roadside verges.

The next steps for bee indicator species identification would be to explore the differences between data collected in roadside verges to data collected in the broader landscape. Since only 55% of the known Manitoba bee species were included in this analysis, imperfect detection of species due to sampling methods or sampling locations is likely (Urban et al. 2012). Additionally, species identified as indicators will need to be tested for the components within the landscape and life history traits that could be affecting their populations in parallel to any changes within the environment that might affect the broader bee community (Kevan 1999, Chowdhury et al. 2023). Different species were identified in this analysis as potential indicators, though their use of the landscape, flight periods, nesting strategies, and floral associations vary, potentially indicating other components of change or variation in the environment. Further detection and exploration of landscape heterogeneity's role in the environment, by exploring how a variety of genera are influenced by landscape components could identify a genera or species to be a representative of the greater bee community, informing conservation efforts on the best practices to maintain a healthy and diverse bee community (Schindler et al. 2013, Harrison et al. 2018, Naeem et al. 2020).

GENERAL DISCUSSION AND CONCLUSIONS

Based on the findings, a conversation between conservationists, Rural Municipality infrastructure managers, and producers surrounding the importance of connectivity, landscape complexity, habitat creation, and habitat maintenance is required to consolidate efforts in wild bee conservation initiatives. Conservationists lobbying for conservation policies will need to ensure that management solutions to reduce the amount of shrubland, preserve mixed wood forests, promote flowering plant species, and grass cover occurs. The area of non-rewarding and rewarding agriculture not being significant drivers of bee community dynamics suggests to me that focus should not be on how much space the agricultural area is occupying, but the quality and diversity of natural areas or naturalized areas near the agricultural areas. Land cover types that showed positive impacts on bee diversity were areas with increased compositional and configurational heterogeneity, such as pasture and mixed wood land. This suggests that having consistent naturalized habitat types in proximity to agricultural areas, regardless of whether the crop is rewarding or not rewarding to bees, is essential to supporting diverse bee communities. Conservationists and natural habitat restorers could assist the producers, landowners, and Rural Municipalities in developing patchy landscapes, informing stakeholders on key habitat types, like pasture or mixedwood stands, that would have the most impact in supporting bee communities while diminishing the impacts of conversion of agricultural land for conservation initiatives. This would support the fragmentation, corridor, and habitat isolation theories, following the need for connected and diverse patches of natural habitat to support and maintain a diverse and abundant wild bee community.

Rural Municipality Infrastructure Managers would need to revise their mowing practices, delaying mowing to allow for flowering and seeding to occur, allowing for the provisioning of

wild bees and the continued growth of the flowering plant community within roadside verges. Roadside verges could be supporting the movement of bees through the landscapes, increasing connectivity between patches within the landscape by hosting a variety of resources essential to bees, such as nesting habitat, forage, and overwintering refugia. Since road margins often remain the only source of diverse flowering plants in non rewarding landscapes and provide linear movement avenues in natural ecosystems, ensuring additional stressors like pesticides, herbicides, illegal burning, and excessive mowing are avoided would provide a relatively safe avenue and habitat for wild bee conservation.

Producers could use these findings to understand the impacts the agricultural practices have on the surrounding landscape, emphasizing the need for no-mow initiatives, encouraging the colonization of endemic flowering plant species in field margins and roadside verges for the betterment of the pollination services provided by wild bees. Allowing maturing forest stands, like mixed wood stands, reducing shrubby encroachment, and planting native flower species in field margins or fallow areas would provide ample areas for provisioning a diverse bee community in an agricultural setting. Better understanding the movement of bees through the landscape, key habitat areas (pasture land and mixed wood stands as an example), and essential resources at different points in the year would inform best practices for pesticide and herbicide use, along with limiting the competition with managed bee stock by understanding the wild bee population dynamics relationship with flowering plants within the area.

The continued participation, and investment in wild bee conservation initiatives by conservationists, producers, and key stakeholders relies on continued research into the landscape's effects on wild bee diversity and abundance. It also relies on the investment of the community, in holding their representatives accountable to promote conservation initiatives to

key stakeholders, emphasizing their desire to support an ecologically diverse, healthy, and disturbance-resistant natural landscape, wherever possible. Compromising, being open to change, engaging in conversation, and a desire to learn more will ensure that the future impacts of climate change, agricultural intensification, and urbanization do not homogenize the landscape, reducing all diversity to the bare minimum required to sustain necessary ecological relationships.

In conclusion, landscape heterogeneity has a complex impact on the wild bee community, with variations in effects based on location, site type, year, time of year, and species. Significant variation between site types between agricultural and natural sites, suggesting that maintaining delineations between site types could continue to show varying effects on wild bee communities. Semi-natural sites may not need to be directly tested if they have had no significant impact on any of the models. Combining the semi-natural sites with natural and ag sites would simplify analysis, though may not effectively represent relationships seen in every region. Caution would need to be exercised in how the combining would occur, in order not to mask any variation seen in purely agricultural or natural site types, requiring a land cover type gradient instead of clear categorical distinctions. Variation in the sampling rounds typically had early spring, early summer species flowering at the same time, along with the bees that depend on those species matching that flower phenology, following the trends seen in other studies. Compositional landscape heterogeneity metrics in urban areas, pasturelands, mixed wood stands, and shrubland had a significant impact on wild bee diversity depending on year sampled, with no impact on bee abundance. To fully explore the impacts of sample round variation and year to year variation, longer time frame studies would need to be completed.

Configurational landscape heterogeneity metrics, mean shape index, and patch area, were potentially important factors in the analysis, requiring the need for continued research into the impacts of fragmentation, corridors, patch dynamics, and the overall heterogeneity of the landscape. A landscape with increased complexity would be able to support a more diverse bee community via the creating of additional niche habitats and supporting functional complementarity, while a lack of complexity reduces both niche habitats and functional complementarity. Complexity of the landscape and the amount of natural habitat are seen as essential even in the compositional heterogeneity analysis, with factors like pastureland, mixed wood, shrubland, and urban area proving impactful on the bee community. These factors all typically create some form of heterogeneity within a landscape, further supporting the trend that bee communities are impacted by the local and broader landscape features. Blanket statements on the relationships seen between the bee and flowering plant community to the landscapes in Manitoba, are not as easy to interpret and will often not show any variation across the province. But examining the area with greater detail, clearly defining ecosystem features, and allowing for each component to be tested separately proves that there is variation in bee communities across the province. Including the scale of the landscape examined into landscape heterogeneity analysis and the variability of which the ecological communities change depending on scale, will highlight the variation in impact of heterogeneous landscapes based on province, region, and local scale, providing greater context of the impacts seen on the wild bee communities.

Indicator species analysis showed some promising results, though it would require further refinement of sampling techniques and analysis techniques to properly identify significant indicator species. Precambrian Boreal and Lake of the Woods had many species that were significantly associated with the ecoregion, with stronger relationships in comparison to the other

ecoregions. Tall Grass Prairie and Assiniboine Delta may be relying on other pollinators more than bees, in particular Syrphidae or Lepidoptera species. Since sampling ends in August, there were a few bee and plant species missing in the analysis, again potentially missing key species for the various ecoregions. *Melissodes agilis* and *Halictus confusus* caused issues with outliers in 2022, due to 982 *Melissodes agilis* and 737 *Halictus confusus* being caught over the sampling season. Additional analysis to consider in a future indicator species analysis would be whether the indicator species can be linked to a particular species composition, potentially highlighting a species of indicator that would indicate the presence of rare or essential bee species in a specific habitat type.

Further research will need to be completed to substantiate the landscape heterogeneity results presented in this thesis. Increasing the sampling effort to encompass more areas, with a longer sampling season, would provide an opportunity for situations where outliers, abnormal year variation, or unexplained variation would have less of an impact on the overall model. Including a more rigorous sampling regime across the province, including more within-landscape sampling instead of focusing on roadside verges, would benefit the landscape heterogeneity and indicator species analysis, providing further insight into the relationships seen across Southern Manitoba.

SUPPLEMENTARY TABLES AND FIGURES

Figures:

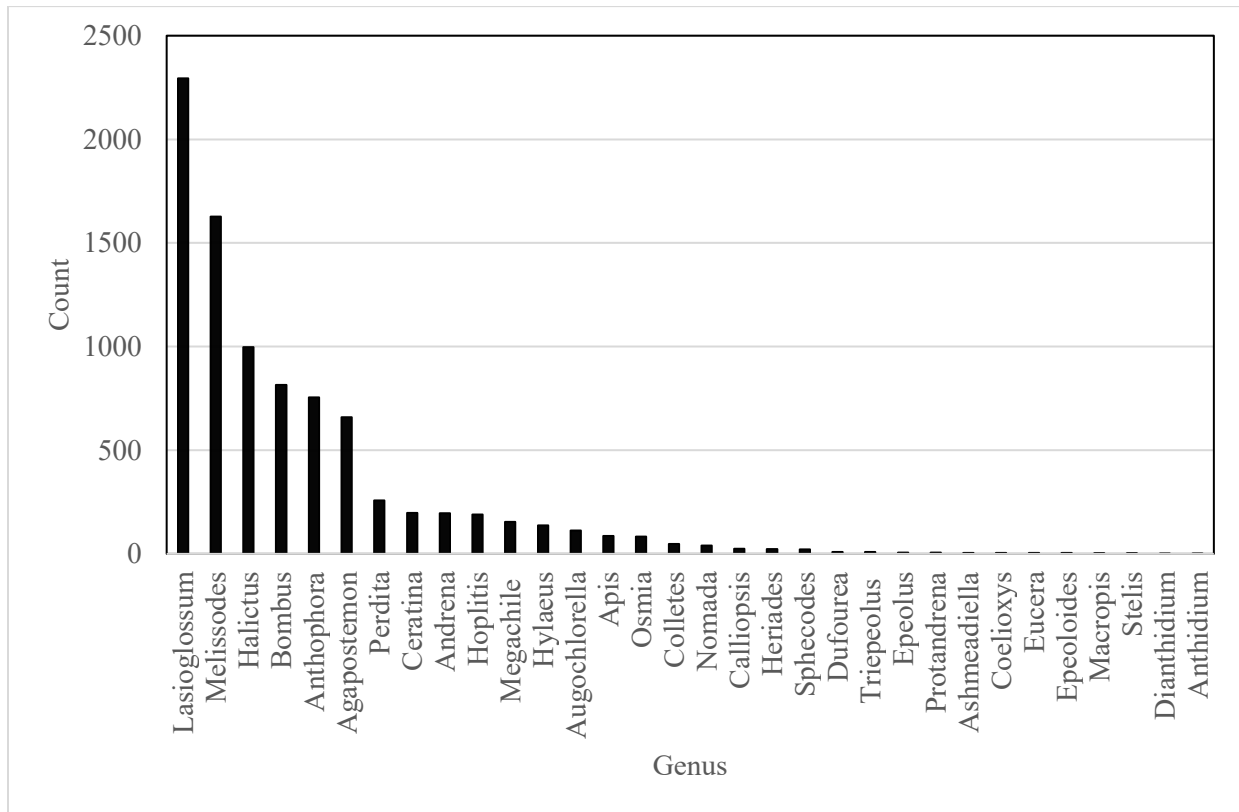


Figure S1: Abundance of genera captured using passive and active sampling techniques for 2021 and 2022.

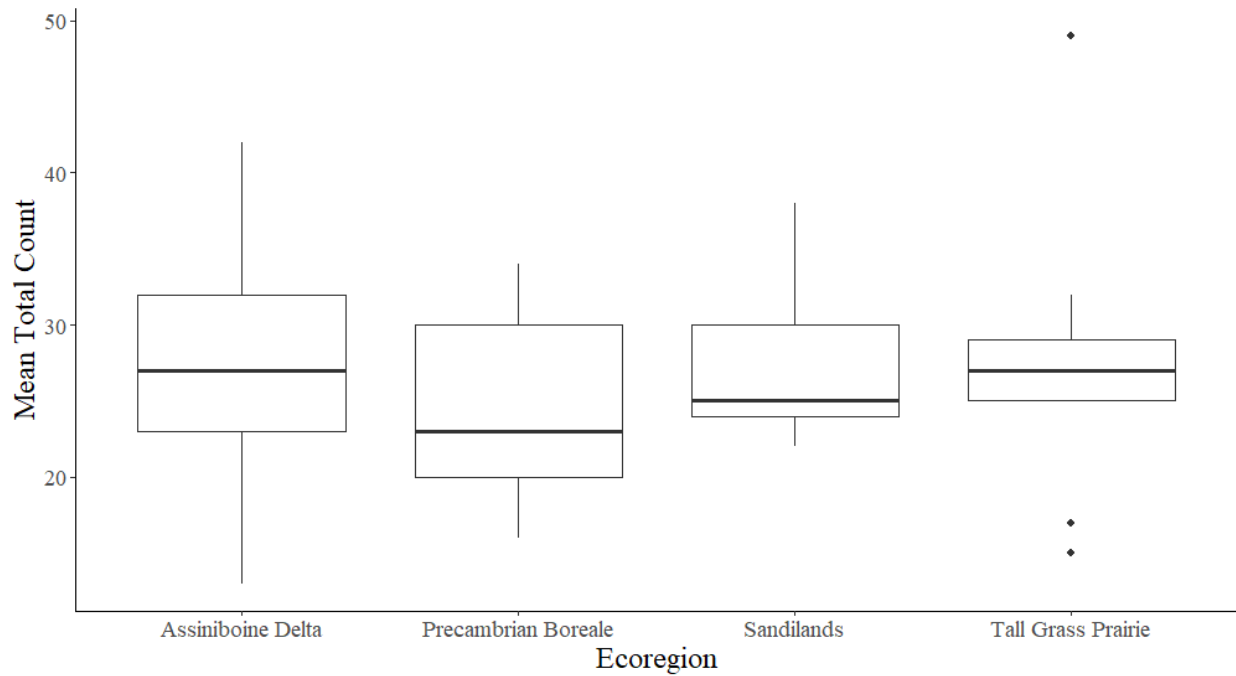


Figure S2: Mean bee abundance per ecoregion per sample season for both active and passive sampling (2021) (n=36).

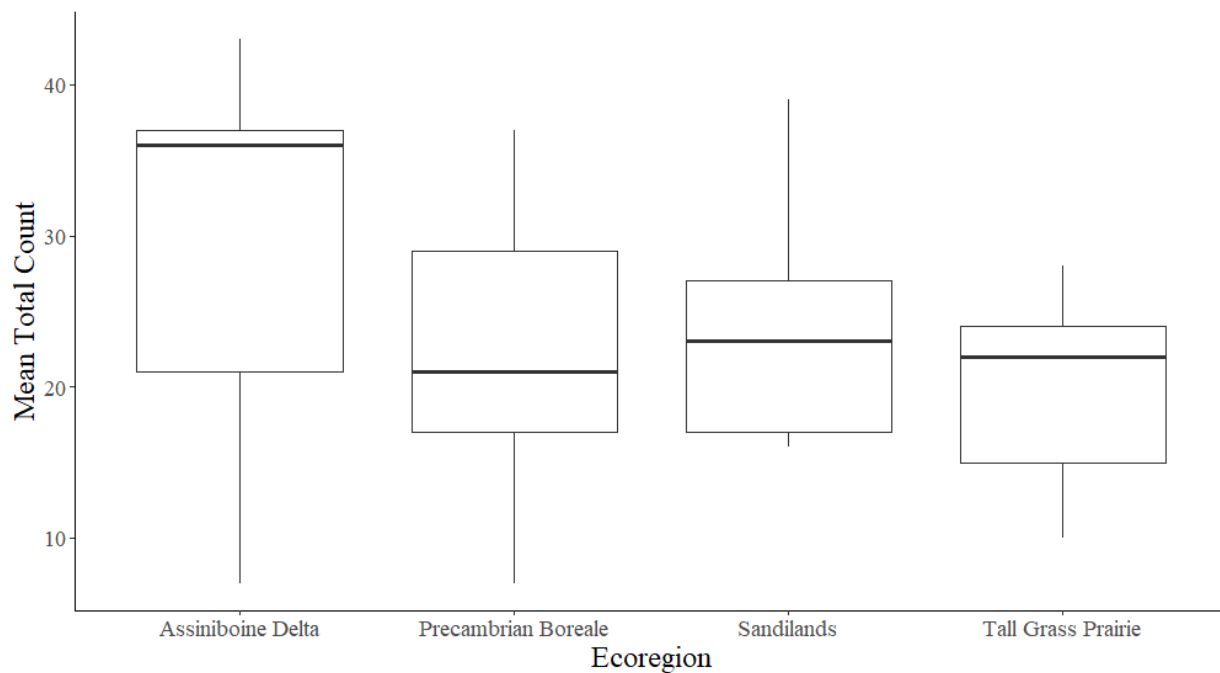


Figure S3: Mean bee abundance per ecoregion per sample season for both active and passive sampling (2022) (n=36).

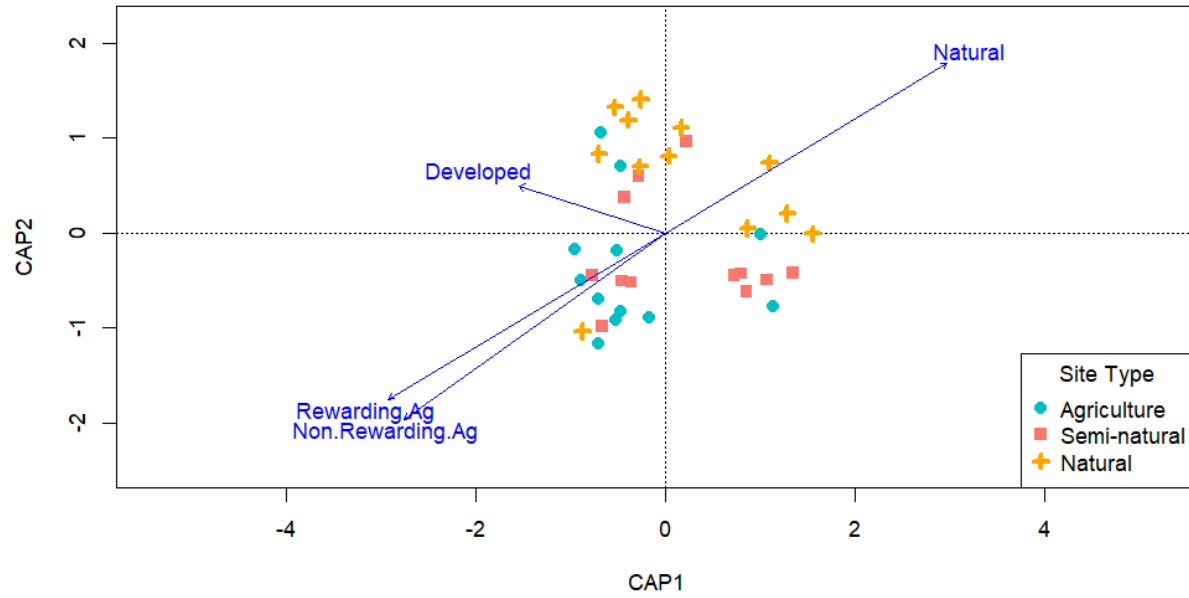


Figure S4: Distance-based redundancy analysis of bee species in 2021 round 1 of sampling (n=36). Bee counts by site were also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

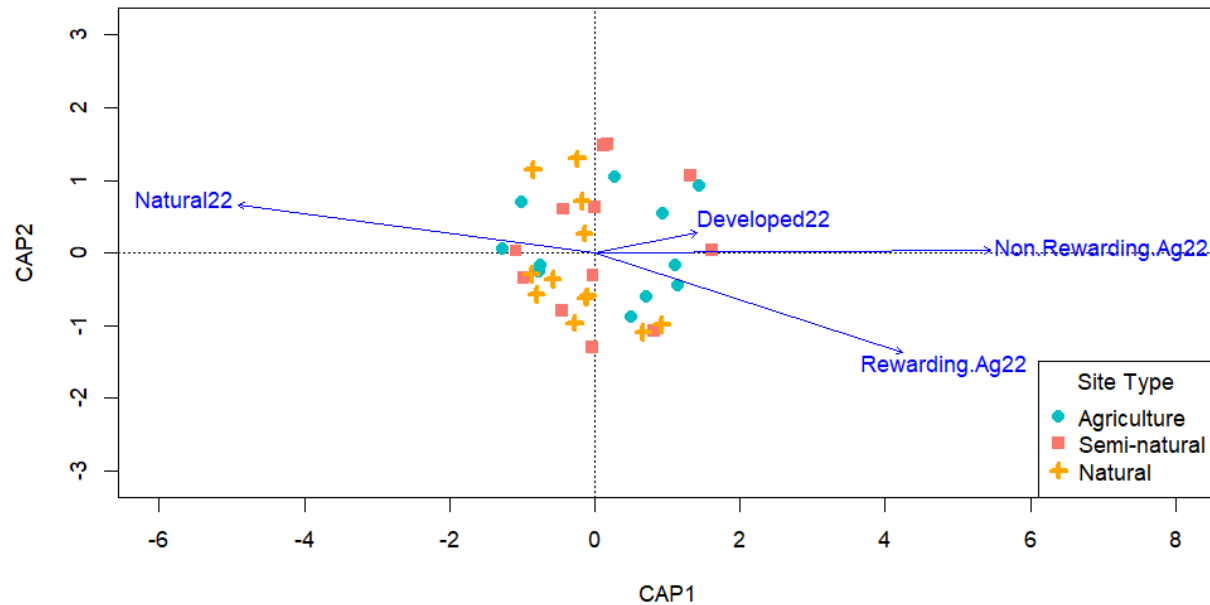


Figure S5: Distance based redundancy analysis of bee species in 2022 round 1 of sampling (n=36). Bee counts by site were also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

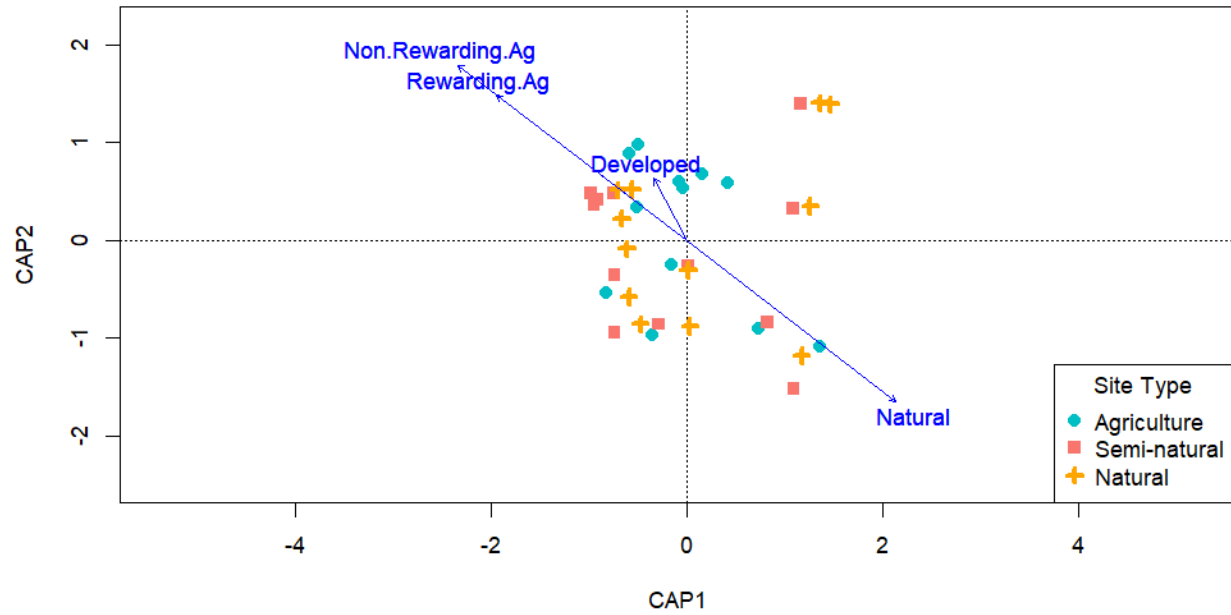


Figure S6: Distance based redundancy analysis of bee species in 2021 round 2 of sampling (n=36). Bee counts by site were also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

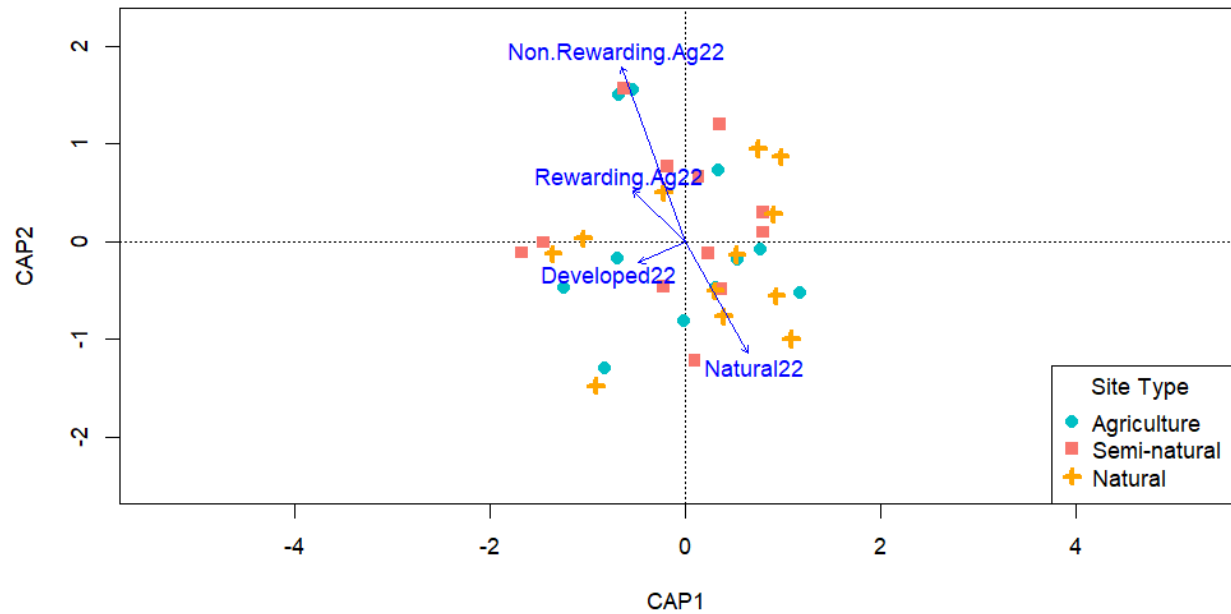


Figure S7: Distance based redundancy analysis of bee species in 2022 round 2 of sampling (n=36). Bee counts by site were also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

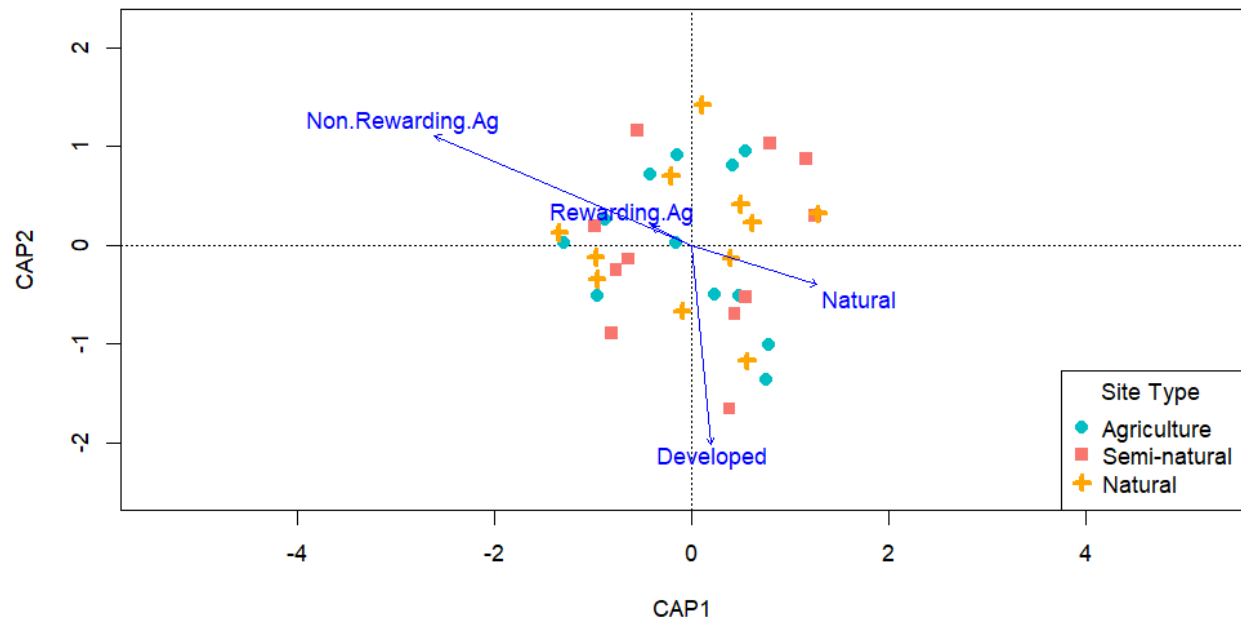


Figure S8: Distance based redundancy analysis of bee species in 2021 round 3 of sampling (n=36). Bee counts by site were also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

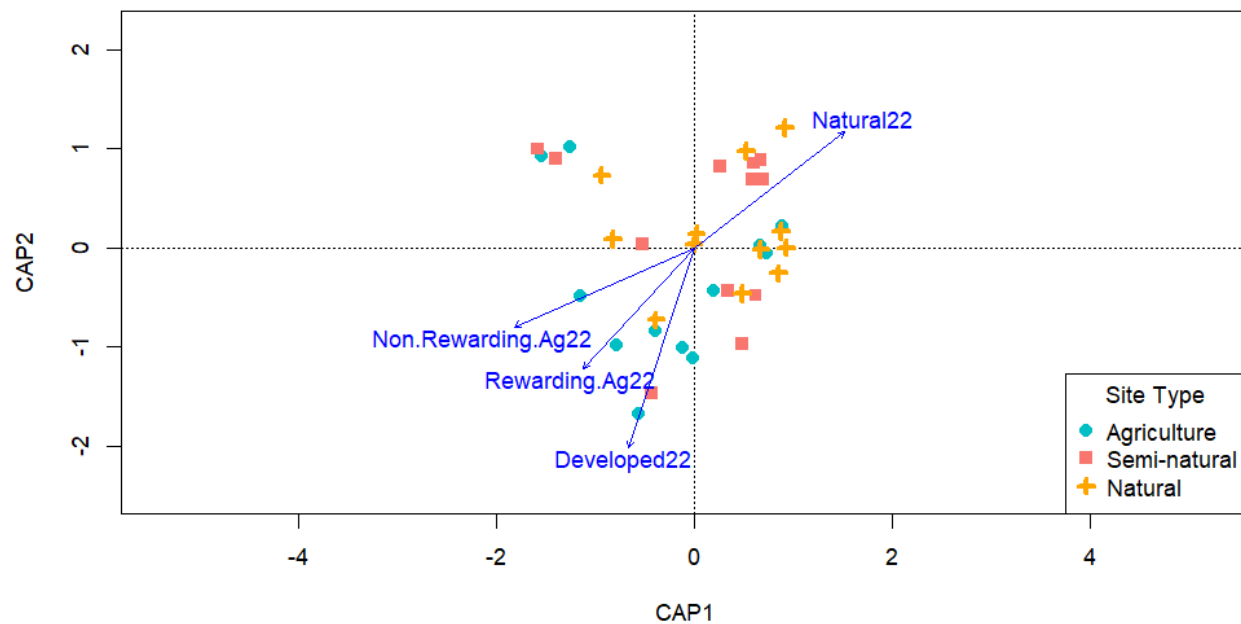


Figure S9: Distance based redundancy analysis of bee species in 2022 round 3 of sampling (n=36). Bee counts by site were also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

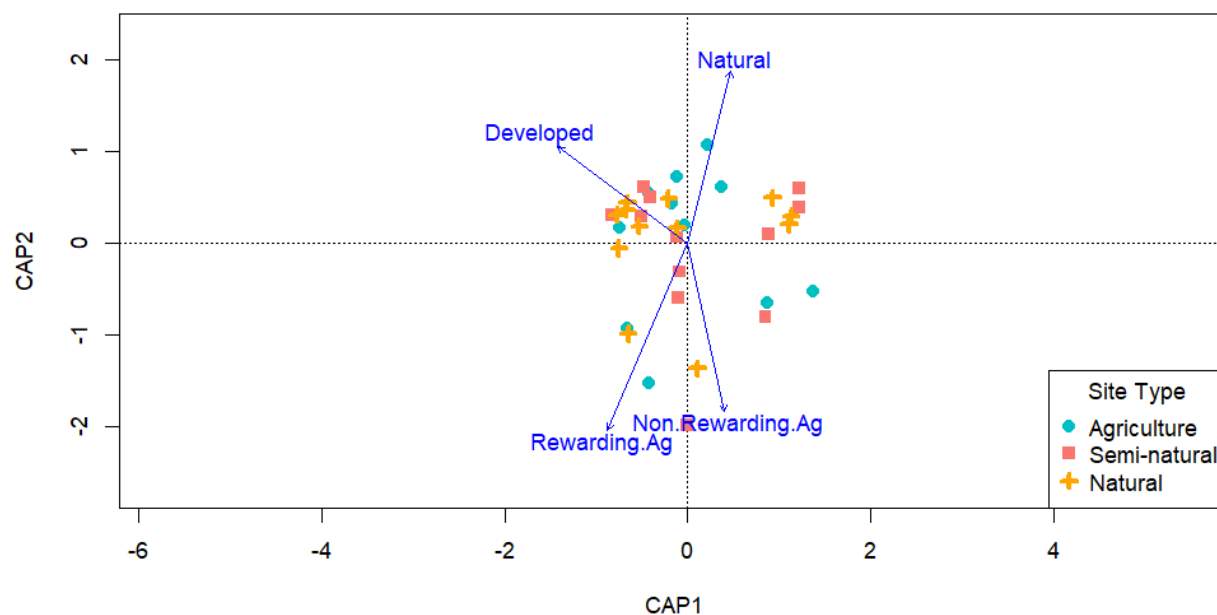


Figure S10: Distance based redundancy analysis of floral species in 2021 round 1 of sampling(n=36). Bee counts by site were also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

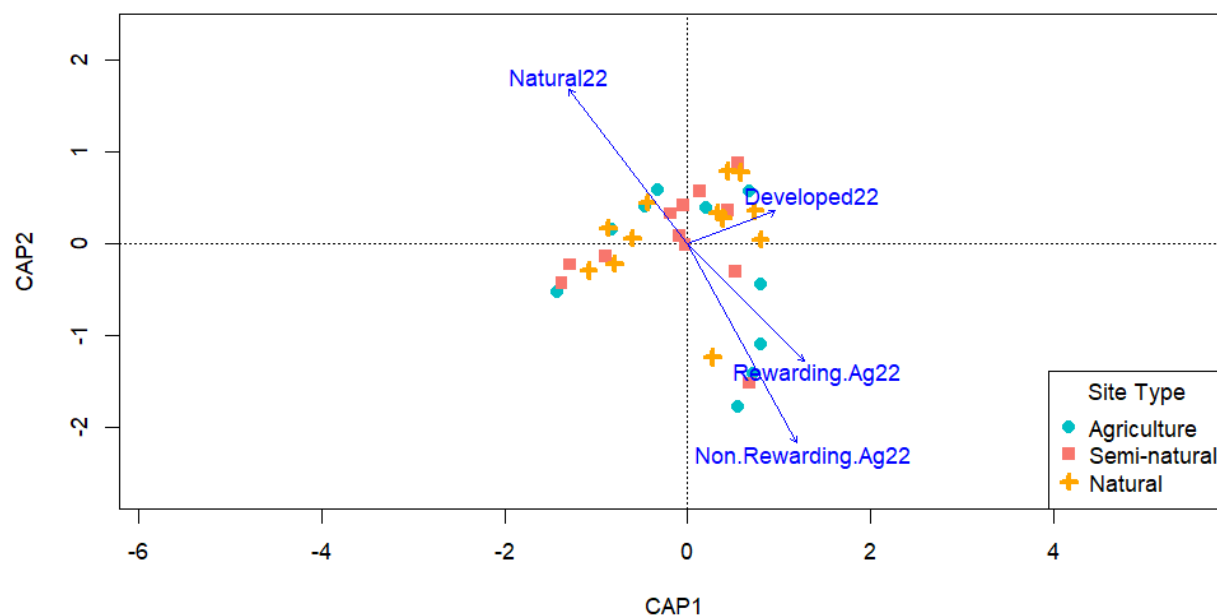


Figure S11: Distance based redundancy analysis of floral species in 2022 round 1 of sampling(n=36). Flowering plant cover by site was also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

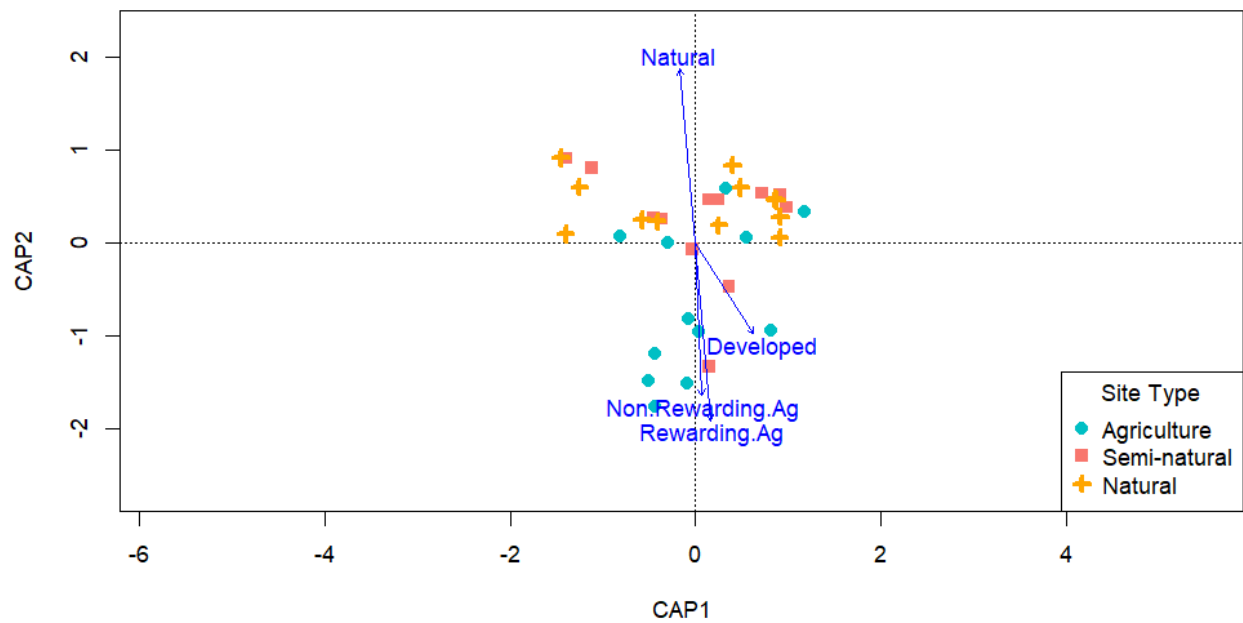


Figure S12: Distance based redundancy analysis of floral species in 2021 round 2 of sampling (n=36). Flowering plant cover by site was also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

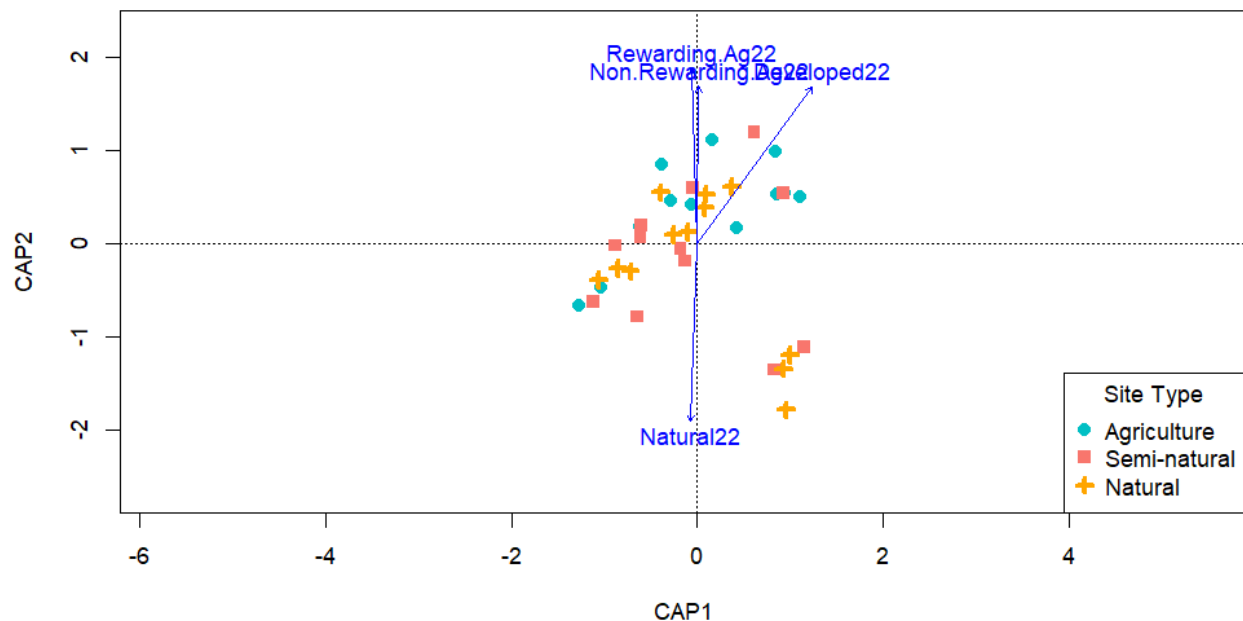


Figure S13: Distance based redundancy analysis of floral species in 2022 round 2 of sampling (n=36). Flowering plant cover by site was also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

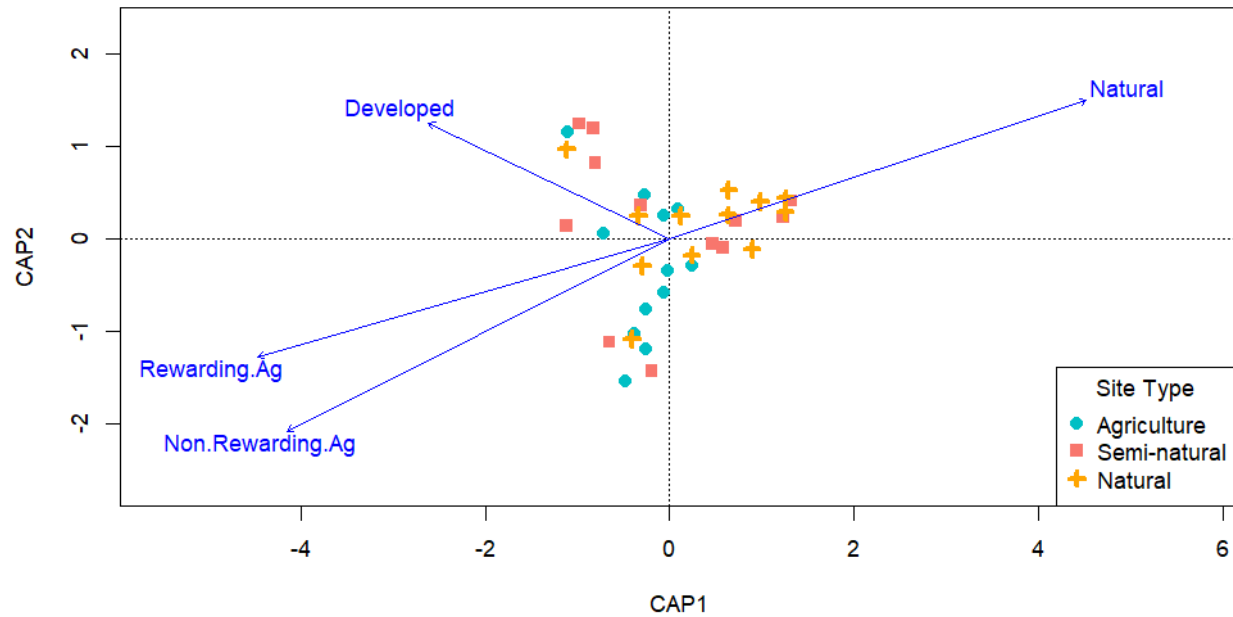


Figure S14: Distance based redundancy analysis of floral species in 2021 round 3 of sampling(n=36). Flowering plant cover by site was also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

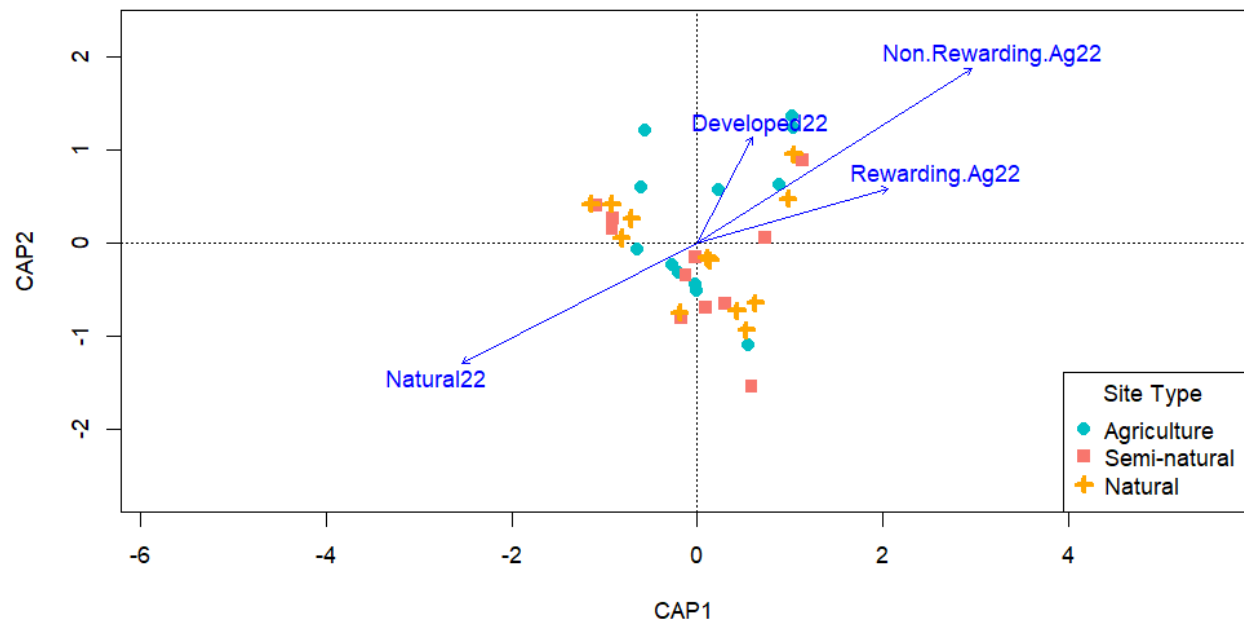


Figure S15: Distance based redundancy analysis of floral species in 2022 round 3 of sampling(n=36). Flowering plant cover by site was also constrained by landscape components: natural land, developed land, non-rewarding agriculture, and rewarding agriculture.

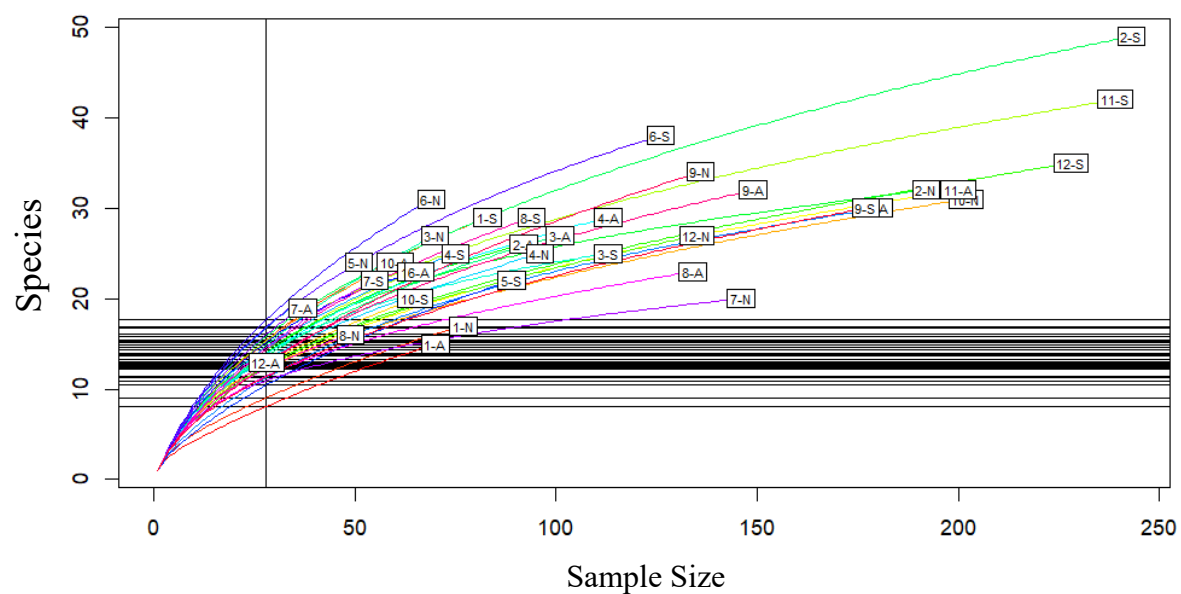


Figure S16: Rarefaction Curve for all sites in 2021.

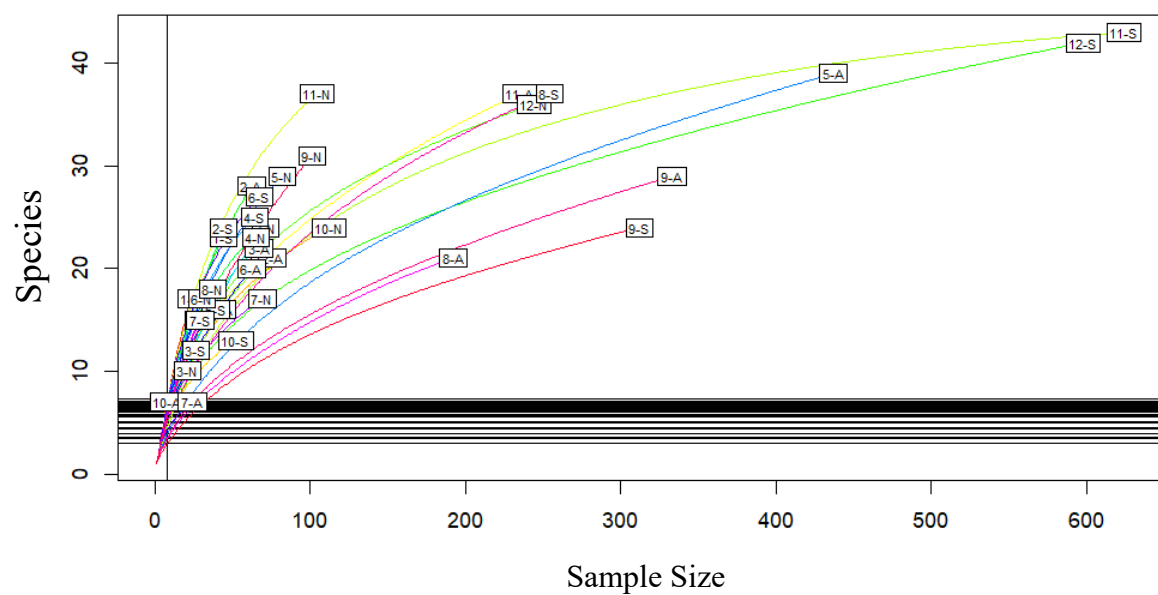


Figure S17: Rarefaction curve for all sites in 2022.

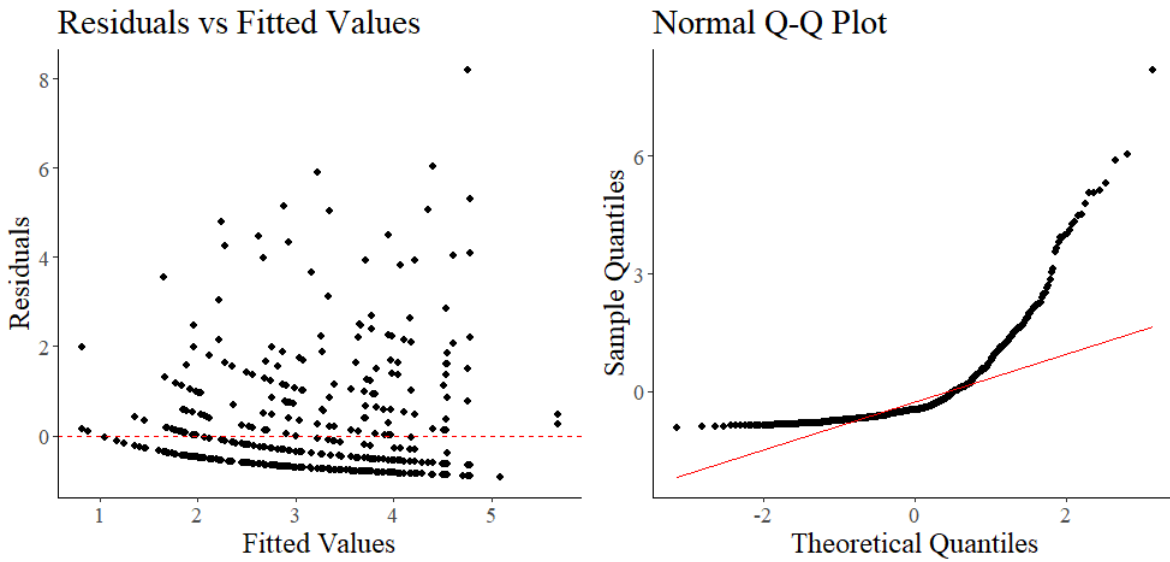


Figure S18: QQ plot and heteroscedasticity diagnostic plots for indicator species 2021 generalized linear mixed effects models.

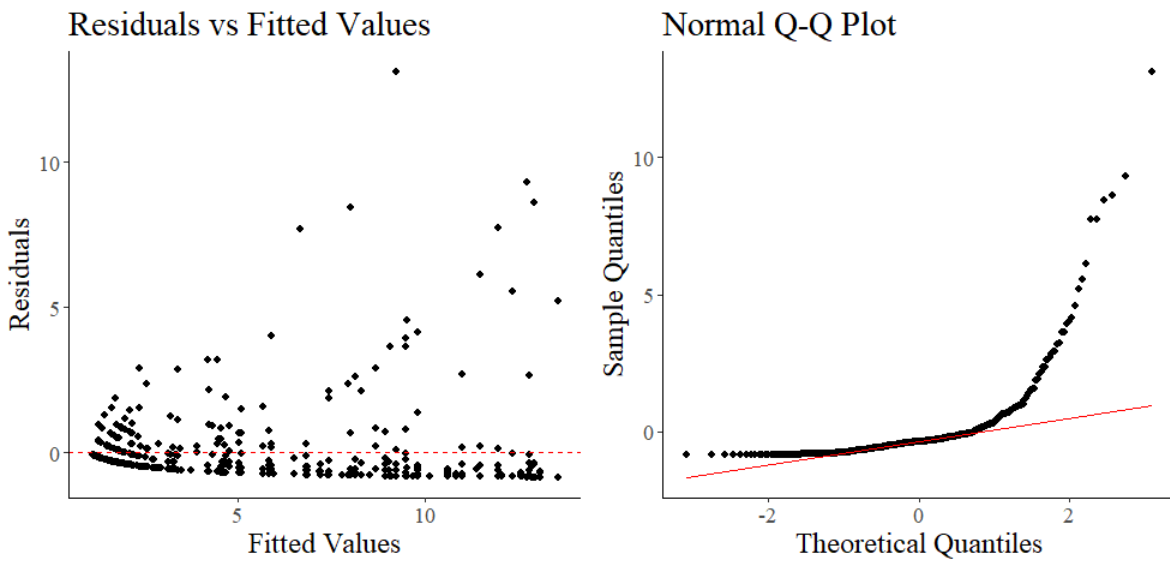


Figure S19: QQ plot and heteroscedasticity diagnostic plots for indicator species 2022 generalized linear mixed effects models.

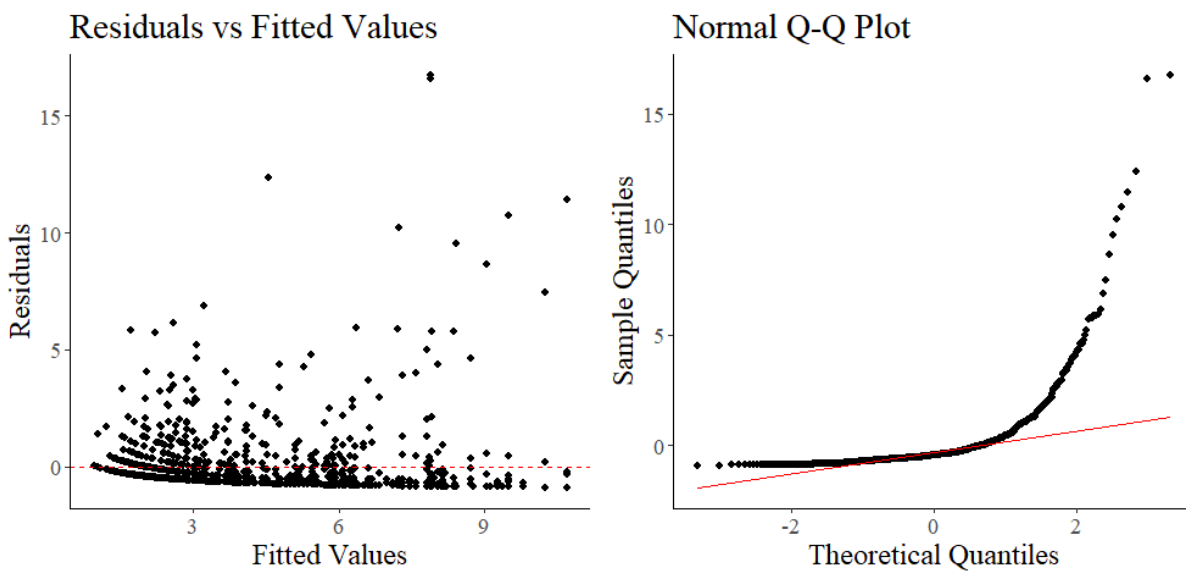


Figure S20: QQ plot and heteroscedasticity diagnostic plots for indicator species for both sample years (2021-2022) generalized linear mixed effects models.

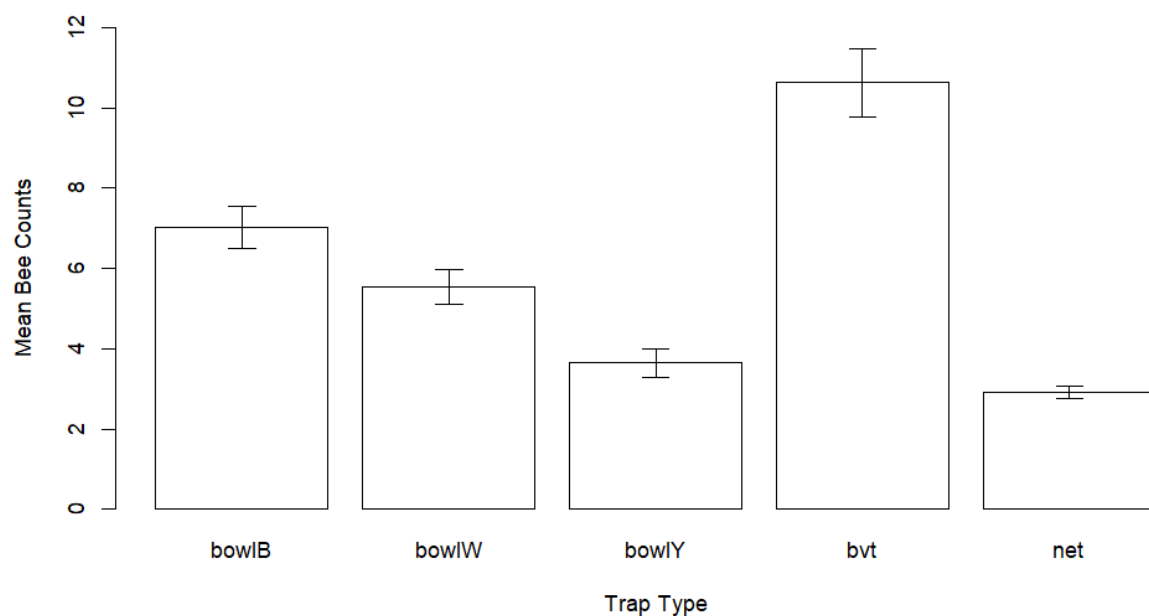


Figure S21: Passive and active trap types effects on mean bee abundance for 2021 and 2022.

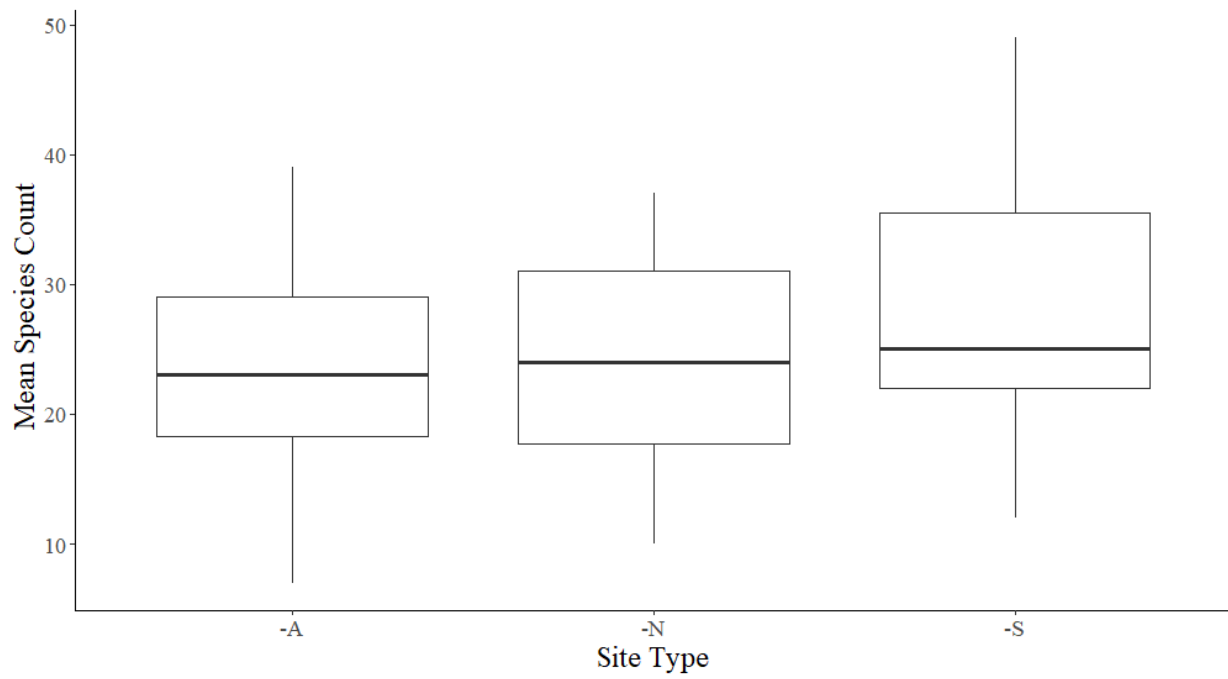


Figure S22: Mean species diversity across the site types for 2021 and 2022 (n=36).

Tables:

Table S1: Site location coordinates and sample dates for 2021 and 2022 sampling season (May-August).

Site Locations				Sample Dates			
	Latitude	Longitude	Type	Cluster	Sample Round	Year	
TGP						2021	2022
Cluster 1	49.133	-97.033	Ag	1	Round 1	10/06/2021	24/06/2022
	49.133	-96.854	Semi-Natural	1	Round 2	13/07/2021	21/07/2022
	49.133	-96.741	Natural	1	Round 3	12/08/2021	15/08/2022
Cluster 2	49.148	-96.562	Ag	2	Round 1	14/06/2021	23/06/2022
	49.111	-96.562	Semi-Natural	2	Round 2	14/07/2021	20/07/2022
	49.059	-96.558	Natural	2	Round 3	13/08/2021	12/08/2022
Cluster 3	49.34	-96.714	Ag	3	Round 1	15/06/2021	22/06/2022
	49.296	-96.713	Semi-Natural	3	Round 2	15/07/2021	18/07/2022
	49.245	-96.691	Natural	3	Round 3	19/08/2021	11/08/2022
Lake of the Woods							
Cluster 4	49.067	-95.98	Ag	4	Round 1	09/06/2021	17/06/2022
	49.109	-95.979	Semi-Natural	4	Round 2	07/07/2021	14/07/2022
	49.161	-95.979	Natural	4	Round 3	11/08/2021	10/08/2022
Cluster 5	49.311	-95.968	Ag	5	Round 1	08/06/2021	10/06/2022
	49.311	-96.058	Semi-Natural	5	Round 2	06/07/2021	13/07/2022
	49.302	-95.849	Natural	5	Round 3	10/08/2021	08/08/2022
Cluster 6	49.502	-96.511	Ag	6	Round 1	07/06/2021	09/06/2022
	49.517	-96.42	Semi-Natural	6	Round 2	05/07/2021	12/07/2022
	49.528	-96.359	Natural	6	Round 3	06/08/2021	05/08/2022
Whiteshell							
Cluster 7	49.752	-96.662	Ag	7	Round 1	02/06/2021	08/06/2022
	49.752	-96.57	Semi-Natural	7	Round 2	30/06/2021	08/07/2022
	49.766	-96.399	Natural	7	Round 3	05/08/2021	04/08/2022
Cluster 8	50.046	-96.026	Ag	8	Round 1	01/06/2021	07/06/2022
	50.112	-96.039	Semi-Natural	8	Round 2	29/06/2021	07/07/2022
	50.149	-95.93	Natural	8	Round 3	04/08/2021	03/08/2022
Cluster 9	50.297	-96.236	Ag	9	Round 1	31/05/2021	06/06/2022
	50.325	-96.214	Semi-Natural	9	Round 2	28/06/2021	05/07/2022
	50.36	-96.215	Natural	9	Round 3	03/08/2021	29/07/2022
Spruce Woods							
Cluster 10	49.856	-99.349	Ag	10	Round 1	22/07/2021	29/06/2022
	49.812	-99.348	Semi-Natural	10	Round 2	24/06/2021	27/07/2022
	49.775	-99.339	Natural	10	Round 3	25/08/2021	19/08/2022
Cluster 11	49.62	-98.915	Ag	11	Round 1	22/06/2021	27/06/2022
	49.649	-98.938	Semi-Natural	11	Round 2	19/07/2021	22/07/2022

Cluster 12	49.678	-98.935	Natural	11	Round 3	23/08/2021	16/08/2022
	49.547	-99.302	Ag	12	Round 1	23/06/2021	28/06/2022
	49.591	-99.302	Semi-Natural	12	Round 2	21/07/2021	25/07/2022
	49.621	-99.257	Natural	12	Round 3	24/08/2021	17/08/2022

Table S2: Bees species (Family, Genus, Subgenus, Species, Author) and counts by trap type (Bee Bowl, Blue Vane Trap, Aerial Netting) for 2021 and 2022.

Genus	Subgenus	Author	Bee Bowl	BVT	Net	Grand Total
Andrenidae			323	66	97	486
<i>Andrena</i>			90	34	72	196
<i>barbilabris</i>	(<i>Leucandrena</i>)	(Kirby 1802)	2		1	3
<i>canadensis</i>	(<i>Cnemidandrena</i>)	(Dalla Torre 1896)		1	1	2
<i>chromotricha</i>	(<i>Cnemidandrena</i>)	Cockerell 1899			1	1
<i>commoda</i>	(<i>Melandrena</i>)	Smith 1879	1	3		4
<i>cressonii</i>	(<i>Holandrena</i>)	Robertson 1891			1	1
<i>cyanophila</i>	(<i>Trachandrena</i>)	Cockerell 1906	30	9	1	40
<i>dunningi</i>	(<i>Melandrena</i>)	Cockerell 1898			2	2
<i>erythrogaster</i>	(<i>Melandrena</i>)	(Ashmead 1890)	2			2
<i>helianthi</i>	(<i>Callendrena s.l.</i>)	Robertson 1891			1	1
<i>lupinorum</i>	(<i>Melandrena</i>)	Cockerell 1906	46	17	15	78
<i>melanochroa</i>	(<i>Micrandrena</i>)	Cockerell 1898	1			1
<i>miranda</i>	(<i>Trachandrena</i>)	Smith 1879	1	1		2
<i>miserabilis</i>	(<i>Larandrena</i>)	Cresson 1872	1		1	2
<i>nivalis</i>	(<i>Melandrena</i>)	Smith 1853	4		10	14
<i>nubecula</i>	(<i>Micrandrena</i>)	Smith 1853			1	1
<i>persimulata</i>	(<i>Gonandrena</i>)	Viereck 1917	2		10	12
<i>rufosignata</i>	(<i>Andrena</i>)	Cockerell, 1902			3	3
<i>thaspiae</i>	(<i>Andrena</i>)	Graenicher 1903		1	3	4
<i>vicina</i>	(<i>Melandrena</i>)	Smith 1853			2	2
<i>wilkella</i>	(<i>Taeniandrena</i>)	(Kirby 1802)		2	10	12
<i>w-scripta</i>	(<i>Thysandrena</i>)	Viereck 1904			1	1
<i>ziziae</i>	(<i>Micrandrena</i>)	Robertson 1891			8	8
<i>Calliopsis</i>			25			25
<i>andreniformis</i>	(<i>Calliopsis</i>)	Smith 1853	25			25
<i>Perdita</i>			207	28	23	258

<i>albipennis</i>	(<i>Cockerellia</i>)	Crawford 1912	28	2	16	46
<i>perpallida</i>	(<i>Perdita</i>)	Cockerell 1901	23	19	7	49
<i>swenkii</i>	(<i>Perdita</i>)	Crawford 1915	156	7		163
<i>Protandrena</i>			1	4	1	6
<i>perlaevis</i>	(<i>Pterosarus</i>)	(Cockerell 1896b)	1	4	1	6
Apidae			513	2263	769	3545
<i>Anthophora</i>			31	679	45	755
<i>bomboides</i>	(<i>Melea</i>)	Kirby 1837		12	2	14
<i>occidentalis</i>	(<i>Melea</i>)	Cresson 1896	11	333	5	349
<i>terminalis</i>	(<i>Clisodon</i>)	Cresson 1896	20	334	38	392
<i>Apis</i>			9	26	52	87
<i>mellifera</i>		Linnaeus 1758	9	26	52	87
<i>Bombus</i>			90	281	444	815
<i>bimaculatus</i>	(<i>Pyrobombus</i>)	Cresson 1863		4	4	8
<i>borealis</i>	(<i>Subterraneobombus</i>)	Kirby 1837	12	97	36	145
<i>citrinus</i>	(<i>Psithyrus</i>)	(Smith 1854)		4		4
<i>fervidus</i>	(<i>Thoracobombus</i>)	(Fabricius 1798)	4	24	6	34
<i>flavidus</i>	(<i>Psithyrus</i>)	(Franklin 1911)			2	2
<i>flavifrons</i>	(<i>Pyrobombus</i>)	Cresson 1863	1			1
<i>frigidus</i>	(<i>Pyrobombus</i>)	Smith 1854		1		1
<i>griseocollis</i>	(<i>Cullumanobombus</i>)	(DeGeer 1773)	11	2	25	38
<i>insularis</i>	(<i>Psithyrus</i>)	(Smith 1861)		2		2
<i>melanopygus</i>	(<i>Pyrobombus</i>)	Nylander 1848		2	3	5
<i>perplexus</i>	(<i>Pyrobombus</i>)	Cresson 1863			8	8
<i>rufocinctus</i>	(<i>Cullumanobombus</i>)	Cresson 1863	5	11	23	39
<i>sandersoni</i>	(<i>Pyrobombus</i>)	Franklin 1913	1		15	16
<i>ternarius</i>	(<i>Pyrobombus</i>)	Say 1837	41	110	209	360
<i>terricola</i>	(<i>Bombus</i>)	Kirby 1837	2	2	9	13
<i>vagans</i>	(<i>Pyrobombus</i>)	Smith 1854	13	22	104	139
<i>Ceratina</i>			114	26	57	197
<i>calcarata</i>	(<i>Zadontomerus</i>)	Robertson 1900	2		1	3
<i>dupla</i>	(<i>Zadontomerus</i>)	Say 1837	23	14	10	47

<i>mikmaqi</i>	(<i>Zadontomerus</i>)	Rehan & Sheffield 2011	89	12	46	147
<i>Epeoloides</i>			2		2	4
<i>pilosulus</i>		(Cressson 1878)	2		2	4
<i>Epeolus</i>			3		3	6
<i>minimus</i>		(Robertson 1902)	3		2	5
<i>scutellaris</i>		(Say 1824)			1	1
<i>Eucera</i>				5		5
<i>atriventris</i>		(Smith 1854)		5		5
<i>Melissodes</i>			236	1242	149	1627
<i>agilis</i>	(<i>Eumelissodes</i>)	Cresson 1878	115	809	58	982
<i>bimaculatus</i>	(<i>Melissodes</i>)			1		1
<i>confusus</i>	(<i>Eumelissodes</i>)	Cresson 1878	54	90	20	164
<i>druriellus</i>	(<i>Eumelissodes</i>)	(Kirby 1802)	12	42	5	59
<i>illatus</i>	(<i>Eumelissodes</i>)	Levell & Cockerell 1906	3		2	5
<i>microstrictus</i>			2			2
<i>pallidisignatus</i>	(<i>Eumelissodes</i>)	Cockerell 1905		6	3	9
<i>subillatus</i>	(<i>Eumelissodes</i>)	LaBerge 1961		2	1	3
<i>trinodis</i>	(<i>Eumelissodes</i>)	Robertson 1901	45	286	58	389
<i>wheeleri</i>	(<i>Eumelissodes</i>)	Cockerell 1906	5	6	2	13
<i>Nomada</i>			22	3	15	40
<i>alpha</i>		Cockerell 1905	1			1
<i>articulata</i>		Smith 1854	1	1	1	3
<i>australis</i>		Mitchell 1962		1	1	2
<i>crawfordi</i>		Cockerell 1905			1	1
<i>cressonii</i>		Robertson 1893	1		1	2
<i>denticulata</i>		Robertson 1902			1	1
<i>florilega</i>		Lovell & Cockerell 1905	3	1	1	5
<i>imbricata</i>		Smith 1854	1			1
<i>integerrima</i>		Dalla Torre 1896	2			2
<i>lehighensis</i>		Cockerell 1903	4		2	6
<i>maculata</i>		Cresson 1863			2	2

<i>obliterata</i>		Cresson 1863	7		7
<i>quadrimaculata</i>		Robertson 1903	1	1	2
<i>sayi</i>		Robertson 1893	1	3	4
<i>vincta</i>		Say 1837		1	1
<i>Triepeolus</i>			6	1	9
<i>grindeliae</i>		Cockerell 1907	1		1
<i>helianthi</i>		(Robertson 1897)	1	1	2
<i>michiganensis</i>		Mitchell 1962		1	1
<i>obliteratus</i>		Graenicher 1911	3		3
<i>pectoralis</i>		(Robertson 1897)	1	1	2
Colletidae			92	12	186
<i>Colletes</i>			13	8	48
<i>hyalinus</i>		Provancher 1888	1	6	7
<i>kincaidii</i>		Cockerell 1898	10	8	29
<i>susannae</i>		Swenk 1925	2	10	12
<i>Hylaeus</i>			79	4	138
<i>affinis</i>	(<i>Hylaeus</i>)	(Smith 1853)	55	28	83
<i>annulatus</i>	(<i>Hylaeus</i>)	(Linnaeus 1758)	3	5	10
<i>fedorica</i>	(<i>Hylaeus</i>)	(Cockerell 1896)		1	1
<i>gaigei</i>	(<i>Prosopis</i>)	(Cockerell 1916)	1	1	3
<i>illinoensis</i>	(<i>Prosopis</i>)	(Robertson 1896)		1	1
<i>leptocephalus</i>	(<i>Hylaeus</i>)	(Morawitz 1871)	1	1	2
<i>mesillae</i>	(<i>Hylaeus</i>)	(Cockerell 1896)	10	1	23
<i>modestus</i>	(<i>Prosopis</i>)	Say 1837	2	1	3
<i>modestus group</i>	(<i>Prosopis</i>)	Say 1837	4	2	6
<i>nelumbonis</i>	(<i>Prosopis</i>)	(Robertson 1890)	2	1	3
<i>saniculae</i>	(<i>Hylaeus</i>)	(Robertson 1896)		1	1
<i>species A</i>	(<i>Prosopis</i>)		1		1
<i>verticalis</i>	(<i>Hylaeus</i>)	(Cresson 1869)		1	1
Halictidae			2647	1072	4063
<i>Agapostemon</i>			413	229	659
<i>sericeus</i>	(<i>Agapostemon</i>)	(Forster 1771)	86	15	104

<i>splendens</i>	(<i>Agapostemon</i>)	(Lepeletier 1841)	88	10	5	103
<i>subtilior</i>	(<i>Agapostemon</i>)	Cresson 1872	227	196	9	432
<i>virescens</i>	(<i>Agapostemon</i>)	(Fabricius 1775)	12	8		20
<i>Augochlorella</i>			70	2	41	113
<i>aurata</i>		(Smith 1853)	70	2	41	113
<i>Dufourea</i>			3	1	5	9
<i>harveyi</i>		(Cockerell 1906)	3		5	8
<i>maura</i>		(Cresson 1878)		1		1
<i>Halictus</i>			747	184	29	960
<i>confusus</i>		Smith 1853	709	47	19	775
<i>ligatus</i>		Say 1837	1		1	2
<i>parallelus</i>		Say 1837	2	26	1	29
<i>rubicundus</i>		(Christ 1791)	68	113	11	192
<i>Lasioglossum</i>			1396	656	248	2300
<i>abanci</i>	(<i>Dialictus</i>)	(Crawford 1932)	2		3	5
<i>absimile</i>	(<i>Dialictus</i>)	(Sandhouse 1924)	29	4	2	35
<i>admirandum</i>	(<i>Dialictus</i>)	(Sandhouse 1924)	11		1	12
<i>albipenne</i>	(<i>Dialictus</i>)	(Robertson 1890)	54	53	3	110
<i>athabascense</i>	(<i>Lasioglossum</i>)	(Sandhouse 1933)		1	1	2
<i>cinctipes</i>	(<i>Evylaeus</i>)	(Provancher 1888)	2	2	1	5
<i>coriaceum</i>	(<i>Lasioglossum</i>)	(Smith 1853)	55	17	14	86
<i>coeruleum</i>	(<i>Dialictus</i>)	(Robertson 1893)	2	1		3
<i>cressonii</i>	(<i>Dialictus</i>)	(Robertson 1890)	13		2	15
<i>ellisiae</i>	(<i>Dialictus</i>)	(Sandhouse 1924)	5		1	6
<i>imitatum</i>	(<i>Dialictus</i>)	(Smith 1853)		1		1
<i>inconditum</i>	(<i>Hemihalictus</i>)	(Cockerell 1916)	3		1	4
<i>laevissimum</i>	(<i>Dialictus</i>)	(Smith 1853)	21	4	9	34
<i>leucocomus</i>	(<i>Dialictus</i>)	(Lovell 1908)	98	10	9	117
<i>leucozonium</i>	(<i>Leuchalictus</i>)	(Schrank 1781)	85	29	41	155
<i>lineatulum</i>	(<i>Dialictus</i>)	(Crawford 1906)	24	1	4	29
<i>macoupinense</i>	(<i>Hemihalictus</i>)	(Robertson 1895)	5	1	1	7
<i>nigroviride</i>	(<i>Dialictus</i>)	(Graenicher 1911)	3		15	18

<i>novascotiae</i>	(<i>Dialictus</i>)	(Mitchell 1960)	58	114	16	188
<i>oblongum</i>	(<i>Dialictus</i>)	(Lovell 1905)	10	1	5	16
<i>occidentale</i>	(<i>Dialictus</i>)	(Crawford 1902)	15	2		17
<i>paraforbesii</i>	(<i>Lasioglossum</i>)	McGinley 1986	99	88	9	196
<i>pectorale</i>	(<i>Hemihalictus</i>)	(Smith 1853)	23		3	26
<i>perpunctatum</i>	(<i>Dialictus</i>)	(Ellis 1913)	63	19	35	117
<i>pictum</i>	(<i>Dialictus</i>)	(Crawford 1902)	58	1	4	63
<i>pilosum</i>	(<i>Dialictus</i>)	(Smith 1853)	245	67	26	338
<i>planatum</i>	(<i>Dialictus</i>)	(Lovell 1905)	7		2	9
<i>pruinatum</i>	(<i>Dialictus</i>)	(Robertson 1892)	1	1		2
<i>quebecense</i>	(<i>Sphecodogastra</i>)	(Crawford 1907)	1	1	1	3
<i>sagax</i>	(<i>Dialictus</i>)	(Sandhouse 1924)	16	6	4	26
<i>semicaeruleum</i>	(<i>Dialictus</i>)	(Cockerell 1895)	40	11	2	53
<i>subversans</i>	(<i>Dialictus</i>)	(Mitchell 1960)	11			11
<i>subviridatum</i>	(<i>Dialictus</i>)	(Cockerell 1938)	4	1	3	8
<i>timothyi</i>	(<i>Dialictus</i>)	Gibbs 2010	6	1		7
<i>truncatum</i>	(<i>Sphecodogastra</i>)	(Robertson 1901)	1	1	1	3
<i>versans</i>	(<i>Dialictus</i>)	(Lovell 1905)	2		3	5
<i>versatum</i>	(<i>Dialictus</i>)	(Robertson 1902)	4	2		6
<i>vierecki</i>	(<i>Dialictus</i>)	(Crawford 1904)	87		1	88
<i>viridatum</i>	(<i>Dialictus</i>)	(Lovell 1905)	103	30	16	149
<i>zonulus</i>	(<i>Leuchalictus</i>)	(Smith 1848)	111	199	9	319
<i>Sphecodes</i>			18		4	22
<i>atlantis</i>		Mitchell 1956	3			3
<i>banksii</i>		Lovell 1909	2		1	3
<i>clematidis</i>		Robertson 1897			1	1
<i>confertus</i>		Say 1837	1			1
<i>coronus</i>		Mitchell 1956	7			7
<i>dichrous</i>		Smith 1853	3			3
<i>illinoensis</i>		(Robertson 1903)	1			1
<i>mandibularis</i>		Cresson 1872	1			1
<i>pecosensis</i>		Cockerell 1904			2	2

Megachilidae			208	93	166	467
<i>Anthidium</i>				1		1
<i>tenuiflorae</i>	(<i>Anthidium</i>)	Cockerell 1907		1		1
<i>Ashmeadiella</i>			3	1	1	5
<i>bucconis</i>	(<i>Ashmeadiella</i>)	(Say 1837)	3	1	1	5
<i>Coelioxys</i>			1	1	3	5
<i>editus</i>	(<i>Xerocoelioxys</i>)	Cresson 1872	1			1
<i>rufitarsis</i>	(<i>Boreocoelioxys</i>)	Smith 1854		1	3	4
<i>Dianthidium</i>			1	1		2
<i>simile</i>	(<i>Dianthidium</i>)	(Cresson 1864)	1	1		2
<i>Heriades</i>			2	12	9	23
<i>carinata</i>	(<i>Neotrypetes</i>)	Cresson 1864	2	9	9	20
<i>variola</i>	(<i>Neotrypetes</i>)	(Cresson 1872)		3		3
<i>Hoplitis</i>			109	37	44	190
<i>albifrons</i>	(<i>Alcidamea</i>)	(Kirby 1837)	1	2	1	4
<i>pilosifrons</i>	(<i>Alcidamea</i>)	(Cresson 1864)	51	31	14	96
<i>producta</i>	(<i>Alcidamea</i>)	(Cresson 1864)	41	3	23	67
<i>robusta</i>	(<i>Formicapis</i>)	(Nylander 1848)			1	1
<i>spoliata</i>	(<i>Alcidamea</i>)	(Provancher 1888)	12	1	4	17
<i>truncata</i>	(<i>Alcidamea</i>)	(Cresson 1878)	4		1	5
<i>Megachile</i>			53	17	92	162
<i>brevis</i>	(<i>Litomegachile</i>)	Say 1837	2		2	4
<i>campanulae</i>	(<i>Chelostomoides</i>)	(Robertson 1903)	3		2	5
<i>centuncularis</i>	(<i>Megachile</i>)	(Linnaeus 1758)			1	1
<i>circumcincta</i>	(<i>Xanthosarus</i>)	(Kirby 1802)	1			1
<i>inermis</i>	(<i>Megachile</i>)	Provancher 1888	18	5	23	46
<i>latimanus</i>	(<i>Xanthosarus</i>)	Say 1823	8	8	25	41
<i>melanophaea</i>	(<i>Xanthosarus</i>)	Smith 1853	3	2	3	8
<i>montivaga</i>	(<i>Megachile</i>)	Cresson 1878	1		2	3
<i>pugnata</i>	(<i>Sayapis</i>)	Say 1837	1		3	4
<i>relativa</i>	(<i>Megachile</i>)	Cresson 1878	9		29	38
<i>rotundata</i>	(<i>Eutricharaea</i>)	(Fabricius 1787)	1	1		2

<i>texana</i>	(<i>Litomegachile</i>)	Cresson 1878	1			1
<i>Osmia</i>			38	23	15	76
<i>atriventris</i>	(<i>Melanosmia</i>)	Cresson 1864	9	5	7	21
<i>distincta</i>	(<i>Melanosmia</i>)	Cresson 1864	2		1	3
<i>inermis</i>	(<i>Melanosmia</i>)	(Zetterstedt 1838)			1	1
<i>laticeps</i>	(<i>Melanosmia</i>)	Thomson 1872	1	3	1	5
<i>nigriventris</i>	(<i>Melanosmia</i>)	(Zetterstedt 1838)	10	3	3	16
<i>proxima</i>	(<i>Melanosmia</i>)	Cresson 1864	1			1
<i>simillima</i>	(<i>Melanosmia</i>)	Smith 1853	15	3	4	22
<i>tersula</i>	(<i>Melanosmia</i>)	Cockerell 1912	5	10		15
<i>Stelis</i>			1		2	3
<i>foederalis</i>	(<i>Stelis</i>)	Smith 1854			1	1
<i>labiata</i>	(<i>Stelis</i>)	(Provancher 1888)	1			1
<i>lateralis</i>	(<i>Stelis</i>)	Cresson 1864			1	1
Melittidae					3	3
<i>Macropis</i>					3	3
<i>nuda</i>	(<i>Macropis</i>)	(Provancher 1882)			3	3
Grand Total			3797	3521	1463	8781

Table S3: Number of species per ecoregion and site type for 2021 and 2022(n=36).

Site	Year	Ecoregion	Number of Species	Site Type	Year	Ecoregion	Number of Species	Site Type
1-A	2021	Tall Grass Prairie	15	A	2022	Tall Grass Prairie	15	A
1-N	2021	Tall Grass Prairie	17	N	2022	Tall Grass Prairie	17	N
1-S	2021	Tall Grass Prairie	29	S	2022	Tall Grass Prairie	23	S
10-A	2021	Assiniboine Delta	24	A	2022	Assiniboine Delta	7	A
10-N	2021	Assiniboine Delta	31	N	2022	Assiniboine Delta	24	N
10-S	2021	Assiniboine Delta	20	S	2022	Assiniboine Delta	13	S
11-A	2021	Assiniboine Delta	32	A	2022	Assiniboine Delta	37	A
11-N	2021	Assiniboine Delta	23	N	2022	Assiniboine Delta	37	N
11-S	2021	Assiniboine Delta	42	S	2022	Assiniboine Delta	43	S
12-A	2021	Assiniboine Delta	13	A	2022	Assiniboine Delta	21	A
12-N	2021	Assiniboine Delta	27	N	2022	Assiniboine Delta	36	N
12-S	2021	Assiniboine Delta	35	S	2022	Assiniboine Delta	42	S
2-A	2021	Tall Grass Prairie	26	A	2022	Tall Grass Prairie	28	A
2-N	2021	Tall Grass Prairie	32	N	2022	Tall Grass Prairie	24	N
2-S	2021	Tall Grass Prairie	49	S	2022	Tall Grass Prairie	24	S
3-A	2021	Tall Grass Prairie	27	A	2022	Tall Grass Prairie	22	A
3-N	2021	Tall Grass Prairie	27	N	2022	Tall Grass Prairie	10	N
3-S	2021	Tall Grass Prairie	25	S	2022	Tall Grass Prairie	12	S
4-A	2021	Lake of the Woods	29	A	2022	Lake of the Woods	16	A
4-N	2021	Lake of the Woods	25	N	2022	Lake of the Woods	23	N
4-S	2021	Lake of the Woods	25	S	2022	Lake of the Woods	25	S
5-A	2021	Lake of the Woods	30	A	2022	Lake of the Woods	39	A
5-N	2021	Lake of the Woods	24	N	2022	Lake of the Woods	29	N
5-S	2021	Lake of the Woods	22	S	2022	Lake of the Woods	16	S
6-A	2021	Lake of the Woods	23	A	2022	Lake of the Woods	20	A
6-N	2021	Lake of the Woods	31	N	2022	Lake of the Woods	17	N
6-S	2021	Lake of the Woods	38	S	2022	Lake of the Woods	27	S
7-A	2021	Precambrian Boreal	19	A	2022	Precambrian Boreal	7	A
7-N	2021	Precambrian Boreal	20	N	2022	Precambrian Boreal	17	N

7-S	2021	Precambrian Boreal	22	S	2022	Precambrian Boreal	15	S
8-A	2021	Precambrian Boreal	23	A	2022	Precambrian Boreal	21	A
8-N	2021	Precambrian Boreal	16	N	2022	Precambrian Boreal	18	N
8-S	2021	Precambrian Boreal	29	S	2022	Precambrian Boreal	37	S
9-A	2021	Precambrian Boreal	32	A	2022	Precambrian Boreal	29	A
9-N	2021	Precambrian Boreal	34	N	2022	Precambrian Boreal	31	N
9-S	2021	Precambrian Boreal	30	S	2022	Precambrian Boreal	24	S

Table S4: Landscape Metrics measured at the 1500m buffer size for 2021 and 2022 across 36 sites in Southern Manitoba.

Landscape Metrics			
Diversity Metric	Equation	Heterogeneity Measured	Description
Shannon Diversity Index	$SHDI = - \sum_{i=1}^m (P_i * \ln P_i)$	Compositional Heterogeneity	Takes the proportionate abundance of each class of landscape type and the number of classes found in the landscape to create a diversity metric.
Edge Density	$ED = \frac{E}{A} * 10000$	Compositional Heterogeneity	Represents all the edges found in the landscape. Each patch will have a measure of edge as metres per hectare.
Mean of Patch Area	$AREA_{MN} = mean(AREA[patch_{ij}])$	Compositional Heterogeneity	Creates a summary of the landscape by taking the mean of the patch area in the landscape.
Aggregation Index	$AI = \left[\sum_{i=1}^m \left(\frac{g_{ii}}{max - g_{ii}} \right) P_i \right] (100)$	Configurational Heterogeneity	Takes the actual number of classes that are found adjacent in the landscape divided by the theoretical number of like adjacencies for each class, summed over each class for the whole landscape.
Cohesion Index	$COHESION = 1 - \left(\frac{\sum_{i=1}^m \sum_{j=1}^n p_{ij}}{\sum_{i=1}^m \sum_{j=1}^n p_{ij} \sqrt{a_{ij}}} \right) * \left(1 - \frac{1}{\sqrt{Z}} \right)^{-1} * 100$	Configurational Heterogeneity	Measures the connectivity in the landscape of the same patch type.
Mean Shape Index	$SHAPE_{MN} = mean(SHAPE[patch_{ij}])$	Configurational Heterogeneity	Describes the complexity of the patch shapes in the landscape, taking the perimeter of patches comparing to the square root of the patch area creating a ratio.

Table S5: Indicator species determined for ecoregion groupings, site types, and site groupings for 2021 and 2022 bee species caught in roadside verges at Southern Manitoba sites, across 36 sample sites sampled three times per year. Life history information included to determine defining traits of each species. ($\alpha=0.05$).

Species	Grouping	Indicator Value(IV)	p-value	Year	Grouping Type	Sociality	Nesting	Lecty
<i>Andrena cyanophila</i>	Tall Grass Prairie	0.658	0.026	2021	Ecoregion	Solitary	Ground	Polylectic
<i>Lasioglossum subversans</i>	Lake of the Woods	0.632	0.028	2021	Ecoregion	Eusocial	Ground	Polylectic
<i>Halictus rubicundus</i>	Precambrian Boreal	0.766	0.003	2021	Ecoregion	Eusocial	Ground	Polylectic
<i>Bombus griseocollis</i>	Tall Grass Prairie and Assiniboine Delta	0.69	0.02	2021	Ecoregion	Eusocial	Hive	Polylectic
<i>Bombus vagans</i>	Assiniboine Delta and Lake of the Woods	0.822	0.007	2021	Ecoregion	Eusocial	Hive	Polylectic
<i>Ceratina dupla</i>	Lake of the Woods and Precambrian Boreal	0.748	0.018	2021	Ecoregion	Subsocial	Stem	Polylectic
<i>Lasioglossum novascotiae</i>	Precambrian Boreal	0.713	0.027	2021	Ecoregion	Eusocial	Ground	Polylectic
<i>Halictus confusus</i>	Precambrian Boreal	0.904	0.016	2022	Ecoregion	Eusocial	Ground	Polylectic
<i>Lasioglossum cressonii</i>	Precambrian Boreal	0.645	0.01	2022	Ecoregion	Eusocial	Wood	Polylectic
<i>Lasioglossum leucocomus</i>	Tall Grass Prairie and Assiniboine Delta	0.684	0.047	2022	Ecoregion	Eusocial	Ground	Polylectic
<i>Lasioglossum semicaeruleum</i>	Tall Grass Prairie and Assiniboine Delta	0.657	0.05	2022	Ecoregion	Eusocial	Ground	Polylectic
<i>Halictus rubicundus</i>	Lake of the Woods and Precambrian Boreal	0.729	0.026	2022	Ecoregion	Eusocial	Ground	Polylectic
<i>Lasioglossum novascotiae</i>	Precambrian Boreal	0.694	0.013	2022	Ecoregion	Eusocial	Ground	Polylectic
<i>Agapostemon splendens</i>	Ag	0.707	0.004	2021	Site Type	Solitary	Ground	Polylectic
<i>Lasioglossum leucocomus</i>	Ag	0.706	0.002	2021	Site Type	Eusocial	Ground	Polylectic
<i>Lasioglossum paraforbesii</i>	Ag	0.681	0.019	2021	Site Type	Solitary	Ground	Polylectic

<i>Andrena cyanophila</i>	Ag	0.645	0.009	2021	Site Type	Solitary	Ground	Polylectic
<i>Lasioglossum pictum</i>	Ag	0.645	0.011	2021	Site Type	Eusocial	Ground	Polylectic
<i>Andrena lupinorum</i>	Ag	0.63	0.029	2021	Site Type	Solitary	Ground	Oligolectic
<i>Agapostemon sericeus</i>	Ag	0.619	0.02	2021	Site Type	Solitary	Ground	Polylectic
<i>Bombus vagans</i>	Natural	0.805	0.006	2021	Site Type	Eusocial Subsocial	Hive	Polylectic
<i>Ceratina dupla</i>	Semi-natural	0.799	0.001	2021	Site Type	1	Stem	Polylectic
<i>Halictus rubicundus</i>	Semi-natural	0.729	0.005	2021	Site Type	Eusocial	Ground	Polylectic
<i>Melissodes agilis</i>	Ag and Natural	0.88	0.01	2021	Site Type	Solitary	Ground	Oligolectic
<i>Melissodes trinodis</i>	Ag and Natural	0.848	0.009	2021	Site Type	Solitary	Ground	Oligolectic
<i>Bombus griseocollis</i>	Ag and Natural	0.645	0.03	2021	Site Type	Eusocial	Hive	Polylectic
<i>Halictus confusus</i>	Natural and Semi-natural	0.878	0.014	2021	Site Type	Eusocial Subsocial	Ground	Polylectic
<i>Ceratina mikmaqi</i>	Natural and Semi-natural	0.862	0.009	2021	Site Type	1	Stem	Polylectic
<i>Hoplitis pilosifrons</i>	Natural and Semi-natural	0.77	0.043	2021	Site Type	Solitary	Stem	Polylectic
<i>Lasioglossum novascotiae</i>	Natural and Semi-natural	0.704	0.01	2021	Site Type	Eusocial	Ground	Polylectic
<i>Augochlorella aurata</i>	Natural and Semi-natural	0.701	0.029	2021	Site Type	Eusocial	Ground	Polylectic
<i>Hoplitis producta</i>	Natural and Semi-natural	0.645	0.03	2021	Site Type	Solitary	Stem	Polylectic
<i>Lasioglossum leucomus</i>	Ag	0.726	0.007	2022	Site Type	Eusocial	Ground	Polylectic
<i>Agapostemon splendens</i>	Ag	0.707	0.001	2022	Site Type	Solitary	Ground	Polylectic
<i>Lasioglossum vierecki</i>	Ag	0.645	0.006	2022	Site Type	Solitary	Ground	Polylectic
<i>Anthophora occidentalis</i>	Ag	0.645	0.008	2022	Site Type	Solitary	Ground	Polylectic
<i>Lasioglossum pictum</i>	Ag	0.636	0.011	2022	Site Type	Eusocial	Ground	Polylectic
<i>Agapostemon sericeus</i>	Ag	0.636	0.015	2022	Site Type	Solitary	Ground	Polylectic
<i>Bombus griseocollis</i>	Ag	0.618	0.05	2022	Site Type	Eusocial	Hive	Polylectic
<i>Lasioglossum pectorale</i>	Ag	0.606	0.017	2022	Site Type	Solitary	Ground	Polylectic

<i>Perdita swenkii</i>	Ag	0.603	0.008	2022	Site Type	Solitary	Ground	Oligolectic
<i>Lasioglossum pilosum</i>	Ag	0.576	0.022	2022	Site Type	Eusocial	Ground	Polylectic
<i>Halictus confusus</i>	Semi-natural	0.927	0.004	2022	Site Type	Eusocial	Ground	Polylectic
<i>Halictus rubicundus</i>	Semi-natural	0.756	0.007	2022	Site Type	Eusocial	Ground	Polylectic
<i>Lasioglossum novascotiae</i>	Semi-natural	0.655	0.028	2022	Site Type	Eusocial	Ground	Polylectic
<i>Melissodes trinodis</i>	Ag and Natural	0.786	0.042	2022	Site Type	Solitary	Ground	Oligolectic
<i>Lasioglossum viridatum</i>	Natural and Semi-natural	0.677	0.026	2022	Site Type	Eusocial	Ground	Polylectic
<i>Lasioglossum admirandum</i>	1 and 5	0.77	0.039	2021	Cluster	Eusocial	Ground	Polylectic
<i>Lasioglossum subversans</i>	7 and 8	0.775	0.044	2021	Cluster	Eusocial	Ground	Polylectic
<i>Agapostemon splendens</i>	2 and 3 and 4	0.816	0.017	2021	Cluster	Solitary Subsocial	Ground	Polylectic
<i>Ceratina dupla</i>	9 and 10 and 12	0.859	0.012	2021	Cluster	1	Stem	Polylectic
<i>Melissodes trinodis</i>	1 and 3 and 5 and 6 and 7	0.941	0.007	2021	Cluster	Solitary	Ground	Oligolectic
<i>Halictus confusus</i>	5 and 9 and 10 and 11 and 12	0.932	0.044	2021	Cluster	Eusocial	Ground	Polylectic
<i>Bombus vagans</i>	5 and 6 and 7 and 8 and 9 and 12	0.875	0.019	2021	Cluster	Eusocial	Hive	Polylectic
<i>Hoplitis pilosifrons</i>	1 and 3 and 5 and 6 and 7 and 9 and 10 and 12	0.881	0.021	2021	Cluster	Solitary	Stem	Polylectic
<i>Anthophora terminalis</i>	2 and 3 and 4 and 5 and 6 and 7 and 9 and 11	0.947	0.041	2021	Cluster	Solitary	Wood	Polylectic
<i>Agapostemon texanus</i>	2 and 3 and 4 and 5 and 6 and 8 and 9 and 10	0.952	0.04	2021	Cluster	Solitary	Ground	Polylectic
<i>Anthophora occidentalis</i>	3	0.887	0.005	2022	Cluster	Solitary	Ground	Polylectic
<i>Lasioglossum pilosum</i>	3 and 4	0.815	0.019	2022	Cluster	Eusocial	Ground	Polylectic
<i>Agapostemon sericeus</i>	3 and 4	0.798	0.042	2022	Cluster	Solitary	Ground	Polylectic
<i>Lasioglossum pictum</i>	3 and 4	0.792	0.029	2022	Cluster	Eusocial	Ground	Polylectic

<i>Lasioglossum vierecki</i>	3 and 4	0.787	0.018	2022	Cluster	Solitary	Ground	Polylectic
<i>Bombus sandersonii</i>	5 and 12	0.764	0.042	2022	Cluster	Eusocial	Hive	Polylectic
<i>Halictus rubicundus</i>	11 and 12	0.877	0.01	2022	Cluster	Eusocial	Ground	Polylectic
<i>Agapostemon texanus</i>	3 and 4 and 8	0.961	0.002	2022	Cluster	Solitary	Ground	Polylectic
<i>Lasioglossum cressonii</i>	3 and 10 and 12	0.782	0.018	2022	Cluster	Eusocial	Wood	Polylectic
	5 and 7 and 9 and 10							
<i>Lasioglossum viridatum</i>	and 11	0.805	0.024	2022	Cluster	Eusocial	Ground	Polylectic
	1 and 3 and 4 and 5 and							
<i>Apis mellifera</i>	6 and 9	0.857	0.03	2022	Cluster	Eusocial	Hive	Polylectic
	3 and 4 and 5 and 9 and							
<i>Halictus confusus</i>	11 and 12	0.989	0.002	2022	Cluster	Eusocial	Ground	Polylectic
	1 and 2 and 3 and 4 and							
<i>Melissodes agilis</i>	5 and 8 and 11 and 12	0.99	0.009	2022	Cluster	Solitary	Ground	Oligolectic
	1 and 3 and 4 and 5 and							
<i>Lasioglossum zonulum</i>	6 and 7 and 11 and 12	0.898	0.024	2022	Cluster	Solitary	Ground	Polylectic

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