

**The effects of human-driven landscape disturbance on wild bee communities
and plant-bee networks across southern Manitoba, Canada**

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ABSTRACT

Landscape disturbance caused by human activities like large-scale cropping and urbanization is one of the main drivers of wild bee declines and changes to plant-pollinator networks worldwide. Factors such as land cover diversity and fragmentation can also influence bee communities and networks, but published effects are mixed and often depend on location, community composition, and scale of disturbance. I investigated the effects of local and landscape level disturbance on bee communities and plant-bee networks across southern Manitoba, Canada, with the goal of informing policies aimed at conserving wild bee populations and network functionality. I collected 21,000 bees over two years using coloured pan traps and blue vane traps (for community analyses) and 2,189 using aerial nets (for network analyses). Using linear modelling, I found that crop cover reduced bee abundance and richness, and negatively affected network stability, indicating that greater amounts of crop cover in the landscape have widespread negative effects on both bees and networks. Conversely, fragmentation and land cover diversity benefitted bee abundance, richness, and community functional dispersion in most ecoregions, and enhanced network size and stability. This suggests that areas with greater amounts of edge, as well as a diverse array of land cover types, can benefit bees and networks. Finally, I found that the number of introduced plant species at the local scale enhanced bee community functional dispersion without negative effects on bee abundance or richness, suggesting that introduced plants in field margins help rather than hurt bee communities where native plants have been lost due to disturbance. Extensively removing introduced plant species from field margins should be reconsidered since these species help to support wild bee communities in disturbed areas. Land management policies promoting more extensive field edges and increasing land cover diversity are needed to maintain an abundant and diverse assemblage of bees and to enhance plant-bee network size and stability.

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INTRODUCTION

In this study, I examine how human-driven landscape disturbance impacts wild bee communities and plant-bee networks across southern Manitoba, Canada. My thesis is structured into four parts, starting with a literature review (Chapter one) followed by research manuscripts on bee communities (Chapter two) and plant-bee networks (Chapter three) and ending with a brief section on conclusions and implications of findings. Chapter two focuses on the effects of disturbance at the landscape-level (cropped area, urbanization, fragmentation, and habitat diversity) and local-level (vegetation structure and flower diversity) on bee abundance, richness, functional trait diversity, and community composition. I also explore how ecoregional context can influence landscape-level trends. Chapter three focuses on the impacts of landscape-level disturbance on network size, structure (nestedness, connectance, modularity), and stability, using simulated plant extinctions.

The objectives of this thesis are:

- i. Document Manitoba's bee diversity and contribute to provincial and national species records,
- ii. Understand which landscape changes most affect bee communities and networks, and
- iii. Use the findings to inform land management practices for conserving bee communities and plant-bee networks.

Using the published literature reviewed in Chapter one, I predict that bee abundance, species richness, functional dispersion, and community composition will vary along landscape-level disturbance gradients across all sites, but that effects will depend both on the type of disturbance and the broader ecoregional context. I also predict that bee communities will vary along local-level gradients of vegetation structure and floral richness. Finally, I predict that networks will change in size and structure along landscape-level disturbance gradients, and that networks will become less stable with increasing levels of disturbance.

CHAPTER 1: LITERATURE REVIEW

Part 1: Wild bee and plant-pollinator network ecology

Bees (Hymenoptera: Apoidea: Anthophila) are a monophyletic group of insects nested within the apoid wasps (Hymenoptera: Apoidea: Spheciformes) that originated approximately 123 million years ago, coinciding with the diversification of flowering plants (Cardinal and Danforth 2013). Bees underwent a change from consuming a strictly carnivorous diet of other insects to an herbivorous diet consisting of nectar and pollen (although several *Trigona* species in the tropics reverted back to carnivory, see Camargo and Roubik (1991)). Female bees in particular developed extensive, usually plumose, hairs over their body, face, and legs to facilitate pollen transfer (Michener 2007). In return for floral rewards, bees passively disperse pollen (i.e. male gametes) to intraspecific flowers, aiding in sexual reproduction of plants. This is an efficient and favoured means of gamete transfer; more than 87% of extant angiosperms globally utilize insects for sexual reproduction, the majority of which are bees (Ollerton et al. 2011). Bees are therefore a keystone group of insects responsible for maintaining angiosperm diversity and thus supporting ecosystem functioning. Part one briefly examines what is known about the ecology of wild bees and plant-pollinator networks.

Bee diversity

There are more than 20,000 bee species globally (Ascher and Pickering 2019) and over 800 in Canada (Canadian Endangered Species Conservation Council 2016). Bees are currently grouped into seven families, although only six occur in Canada: Andrenidae, Apidae, Colletidae, Halictidae, Megachilidae, and Melittidae (Michener 2007; Hedtke et al. 2013). Several European species have colonized Canada (Russo 2016). Bees exhibit a range of functional traits in terms of their social, nesting, and foraging behaviours. The collection of functional traits in the community is termed functional trait diversity.

Sociality

Bees exhibit a range of social behaviours (Michener 1974). Only about 10% of species are eusocial, in which a single fertile queen produces castes of worker daughters that provision and defend her offspring (e.g., all non-parasitic *Bombus* species and most *Halictus* species) (Danforth et al. 2019). The vast majority are solitary, meaning that a single female lays her eggs and provisions a nest that she constructs herself. Several other strategies are also considered solitary, such as communal living and subsociality. Communal living involves several females independently provisioning cells in a common nest and collectively defending the nest (such as several *Agapostemon*, *Perdita*, *Andrena*, and *Lasioglossum* species). Subsocial species, like some *Ceratina*, produce early-hatching offspring that require parental care, but lack division of labour.

Nest parasitism is a strategy evolved in most bee families (except Andrenidae and Melittidae), and refers either to the usurpation of host nests by mated parasitic females (social parasitism), or deposition of parasitic eggs in the nest of a host species (cleptoparasitism) (Michener 2007). Social parasitism occurs when the nest of a eusocial species is usurped by the parasite, which then uses the host workers to raise parasitic offspring (e.g., *Bombus* in the subgenus *Psithyrus*). Cleptoparasitism is much more common (Sheffield et al. 2014). Estimates of parasitism in Canada ranges from 10–30% of local species diversity, depending on the region (Sheffield et al. 2014).

Nesting biology

All nest-constructing bees are central place foragers, which means that they return to their nests over an extended length of time to complete nest provisioning (Michener 2007). Upwards of 70% of nest-constructing bee species build their nests directly in the ground, while the remainder nest in cavities, stems, rotting wood, and on surfaces (Michener 2007; Packer et al. 2007; Sheffield et al. 2014; Gibbs et al. 2017). Species that makes their nests directly in the ground are found in every family. Some megachilid bees in the genera *Megachile* and *Osmia* nest in tubular cavities and will partition and cap their nests with leaf material, or mud and pebbles. Bumble bees (*Bombus*, Apidae) will use larger cavities, such as rodent holes, to create their cell-partitioned hives. Species nesting in hollowed out stems are found in several families, including

Colletidae (*Hylaeus*), Apidae (*Ceratina*), and Megachilidae (*Hoplitis*, *Heriades*, and some *Megachile*). Wood nesters are rare, but can be found in several families, including Halictidae, Apidae, and Megachilidae.

Diet

Bees feed themselves and provision their nests with nectar, pollen, and occasionally floral oils collected from flowers. Ancestral bees were host-plant specialists, meaning that they visited a very narrow range of flowering plants (Danforth et al. 2006). Over time, some bees adapted to visit a wider range of plant species, and so became host-plant generalists (Murray et al. 2018). This trait is usually reserved for non-parasitic bees only, since parasitic bees do not need to provision their nest and have lost pollen-collecting structures. Many generalist bee species will visit introduced plants in addition to native species, even if native and introduced plants co-occur (Williams et al. 2011).

Phenology

Bees spend the majority of their lives in their nests as immatures or adults, and only emerge for several weeks to mate and produce offspring (Michener 2007). Emergence generally coincides with flowering of host plants, especially for specialist solitary bees (Danforth et al. 2019). Early spring bees like most *Andrena*, *Osmia*, and *Nomada* emerge as soon as the snow starts to melt, and many *Lasioglossum* species emerge shortly after. Other species emerge in early to mid-summer, such as *Melissodes* and *Megachile*. Adults of social species can survive for much longer, but usually die off at the end of the season once a new queen has been laid (Michener 2007). Emergence times of some bee species are changing as a result of climate change (Bartomeus et al. 2011), which can result in asynchrony with plant emergence and thus loss of bee-plant interactions (Memmott et al. 2007; Gilman et al. 2012; Gérard et al. 2020).

Plant-pollinator networks

The complex interactions between plant and pollinators can be mapped out into bipartite networks where each pollinator is ‘linked’ to its host plant(s). When the network consists of a focal group of pollinators, a more detailed term can be used (e.g. plant-bee networks when the

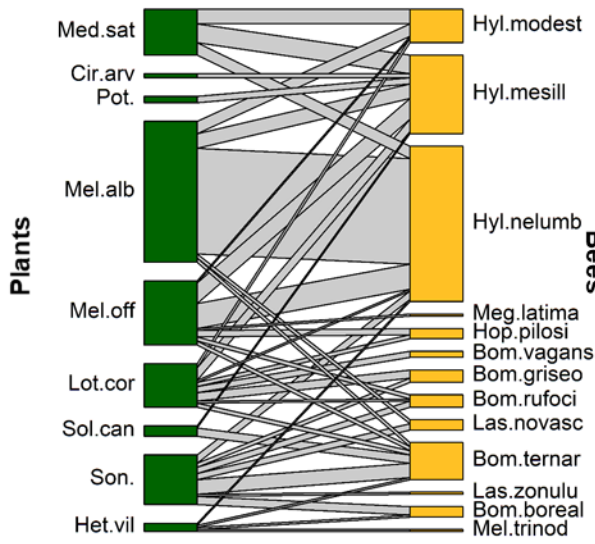
focus is on bee pollinators). Networks are described by their size (number of linked species) and structure (how links aggregate). Although there are many metrics used to describe network size and structure (Dormann et al. 2009), a few common metrics are described below.

Plant-pollinator networks are non-randomly assembled, and all share some key structural features (Bascompte and Jordano 2007). Plant-pollinator networks are formed of a nested structure in which peripheral specialist species are linked to a core of interacting generalist species (Bascompte et al. 2003) ((Next page) Fig. 1). Total specialization of one species on another, and *vice versa*, is the exception rather than the rule (Bascompte et al. 2003). Nestedness increases the number of redundant interactions in the network, which can enhance network stability against species loss (Memmott et al. 2004; Thébault and Fontaine 2010).

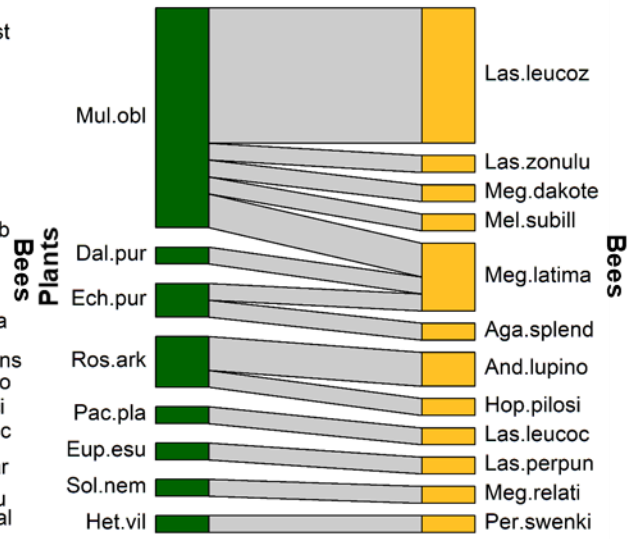
Besides nestedness, networks are described by their connectance (proportion of observed links compared to the number of possible links) and modularity (link-dense areas in the network) ((Next page) Fig. 1). Networks tend to have only 11–18% of total possible links realized (Landi et al. 2018), mainly because specialist species make up the majority of networks but rarely interact with one another. Although the two are related, connectance differs from nestedness in that it does not infer any information about the way in which species are linked as nestedness does (Bascompte et al. 2003). Most networks are modular to some degree and can contain distinct compartmentalized groups of interacting species (Olesen et al. 2007). Modularity is known to increase with network size (Olesen et al. 2007).

((Next page) Fig. 1. Examples of high and low states of connectance, modularity, and nestedness using two networks of similar sizes. For connectance, lines between boxes represent plant-bee interactions and thicker lines indicate greater interaction occurrence. For modularity and nestedness, shaded boxes represent plant-bee interactions and darker shades indicate greater interaction occurrence. Red boxes represent areas of interaction richness within the network. Orange lines represent isocline of perfect nestedness, which would occur if all interactions fell to the left-hand side of the line. Both networks were constructed using data collected in Chapter three. Network one was made using data collected at DMP1N and network two was made using data collected at SHP1D.

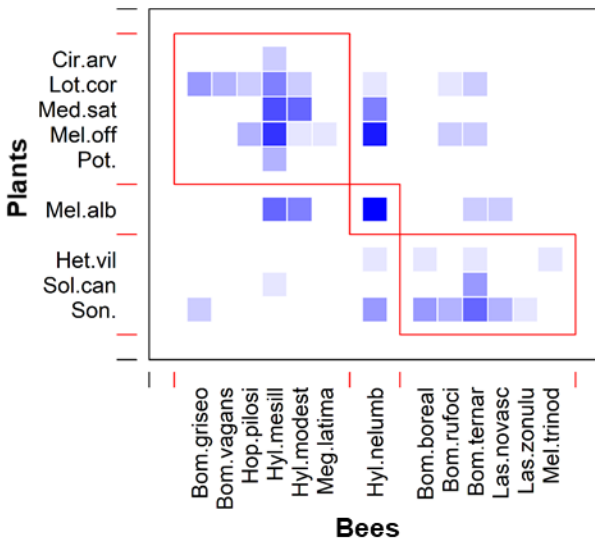
Network 1: High connectance



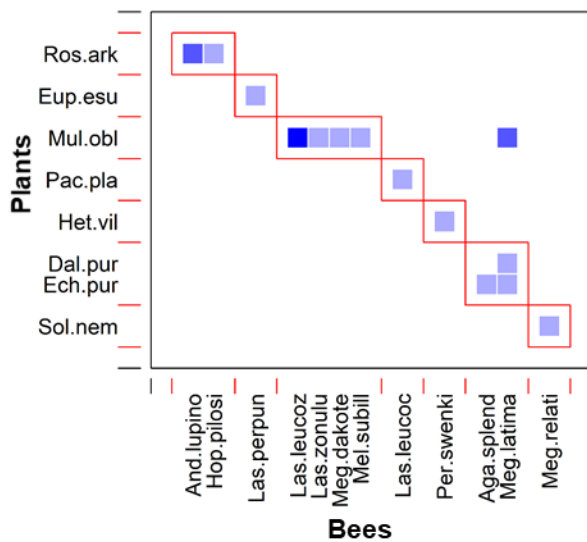
Network 2: Low connectance



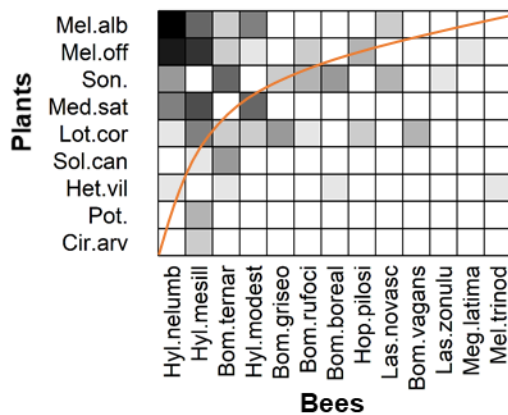
Network 1: Low modularity



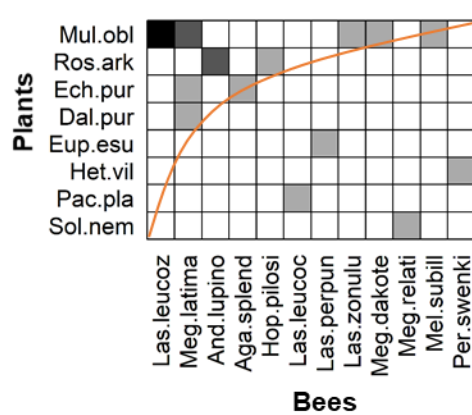
Network 2: High modularity



Network 1: High nestedness



Network 2: Low nestedness



Part 2: Effects of landscape disturbance on bee communities and plant-pollinator networks

Human-driven landscape disturbance involves changes to landscapes from a natural to a modified state following activities such as farming or urban development. Landscape disturbance is one of the leading causes of declines in bee abundance and diversity worldwide (Kearns et al. 1998; Steffan-Dewenter et al. 2005; Biesmeijer et al. 2006; Colla and Packer 2008; Gixti et al. 2009; Potts et al. 2010; Bartomeus et al. 2013) and has recently been shown to change the size and structure of plant-pollinator networks as well (Kearns et al. 1998; Spiesman and Inouye 2013; Burkle et al. 2013). Most studies have taken place in Europe and North America. However, bees are expected to respond in similar ways regardless of location since they are widespread and face similar disturbances occur across the globe (Winfree 2010, Kennedy et al. 2013, Fahrig et al. 2017), but this is not always the case. Part two examines how researchers define and measure landscapes, and explores what is known about bee and network responses to landscape disturbance as they relate to this thesis.

Defining landscapes

A question central to landscape ecology is: How does one define a landscape? Sufficiently large landmasses have many different regions and habitats nested within them. Commonly, several scales are used and evaluated statistically for their effects on biota. The broadest level is that of ecoregion. Ecoregions are defined by their unique set of biotic (i.e. flora and fauna) and abiotic features (i.e. average temperature and precipitation, soil texture and moisture level, etc.) At a finer scale, landscapes can be measured as the area within foraging distance. Bees will typically only forage several hundred metres from the nest to the reduce energetic cost of offspring production (Zurbuchen et al. 2010b, 2010a). The finest scale includes local habitat, which is the vegetation structure and flower richness surrounding nesting sites.

Disturbance changes landscape composition and configuration

Human-driven landscape disturbance can change both the composition and configuration of the landscape. Landscape composition refers to the area and diversity of cover types within a landscape, whereas landscape configuration refers to the geometrical pattern of the landscape

with or without respect to a cover type (McGarigal 2015). Composition is typically used to estimate habitat loss, and configuration is used to estimate landscape fragmentation (McGarigal 2015). Since habitat loss necessarily follows fragmentation, the effects of habitat amount must be distinguished from the effects of fragmentation. Thus, ecologists should strive to use metrics that adequately measure fragmentation *per se* (Fahrig 2003).

There are hundreds of metrics available to measure landscapes (McGarigal 2015), and published studies examining bee ecology vary in the metrics they use. Common metrics used to estimate landscape composition include percent-cover of semi-natural habitat (Tscharntke et al. 2002; Kennedy et al. 2013; Hopfenmüller et al. 2014; Steckel et al. 2014; Shaw et al. 2020) or disturbed habitat (Holzschuh et al. 2010; Shaw et al. 2020), and the Shannon's Landscape Diversity Index (SHDI) (Steckel et al. 2014). Semi-natural habitat includes areas of residual habitat, such as forest patches, meadows, or road verges. Disturbed habitat typically includes cover such as area of concrete or cropland. SHDI is analogous to the Shannon's Diversity index for communities, except that patch area is used in place of species abundance (McGarigal 2015). Metrics for landscape configuration are more diverse, and include, among others: total patch density (Hopfenmüller et al. 2014), shape index (Steckel et al. 2014), interspersion and juxtaposition index (Kennedy et al. 2013), connectivity of semi-natural patches (Bommarco et al. 2010), perimeter-area fractal dimension (Kennedy et al. 2013), and total edge density (Holzschuh et al. 2010). Although all of the above metrics attempt to separate fragmentation from habitat loss (McGarigal 2015), some are better than others (Xianli et al. 2014).

Bee abundance and species diversity

Although some studies report mixed effects depending on the region or landscape context (Carré et al. 2009; Lüscher et al. 2014), most agree that losing semi-natural habitat from the landscape causes declines in bee abundance and diversity (Bommarco et al. 2010; Holzschuh et al. 2010; Le Féon et al. 2010; Steckel et al. 2014; Holland et al. 2015; Denning and Foster 2018; Shaw et al. 2020). In their meta-analysis of 39 studies from around the world, Kennedy et al. (2013) found that bee abundance and richness were enhanced by increasing levels of semi-natural habitat, but unaffected by landscape configuration regardless of the metric the study used and the location of the study. Most bees may be mobile enough to find suitable patches in a fragmented

landscape as long as the total amount of habitat is sufficient (Kennedy et al. 2013). Studies independent of Kennedy et al. (2013) have also demonstrated that landscape configuration has little impact on bee abundance and richness compared to habitat amount (Bommarco et al. 2010; Holzschuh et al. 2010; Steckel et al. 2014). Bommarco et al. (2010) showed that semi-natural habitat loss was the main proponent of species loss in several studies, and that habitat connectivity had little impact on species richness. Holzschuh et al. (2010) and Steckel et al. (2014) agree with Bommarco et al. (2010) that landscape configuration is less influential than landscape composition. However, Holzschuh et al. (2010) and Steckel et al. (2014) only assessed stem-nesting bees, which they caught using artificial stem nests. Ground-nesting bees have the potential to respond differently from stem-nesters (Everaars et al. 2018; Grab et al. 2019).

Landscape ecologists have speculated that a certain amount of habitat is required to maintain species richness, and that a threshold amount of habitat should exist in which species richness dramatically declines if habitat falls below that threshold. The extinction threshold hypothesis predicts that species loss will increase rapidly due to fragmentation effects at a certain level of habitat loss (predicted between 70–80%) (Lande 1987; Fahrig 1998). Modelling simulations provide ample support for this theory (Boswell et al. 1998; Fahrig 1998; With and King, 1999; Hill and Caswell 1999; Flather and Bevers 2002). Yet, some field studies on birds and arthropods found no evidence for an extinction threshold (Trzcinski et al. 1999; Parker and Mac Nally 2002). Because the original theory was produced to assess large-bodied, territorial vertebrates (Lande 1987), our understanding of how small, non-territorial and invertebrate taxa respond to fragmentation at low levels of remaining habitat is weak. One study even indicates that arthropod richness in fragmented landscapes actually increases at higher levels of habitat loss (With 2016). The author proposes that the configuration of the landscape—namely the amount of edge—is a likely proponent in maintaining species richness (With 2016). In her literature review, Fahrig (2017) found no evidence for the extinction-threshold hypothesis in any taxa, including invertebrates, birds, fish, mammals, and even plants. Therefore, researchers studying landscape fragmentation should not assume that the effects of fragmentation are worse at higher levels of habitat loss.

Bee community composition

Landscape disturbance is hypothesized to homogenize bee community composition. Biotic homogenization occurs when sites become taxonomically or functionally similar over time with disturbance (Rooney et al. 2007). Few studies have attempted to explore the effects of landscape disturbance on the community composition of wild bees. Because there are little data available, it is pre-emptive to draw any strong conclusions about community responses to disturbance.

However, at least one study indicates that bee communities can become homogenized in areas of disturbance (Dormann et al. 2007). Dormann et al. (2007) found that bee communities across northwestern Europe became taxonomically homogenized at high levels of habitat loss coupled with high pesticide load, while sites with greater semi-natural habitat had more diverse communities. In this case, only certain bee species were able to tolerate the worst conditions, and intolerant species were lost. Dormann et al. (2007) also found that communities became dissimilar along an increasing fragmentation gradient, which suggests that fragmentation heterogenizes communities. Retaining semi-natural habitat even in highly disturbed areas can help to buffer against changes to community composition.

Phylogenetic and functional trait diversity

Diversity can include deeper information about phylogenetic relatedness and shared life history traits. The purpose of looking beyond a species-richness comparison between communities is to understand the role that behaviour, morphology, and ancestry might have in predicting the survival outcome of a species after a disturbance event. Incorporating bee biology allows researchers to predict how bees with certain traits might respond to landscape disturbance.

Phylogenetic diversity quantifies bee communities based on the ancestral relatedness of its species, while functional diversity measures the variability in life strategies in a community. Functional diversity can be measured using several methods, such as functional dispersion (Sydenham et al. 2016) which measures the average trait distance from a community centroid in trait space (Laliberté and Legendre 2010). Common traits used in functional diversity measurements of bees include social behaviour, nesting strategy, nesting location, diet breadth, and average body size. Other useful traits include phenology (such as month of emergence),

tongue length, dispersal capacity, and even pollen carrying behaviour (for the latter see Portman et al. (2019)).

Phylogenetic and functional diversity are related since closely related species tend to have similar traits, while more distantly related species tend to have distinct traits. For example, most nest-building Megachilidae have pollen-collecting scopal hairs on their sternal segments, whereas all andrenid bees have pollen-collecting hairs on their tibial and femoral leg segments. Because they are related, phylogenetic homogenization (the loss of phylogenetic diversity in a community) can actually drive functional trait homogenization (the loss of functional trait diversity in a community) (Baiser and Lockwood 2011). However, measuring phylogenetic diversity alone does not explicitly test for differences in survival based on functional traits, which is why many researchers choose to use functional diversity or dispersion instead. Functional traits are more informative and can tell us more about which traits in particular might make bees susceptible to disturbance.

Landscape disturbance can drive bee phylogenetic homogenization. Harrison et al. (2018) tested the impact of landscape composition on bee community phylogenetic relatedness using three land-use categories (forested, agricultural, urbanized). They found that urbanized sites became phylogenetically homogenized relative to forested or agricultural sites. Urbanization specifically favoured sweat bees, which is a group that is species rich but not phylogenetically diverse (Harrison et al. 2018). Grab et al. (2019) found a similar result across an agricultural gradient; certain bee clades were being lost due to landscape disturbance, while bumble bees and sweat bees were being disproportionality retained. Grab et al. (2019) noted that disturbance-resistant bee clades shared similar traits like social reproductive behaviour and longer flight periods, which may have allowed them to exist in intensified landscapes. Because they tested phylogenetic rather than functional trait diversity, this remains speculative.

As with phylogenetic homogenization, landscape disturbance can drive bee functional trait homogenization. Much of the functional diversity research surrounding wild bees has been done in agricultural settings (Forrest et al. 2015; Martins et al. 2015; Grab et al. 2019). Forrest et al. (2015) tested the effect of farming strategy (organic or conventional) on the functional diversity of wild female bees using several trait characters. To do this, they net-collected bees on 16 sites

(four conventional, five organic, seven semi-natural controls) that had at least 20% semi-natural land cover within a 1 km radius. Although species richness estimates were higher on both organic farms and natural sites relative to conventional farms, functional diversity was lower on both farm types than natural sites. Forrest et al. (2015) attributed the reduced functional diversity on farms to the loss of solitary, late-emerging, above-ground nesting bees, which were more prevalent in natural systems. They concluded that structural elements common to all farms filters out certain species traits, and that organic farming is not a sufficient method to retain functional trait diversity (a conclusion also supported by Schneider et al. (2014)).

Pollination services can suffer when community functional traits become homogenized due to landscape disturbance (Woodcock et al. 2019). Crop yield and seed set in apple benefit from a diverse array of wild bee functional traits (Martins et al. 2015; Blitzer et al. 2016; Grab et al. 2019). In order to relate functional diversity to the landscape, Martins et al. (2015) modelled bee community functional dispersion from twenty independent apple orchards against a suite of landscape metrics at each site. Bee functional diversity was positively associated with the amount of semi-natural area within a 500 m radius of the sampling sites (specifically meadow and forest area), but not with mean distance to semi-natural patches (Martins et al. 2015). In other words, the composition of the landscape was an influential predictor of functional trait diversity and thus fruit and seed set, while the landscape configuration was not. Orchards set in landscapes containing greater amounts of natural habitat therefore have better access to a greater diversity of bees. Grab et al. (2019) also investigated yield and seed set in apple orchards with similar results, but measured phylogenetic relatedness rather than functional trait diversity *per se*. However, they noticed that bees with specific traits were being lost from the community in agriculturally dominated areas, leading to a change of functional trait diversity between communities (Grab et al. 2019).

Local-scale vegetation and flower richness

Studies examining the effect of local-scale variables on bee abundance and diversity commonly report positive effects of increasing flower cover and richness (Hülsmann et al. 2015; Cole et al. 2017; Andrieu et al. 2018; Rollin et al. 2019). Some studies have found that flower cover and richness have a greater effect on bee abundance and diversity compared to the amount of semi-

natural habitat in the landscape (Hülsmann et al. 2015; Rollin et al. 2019). However, at least one study has shown bee abundance and richness to decline with flower cover (Hass et al. 2018). The authors did not provide an explanation for this unexpected trend. Roulston et al. (2007) suggests that trap-flower competition may be enhanced in areas of greater flower richness and/or density which might drive down the number of specimens and species caught in traps. This phenomenon needs further study.

Plant-pollinator network size, structure, and stability

Plant-pollinator network size and structure can be influenced by landscape disturbance. Network size almost always decreases with habitat loss as species are lost from the environment (Spiesman and Inouye 2013; Burkle et al. 2013; Moreira et al. 2015; Magrach et al. 2018; Ferreira et al. 2020). The corollary is true, such that network size increases with semi-natural habitat (Burkle and Knight 2012; Grass et al. 2018). How fragmentation affects networks is poorly understood (Hadley and Betts 2012; Xiao et al. 2016), but one study suggests that network size declines as patch isolation increases (at least in forests) due to detrimentally long foraging distances (Ferreira et al. 2020). However, caution is needed when interpreting the results of Ferreira et al. (2020) since patch is confounded by habitat amount (Fahrig et al. 2003).

Effects of landscape disturbance on network structure are not consistent across studies (Soares et al. 2017). Nestedness tends to decrease in response to habitat loss, mainly due to a decrease in diet breadth as floral options become limited (Burkle and Knight 2012; Spiesman and Inouye 2013; Burkle et al. 2013; Moreira et al. 2015; Magrach et al. 2018). Ferreira et al. (2020) showed that habitat isolation can also decrease network nestedness. An increase in nestedness after disturbance could theoretically happen, but may only occur if super-generalist species take over the core of the network (Bartomeus et al. 2008). Connectance and modularity have been shown to increase with habitat loss, but effects can work indirectly through decreasing network size such that smaller networks are inherently more connected and modular (Spiesman and Inouye 2013).

Furthermore, some studies report no effect of landscape disturbance on either nestedness (Padrón et al. 2009; Vilà et al. 2009; Nielsen and Totland 2014) or connectance (Aizen et al. 2008;

Nielsen and Totland 2014). Reorganization of interactions can maintain network structure and compensate for lost interactions (Padrón et al. 2009; Vilà et al. 2009; Nielsen and Totland 2014). Interactions lost from the network first tend to involve specialist species (Burkle et al. 2013; Ferreira et al. 2020). Generalist species can take on a specialist role in resource-poor landscapes because they have fewer foraging options available to them (Ferreira et al. 2020). Sometimes network reorganization may disproportionately benefit super-generalist introduced species, which may stabilize the network but exclude native species (Aizen et al. 2008). The inconsistency of disturbance effects on network structure indicates that more studies in a broader range of locations and ecosystems are needed.

The complexity of a network is hypothesized to influence its stability to network perturbations, such as species loss resulting from landscape disturbance (Landi et al. 2018). A sufficient loss of species from the network can theoretically lead to collapse of ecosystem functioning (Lever et al. 2014). Estimating the extinction slopes of bees (or plants) following simulated consecutive species extinctions is a widely used method of testing the stability of networks to habitat disturbance. Studies using this method have shown that networks that are larger and have greater nestedness and connectance and lower modularity are more resilient to species extinctions and can persist for much longer than networks without these features (Memmott et al. 2004; Thébault and Fontaine 2010; Lever et al. 2014; Moreira et al. 2015; Grass et al. 2018; Magrach et al. 2018). However, this remains speculation since real-world examples of network collapse are lacking.

Conclusion

There is a high amount of variation on the published effects of landscape disturbance on bee communities and plant-pollinator networks. Variation in findings are caused by regional context and scale for bee communities, and the types of interactions lost from networks. Future studies should take these in to account when studying bees and plant-pollinator networks.

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CHAPTER 2: FRAGMENTED AND DIVERSE LANDSCAPES SUPPORT WILD BEE COMMUNITIES

Abstract

Background. Human-driven landscape disturbance has caused global declines in abundance and diversity of wild bees (Hymenoptera: Apoidea: Anthophila). Effects of landscape disturbance can depend on geographical context and local drivers such as vegetation structure. In this study, I tested the effects of changing landscape composition, configuration, and local-scale vegetation on wild bee abundance, richness, community functional trait dispersion, and community composition in agriculturally dominated regions of southern Manitoba.

Methods. I sampled 64 sites across a broad area encompassing four ecoregions. I captured bees over two years using coloured pan and blue vane traps to measure bee communities. I hypothesized that crop cover and urban development would negatively impact bee communities, but land cover diversity (Shannon's Landscape Diversity Index) and fragmentation (edge density) would benefit bee communities by providing habitat. I also expected increasing amounts of bare ground, flower cover, and flower richness to benefit bee communities by improving nesting and foraging resources.

Results. I identified 23,189 bees to species or morphospecies. Bee communities were influenced by disturbance at both the landscape and local scales. At the landscape-scale, habitat loss from cereal crops (e.g. wheat, corn) and forb crops (e.g. canola, soybean) had widespread negative effects on bee abundance and species richness, which indicates that areas with greater crop cover support fewer bees and lack the diversity of bees found in areas with less crop cover. Although greater edge density also reduced bee abundance and richness in most ecoregions, the functional dispersion of communities was enhanced. This suggests that landscape configurations which maximize edge habitat support a wider trait assemblage of bees at the cost of bee abundance and richness. In contrast, land cover diversity enhanced bee abundance and richness in most ecoregions but reduced functional dispersion, which suggests that a greater number of land cover types supports abundant and species rich bee communities at the cost of functional traits. At the

local-scale, bee abundance was reduced by flower cover and richness, which could suggest either that some flower species are widespread but support fewer bees, or that adding many low-cover flower species does not significantly improve local foraging resources (or both mechanisms). Finally, introduced flower species enhanced bee community functional dispersion and did not change bee abundance or richness, suggesting that introduced species can potentially benefit bee communities in disturbed areas by adding resources back to landscapes where native varieties have been lost.

Conclusion. My study shows that, in most areas, fragmented landscapes with high amounts of edges and greater land cover diversity support abundant and diverse wild bee communities. Land management policies should be aimed at enhancing edge habitats in the landscape and increasing land cover diversity to maintain an abundant and rich assemblage of bees with a wide array of functional traits. Land managers should also reconsider removing introduced plant species from field margins since these plants are often the only resources available to bees in disturbed areas and they can support a trait-diverse bee community.

Introduction

Wild bees are important pollinators in both natural and agro-ecosystems (Winfree et al. 2011). More than 87% of flowering plants rely on wild bees and other insects to carry out pollination to some degree (Ollerton et al. 2011), including many food crops (Costanza et al. 1997; Klein et al. 2007; Gallai et al. 2009). Unfortunately, wild bees are suffering global declines in abundance and diversity (Kearns et al. 1998; Steffan-Dewenter et al. 2005; Biesmeijer et al. 2006; Colla and Packer 2008; Grixti et al. 2009; Potts et al. 2010; Bartomeus et al. 2013). Habitat loss caused by human activity is considered the primary driver of bee declines (Potts et al. 2010; Winfree 2010; Garibaldi et al. 2011; Kennedy et al. 2013). The foraging behaviour of bees around a central nest (Zurbuchen et al. 2010b, Gathmann and Tschardt 2002) makes them particularly susceptible to landscape disturbance compared to other non-central foraging insects.

Two major contributors to habitat loss are agricultural intensification and urban development. Around half of ice-free land in North America has been converted to either cropland or urban area since the year 1700 (Ellis et al. 2010). Cereal crops are known to reduce bee abundance and

diversity when conventionally farmed (Holzschuh et al. 2007; Le Féon et al. 2013). In contrast, forb crops can sometimes benefit bee communities by providing abundant foraging resources during their bloom period (Holzschuh et al. 2013; Le Féon et al. 2013; Rundlöf et al. 2014; Todd et al. 2016). Urban development, such as city green spaces and gardens, can actually harbour abundant and diverse communities by providing nesting and foraging resources (Normandin et al. 2017), which can compensate for the negative effects of concrete (Hülsmann et al. 2015).

Fragmentation and land cover diversity can both change following landscape disturbance. Fragmentation often accompanies habitat loss, and is defined as the division of contiguous habitat into smaller patches (Fahrig 2003). Separating the effects of fragmentation from habitat loss can only be done at the landscape-scale, since patch-scale estimates like patch isolation are confounded by habitat amount (Fahrig 2003, 2017). Fragmentation can have distinct effects on bees compared to habitat loss (Kennedy et al. 2013; Steckel et al. 2014; Fahrig 2017) and so it is important to evaluate the effects of fragmentation separately from effects of habitat amount. Land cover diversity may increase following disturbance if new habitat types, such as crop fields, are introduced to areas where they were not present pre-disturbance (Hass et al. 2018). However, land cover diversity may actually decrease at higher disturbance levels if it leads to increasing dominance of disturbed habitats (Grime 1973).

Habitat loss, fragmentation, and landscape diversity rarely produce clear effects on wild bee communities. Disturbance from farming and urbanization generally have negative effects on bee communities (Le Féon et al. 2010; Hülsmann et al. 2015), although the effects are sometimes undetectable (Quintero et al. 2010; Fahrig et al. 2015). While some authors report positive effects of increased semi-natural habitat on bee abundance and richness (Holzschuh et al. 2010; Bennett and Isaacs 2014; Sárospataki et al. 2016; Papanikolaou et al. 2017a; Eeraerts et al. 2019; Rollin et al. 2019; Martin et al. 2020), others report mixed effects (Carré et al. 2009; Le Féon et al. 2010; Carrié et al. 2017; Denning and Foster 2018) or no effects (Bukovinszky et al. 2017; Eeraerts et al. 2019). The effects of fragmentation are likewise unclear, such that reported findings range from positive (Kratschmer et al. 2018) or negative effects (Steffan-Dewenter 2003; Papanikolaou et al. 2017b) to mixed (Carrié et al. 2017; Denning and Foster 2018) or no effects (Holzschuh et al. 2010). Landscape diversity may have distinct effects compared to

habitat loss or fragmentation, although effects on bee abundance and richness estimates are often mixed (Carrié et al. 2017; Denning and Foster 2018).

Variability in reported findings are the result of several factors, including spatial scale (Steffan-Dewenter et al. 2002), functional traits of the bee community (Martins et al. 2015), and the geographical location or broader regional context where the study was performed (Martins et al. 2015). Landscape level spatial scale includes the area within a radial buffer surrounding the sampling site, from several hundred meters (Steffan-Dewenter et al. 2002) up to several kilometers (Oliver et al. 2010). The best buffer size can depend on the group of bees in question, since bumble bees, honey bees, and wild bees have all been shown to respond to different sizes (Steffan-Dewenter et al. 2002), and so it is important consider multiple buffers sizes. Functional traits of bees include the diverse ways in which they nest, forage, and behave. The assemblage of traits in the community has been shown to respond differently to landscape disturbance than abundance or richness estimates (Forrest et al. 2015). This makes it a useful characteristic to measure, since the simple loss or gain of a species tells very little of the loss or gain of function (Baiser and Lockwood 2011). Ecoregion (a broad area with distinct vegetation, climate, and abiotic characteristics) may also play a role in determining responses to disturbance, and therefore is an important aspect to consider when understanding how bees respond to the landscape.

Local factors rather than landscape-level processes sometimes explain the greatest proportion of variation in bee responses, especially those relating to flower richness and cover (Hülsmann et al. 2015; Cole et al. 2017; Andrieu et al. 2018; Kratschmer et al. 2018; Eeraerts et al. 2019; Rollin et al. 2019). Usually responses are positive to both flower cover and richness, but at least one study shows that bee abundance and richness can be negatively correlated with flower richness and cover (Hass et al. 2018) although the authors do not give an explanation why. Measuring landscapes at multiple scales is important when studying bee communities, since they can be influenced by local, landscape, and regional scales.

In this study, I examine how human-driven local and landscape disturbance influences wild bee communities across southern Manitoba, Canada. I predict that bee abundance, species richness, and functional dispersion will vary along landscape-level disturbance gradients across all sites,

but that effects will depend both on the type of disturbance and the broader regional context. The traits I used to estimate functional diversity in this study include nesting strategy, sociality, diet breadth, and body size. I am including body size as a functional trait in this study because average body size varies between species and because average species body size of the community can be influenced by disturbance (Bartomeus et al. 2013; Rader et al. 2014). I also predict that bee communities will vary along local-level gradients of vegetation structure and flower richness. The goal of this study is to inform land management policies aimed at conserving wild bee communities.

Materials and methods

Study area

I performed wild bee surveys in the southern portion of Manitoba, Canada, below 50.6°N and between -95.9 to -99.7°W. The climate of southern Manitoba is moderately dry, with average annual precipitation across southern Manitoba ranging from 250–700 mm (McLintock et al. 2019). Because of its central place in continental North America, southern Manitoba receives extreme air temperatures that can range from -40°C in the winter months to 38°C in the summer months, although average monthly temperatures span -13 to 27°C (Scott 1996; McIntock et al. 2019). Snow covers the ground from November through April (McLintock et al. 2019).

Southern Manitoba is separated into several ecoregions, which vary in their mean seasonal temperature, soil moisture level, soil type, and dominant vegetation. The ecoregions I sampled in were, from east to west, Lake of the Woods, Interlake Plain, Lake Manitoba Plain, and Aspen Parkland (Smith et al. 1998). Lake of the Woods is in the southeastern portion of the province and is dominated by mixed boreal forests. Interlake Plain encompasses the area between Lake Manitoba and Lake Winnipeg and extends southward to the international boundary, running alongside the Lake of the Woods ecoregion. It supports trembling aspen forests and shrub land, as well as small amounts of grassland, and is often considered to be a forest-grassland transitional region (Thorpe 2014). The Lake Manitoba Plain and Aspen Parkland ecoregions are part of the Prairie ecozone and make up the central and western portions of the province, respectively. Lake Manitoba Plain is characterized by tall-grass prairie, while Aspen Parkland is dominated by mixed-grass prairie (Scott 1996). Much of the prairie ecozone has been converted

into agricultural land.

Study sites

I sampled 64 sites over two years (32 each in 2018 and 2019, Table S1). Sites were defined as the area within a 2 km radius surrounding my traps. To maximize the number of sites I visited in one day, I chose to sample four sites at one time. Sites are thus clustered by location, with at least 2.1 km between sites (Fig. 2). I selected sites using visual inspection of Google Earth version 7.3.1.5491 based on their proximity to Winnipeg (within 200 km), proximity to natural areas, ease-of-access, and historical significance (sampled in the past). Sites had varying levels of disturbance. I compared what I saw in the landscape to the landscape data layer to ensure that land cover estimates were accurate.

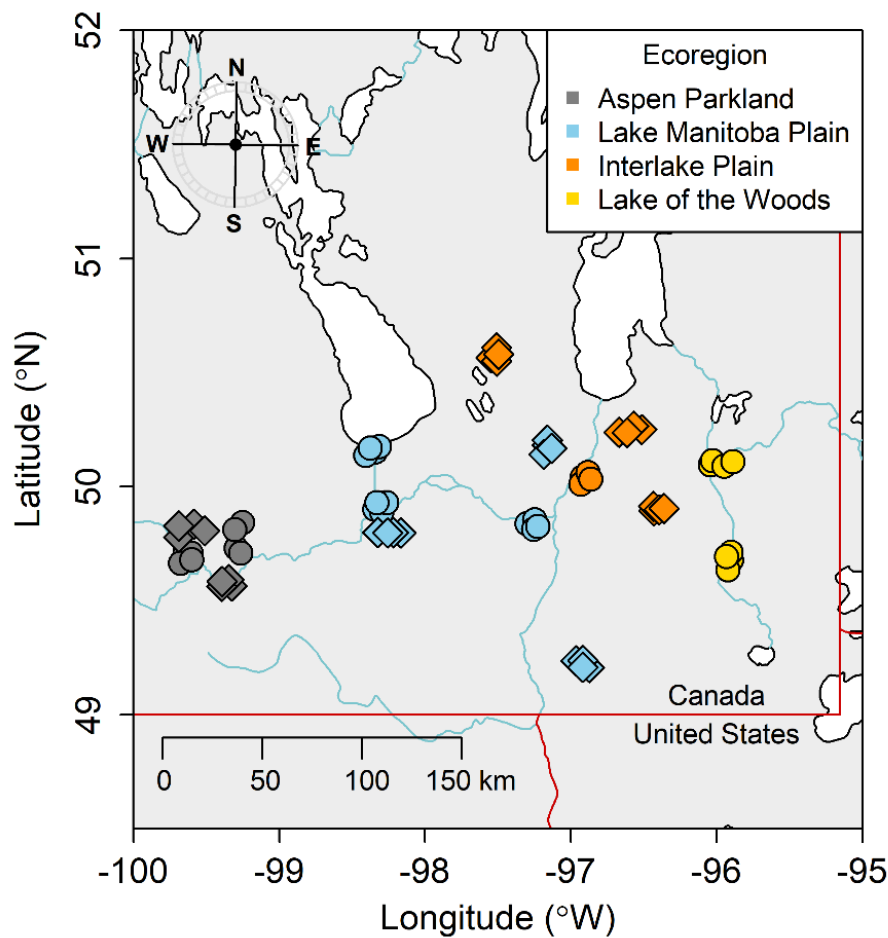


Fig. 2. Study sites across southern Manitoba in 2018 (circles) and 2019 (diamonds).

Sampling procedure

Every sampling method has inherent biases that influences apparent bee community (Joshi et al. 2015; Gibbs et al. 2017b; Prendergast et al. 2020), which is why I used both coloured pan traps and blue vane traps to sample bees. These are widely used attractive traps for collecting bees with minimal user-bias (Leong and Thorp 1999; Stephen and Rao 2005; Toler et al. 2005; Wilson et al. 2008). Pan traps were bought from New Horizons Supported Services, Inc. (Upper Marlboro, Maryland), and were made of plastic 96 mL containers (3.8 cm high and 8.0 cm wide) painted exteriorly with white, fluorescent blue, or fluorescent yellow paint. Blue vane traps were purchased from Springstar, Inc. (Woodinville, Washington). Traps were partially filled with a 2.5 mL/L solution of Dawn Ultra® original scent dishwashing liquid and water. I placed the traps directly on the ground along a road or path near a patch of semi-natural habitat. I arranged the traps linearly with one blue vane trap followed by 12 pan traps in an alternating colour sequence, the order of which was changed at each sampling round. I placed all traps five metres apart to limit competition between traps (Droege et al. 2010b). Three transects were deployed for a total of 36 pan and three blue vane traps per site.

I sampled all sites five times from mid-May through late August in both years, and aimed for three weeks between collection periods. I set out the traps between 09:00 and 10:30 and collected them 5 hours later in the same sequence they were deployed. For each collection period, I changed the order of sites set out on a given day to minimize temporal bias. I collected bees during days that were forecasted to be within optimal foraging conditions, including a temperature between 15 and 32°C and no precipitation or strong winds (Tuell and Isaacs 2010). The forecast was not always accurate, and so the lowest temperature I sampled at was 10°C on May 14th, 2019; I collected several bees even at this temperature. After collection, I stored the specimens in 70% ethanol until they could be processed.

I randomly chose two of the four sites at each location to aerial net for analyzing plant-bee networks in Chapter two. Since I found several species in nets that I did not find using traps, I included them within the biodiversity records. However, I omitted the net data from my statistical analyses on bee communities for this chapter.

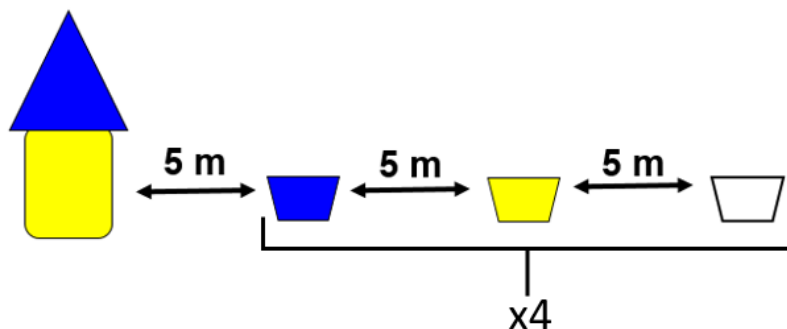


Fig. 3. Schematic of trap placement along road edges, starting with one blue vane trap and followed by 12 pan traps in a repeating colour pattern. Colour pattern was changed at each sampling round. This setup was repeated three times for a total of three blue vane traps and 36 pan traps per site. All traps were five metres apart on the ground and filled with soapy water.

Bee identification

I identified all bees down to the lowest taxonomic rank possible using published taxonomic keys and reference material (Timberlake 1954, 1969; LaBerge 1956, 1961, 1967, 1969, 1971, 1973, 1977, 1980, 1985, 1987, 1989; Mitchell 1960, 1962; Ribble 1967, 1968, 1974; Shinn 1967; Adlakha 1969; LaBerge and Bouseman 1970; LaBerge and Ribble 1972, 1975; Baker 1975; Bouseman and LaBerge 1978; McGinley 1986, 2003; Lavery and Harder 1988; Romankova 2003, 2007; Coelho 2004; Michener 2007; Packer et al. 2007; Rightmyer 2008; Arduser 2009, 2016a, 2016b; Droege et al. 2010a; Gibbs 2010, 2011; Rightmyer et al. 2010; Rehan and Sheffield 2011; Sheffield et al. 2011; Dumesh and Sheffield 2012; Gibbs et al. 2013; Gonzalez and Griswold 2013; Williams et al. 2014; Andrus and Droege 2016a; Droege and Rehan 2016; Droege and Tucker 2016; Griswold et al. 2016; Andrus and Droege 2016b; Larkin et al. 2016; Droege 2016; Gardner 2018; Onuferko 2018; Semmler et al. 2018). Some taxa (e.g., *Nomada*) lack taxonomic treatments sufficient enough to allow all species to be identified reliably. Classification follows Michener (2007), except *Lasioglossum* subgenera follows Gibbs (2018) and Gibbs et al. (2013). Vouchers are deposited at the J. B. Wallis/R. E. Roughley Museum of Entomology at the University of Manitoba and a synoptic set will be held at Agriculture and Agri-food Canada in Brandon, Manitoba.

Bee community metrics

I measured communities for their abundance, rarefied species richness, and functional dispersion at each sampling event. I calculated rarefied species richness using the vegan package (Oksanen et al. 2018). Rarefied richness is a richness estimate taken along a sample-based rarefaction curve at a specified abundance and accounts for differences in richness estimates due to abundance (Hurlbert 1971; Hill 1973; Heck et al. 1975; Chao et al. 2014). I rarefied all richness estimates to the median abundance across all sites (46 specimens).

For functional dispersion, I calculated the functional dispersion index using the FD package (Laliberté et al. 2014). The functional dispersion index incorporates information about abundances and life-history characteristics to estimate dissimilarities between communities (Laliberté and Legendre 2010). The functional dispersion index is defined as $FDis = \sum a_j z_j / \sum a_j$ (Laliberté et al. 2014) where a_j is the abundance of species j , and z_j is the distance of the species to an abundance-weighted community centroid. An increase in the functional dispersion index indicates either that bee communities are gaining uncommon traits, or that the abundance of common traits are declining, or both. The functional dispersion index is computed using principal coordinates analysis, which accounts for high correlation among traits (e.g., all eusocial species are polylectic). I applied a Cailliez correction to eliminate negative eigenvalues. The species traits I used to calculate functional dispersion were sociality, nesting location, diet breadth, and body size (Table 1), the former three of which are all phylogenetically conserved (Odanaka and Rehan 2019). Species traits followed Sheffield et al. (2014) and Gibbs et al. (2017), as well as professional opinion when species traits were unknown. I estimated body sizes using inter-tegular distance (Cane 1987), which is the shortest straight-line distance between the tegulae across the scutum, and is a common measurement used to estimate bee body size (Greenleaf et al. 2007; Kendall et al. 2018). I measured the ITD of 1–478 females (mean 38) per species using the computer program Nikon NIS-Elements (v. F4.30.01) and had only one female specimen for 26 species.

Table 1. Traits used in calculation of functional dispersion index, using the abundance-weighted value of trait diversity in multi-dimensional trait space. Calculated per sampling event following Laliberté et al. (2014).

Sociality	Solitary	Females build own nests
	Communal	Solitary females build nests but share entrances
	Subsocial	Loose colonies formed of foundress and daughters
	Eusocial	Colonies with queen and division of labour
	Cleptoparasitic	Females invade host nest and lay eggs
Nesting	Soil	Nest built directly in the ground
	Hive	Nest of eusocial species
	Cavity	Nest built in pre-existing spaces
	Surface	Nest built directly on hard surfaces
	Stem	Nest built in pith of twigs and stems
	Wood	Nest built in soft, decaying wood
Diet	Oligolectic	Plant specialist, narrow diet range
	Polylectic	Plant generalist, broad diet range
Size	ITD	Species average intertegular distance (mm)

Weather data

I collected morning and afternoon temperature and wind speed data using a Kestrel 2000 Wind Meter for each site at all sampling rounds. For temperature, I took the reading several metres away from the road or car, in the shade and out of the wind. For wind speed, I held up the Kestrel at arms length and slightly above head height. If the temperature or wind speed was fluctuating between values, I took the midpoint of the two extremes. I also measured the amount of sun in the morning and afternoon, which was either fully visible and casting a well-defined shadow (sunny), partially hidden by clouds, but still casting a relatively-defined shadow (partly cloudy), or clouded-over and barely casting a shadow (cloudy). I ran a principal component analysis (PCA) using these weather variables and extracted the first two principal components, which had eigenvalues greater than one (following Kaiser's rule, Kaiser 1960) and collectively explained 55% of the variance. This allowed me to decrease the number of weather variables from six to two, providing several more residual degrees of freedom in my models. The first axis was explained mainly by temperature, and the second axis was explained mainly by wind speed.

Scree plot and PCA were performed in R using the psych and FactoMineR packages, respectively (Le et al. 2008; Revelle 2020).

Floral surveys and quadrat data

In 2019, I gathered local land cover data by visually estimating the percent of flower cover, grass cover, and bare ground in a 1x1 m quadrat, using the charts provided by Anderson (1986) as a guide. I took twenty samples spaced five metres apart in the vegetation within ten metres of the traps at each sampling event. If a species could not be identified in the field using a field guide, it was dry-pressed and taken back to the lab, where I identified it down to the lowest taxonomic rank possible (Scoggan 1957; Reaume 2009; Holm 2017). I sometimes uploaded photographs of plants to iNaturalist to facilitate identifications. Values were averaged across the twenty samples. I also measured the floral richness at each site at every sampling round near traps and categorized each species as either native or introduced based on its status on VASCAN (Brouillet et al. 2021).

Landscape data

I imported the Agriculture and Agri-Food Canada Crop Inventory GEOTIFF layers into R and used the landscapemetrics package to extract landscape data in seven buffers around each site (500, 750, 1000, 1250, 1500, 1750, and 2000 m radii) (Agriculture and Agri-Food Canada 2018, 2019). The Crop Inventory includes 72 unique cover types at a spatial resolution of 30 m². Data are $\geq 94\%$ accurate for crop cover types and $\geq 70\%$ accurate for non-crop cover in Manitoba (Agriculture and Agri-Food Canada 2020). I measured several variables representing landscape composition and one measuring landscape fragmentation (Table 2). For landscape composition, I measured the proportion of disturbed land cover in three main categories:

(i) Cereal crops, including wheat, corn, barley, oats, rye, and triticale. These crops are mainly wind pollinated and so are infrequently visited by bees. Wheat and corn were the most abundant cereal crops. At 2000 m, wheat was found at 53 sites and covered an average of 5.32% total area (max. 33.83%). Corn was found at 43 sites and covered an average of 2.28% total area (max. 26.2%). Average cover of wheat and corn were similar between years.

(ii) Forb crops, including canola, sunflower, flax, soybeans, peas, beans, faba beans, and potatoes. These crops have nectar and/or pollen producing flowers that may be visited by bees. Canola and soybean were the most abundant forb crops. At 2000 m, canola was found at 48 sites and covered an average of 5.84% total area (max. 32.48%). Soybean was found at 51 sites and covered an average of 5.65% total area (max. 31.6%). Average cover of canola and soybean was similar between years.

(iii) Urban area, including roads, highways, buildings, parking lots, and other such developed, hard- to semi-hard- surfaced land cover. Because the smallest pixel size is 30x30 m, road verges and ditches are also included. At 2000 m, urban area covered an average of 7.43% total area (max. 79.08%). Urban area was slightly higher in 2018 than 2019 because I sampled within the city of Winnipeg and nearby Birds Hill Provincial Park, which are well developed compared to other areas of the province.

I also measured the Shannon's Landscape Diversity Index (SHDI), which is derived from Shannon entropy (Shannon and Weaver 1949). SHDI uses all cover types and weights each one by patch area in the landscape to estimate diversity. Therefore, SHDI measures the entire landscape without focusing on any one land cover class, making it ideal when optimal nesting or foraging habitat is unknown, which is the case for many bees. Values are always greater than 0, and greater values indicate higher landscape diversity. For a given number of landcover types, SHDI is maximized when the distribution of area among all covers are of equal proportion (McGarigal 2015).

I used edge density to estimate landscape fragmentation. Edge density is calculated using the formula $ED = E/A(10,000)$, where E =edge length (m) and A =total area in the buffer (ha). Edge density standardizes total edge length (juxtaposing cover types) per unit area (m/ha), so it can be used to directly compare landscapes of different spatial scales (McGarigal 2015). Values are greater than zero, and larger values indicate greater edge density.

Table 2. Land cover variables at the local and landscape scales. Local data were gathered in 2019 only. Landscape data were gathered in both years at seven buffer sizes (500, 750, 1000, 1250, 1500, 1750, and 2000 m).

Scale	Variable	Description
Local	Flower cover	Average area covered by blooming forbs and shrubs (%)
	Grass cover	Average area covered by grass (%)
	Bare ground	Average bare ground (%)
	Flower richness	Number of blooming forb and shrub species.
Landscape (composition)	Cereal crop cover	Area covered by annual grass or grass-like crops (%)
	Forb crop cover	Area covered by annual herbaceous crops (%)
	Urban area	Area covered by human development (%)
	Shannon's Landscape Diversity Index (SHDI)	Measurement of land cover diversity, where cover types are weighted by number of patches
Landscape (fragmentation)	Edge density (ED)	Sum of all edge lengths divided by the total landscape area (m/ha)

Statistical analyses

All of the following analyses were performed in R (R Core Team 2018).

Landscape effects analyses

I constructed generalized linear mixed models (GLMM) using the glmmADMB package (Skaug et al. 2016) to predict the effects of landscapes on trap-collected bee abundance, rarefied richness, and functional dispersion. I first wanted to know whether effects were evident across all sites. In addition to my landscape variables, all of my models included predictor variables of year, Julian day, latitude, longitude, number of traps not tipped over at the end of the day, number of minutes the traps were left in the field, and weather variables (PC1 and PC2 from weather PCA). Every non-landscape predictor variable was scaled and centered around its mean value. Predictor variables were assessed for collinearity using variance inflation factors, but none were found to be strongly collinear (i.e. did not exceed a threshold of 5 (Craney and Surles 2002)). Site was used as a random effect. Trap abundance was fit using a negative binomial distribution, while rarefied richness and functional diversity were fit using a Gaussian

distributions. To select the best buffer size, I ran the same model at each buffer and then used information theory to select the model with the lowest sample-size corrected AIC_c score (Akaike 1973). I considered an effect to be significant if the p-value was smaller than 0.05. I visually inspected all model residuals using heteroscedasticity and quantile-quantile plots for homogeneity of variance and distribution fit, respectively.

I ran a linear model using functional dispersion as a response variable and abundance and richness as predictor variables to explore how the functional dispersion index varies with bee abundance and the number of bee species contributing to its calculation. An increase in the functional dispersion index with abundance may indicate a reduction in abundance of common traits.

To assess whether netting half of the sites influenced abundance, richness, and functional dispersion estimates, I ran independent GLMMs for each using ‘netted’ (yes or no) as a predictor variable. I also included date, location, and sampling event variables as predictors, as well as site as a random effect, to account for residual variation. A significant effect ($\alpha=0.05$) of netting would indicate that community estimates obtained using traps at netted sites were different from non-netted sites due to the presence of net collections.

To determine whether landscape effects depended on ecoregion, I reran the landscape models and included interactions between ecoregion and my five landscape variables. I omitted non-significant, non-landscape variables to improve my degrees of freedom. I then ran separate landscape models in each ecoregion using my five landscape variables to better understand the impacts of landscape structure within each ecoregion.

I used permutational multivariate analysis of variance (perMANOVA) with 999 permutations to predict the effects of disturbed land cover (cereal crop cover, forb crop cover, and urban area) and ecoregion on community composition. Communities were compared using Bray-Curtis dissimilarity at a buffer size of 1000 m. I used a pairwise multiple comparisons test to determine which ecoregion mean community centroids differed in location from one another, which would indicate significantly different species composition. I also ran a perMANOVA followed by a multiple comparisons test on community dispersions to determine if they varied among ecoregions. I visualized communities by plotting the first two constrained axes from a distance-

based redundancy analysis (dbRDA) using disturbed land cover as constraints. I performed perMANOVA, dbRDA, and dispersion analysis using the package *vegan* (Oksanen et al. 2018), and multiple comparisons test using the *pairwiseAdonis* package (Martinez Arbizu 2020). I also ran an abundance-based indicator species analysis using 999 permutations using the *indicspecies* package (De Caceres and Legendre 2009) to further assess associations between less common species and ecoregion(s).

Local effects analysis

I used GLMM to predict the effects of local vegetation structure on trap-collected bee abundance, rarefied richness, and functional dispersion across all sites in 2019. Local model structure was the same as for my landscape models across all sites. My local variables included bare ground, grass cover, flower cover, total flower richness, and introduced flower richness.

Results

I collected 23,189 bees in total, 21,000 of which were collected using traps and used for analyses (Table S2). I identified 273 species or morphospecies using all three methods, and 249 using traps. My total species count represents 72% of the estimated 380 bee species in Manitoba, and 32 out of 37 known genera (Gibbs et al. in press). Sixty species were new records for the province, six of which were also new records for Canada (Table S2). Net collections did not influence trap-based estimates of abundance (GLMM, $df=311$, $z=-0.26$, $p=0.7956$), richness (GLMM, $df=311$, $z=-0.63$, $p=0.5274$), or functional dispersion (GLMM, $df=311$, $z=-1.89$, $p=0.0592$). Functional dispersion decreased slightly as bee abundance increased, based on its negative correlation with abundance (LM, $df=317$, $\beta=-0.0006$, $SE=0.0001$, $p<0.0001$). Functional dispersion also increased weakly as richness increased, based on its positive correlation with richness (LM, $df=317$, $\beta=0.0045$, $SE=0.0008$, $p<0.0001$).

Our trap samples were dominated by halictid bees both in terms of abundance (62% of all individuals) and richness (18% of all species) (Fig. S1). The halictid subgenus *Lasioglossum* (*Dialictus*) accounted for 40% of individuals. The apid genera *Melissodes* and *Bombus* were also highly abundant and accounted for 17% of all individuals collectively (Fig. S1). Most species

were rare (≤ 5 individuals), while ten were highly abundant (Table S2). They were, in descending order (relative abundance in parentheses), *Lasioglossum zonulus* (10.0%), *L. pilosum* (5.8%), *Agapostemon texanus* (5.4%), *L. novascotiae* (5.2%), *Melissodes agilis* (4.9%), *Halictus confusus confusus* (4.1%), *L. leucocomus* (3.7%), *Perdita swenki* (3.2%), *L. vierecki* (2.9%), and *Bombus ternarius* (2.8%).

Across all sites, I caught the greatest average number of bees per site (\pm SD) in Lake Manitoba Plain (341 ± 169 individuals/site), followed by Aspen Parkland (396 ± 133 individuals/site), Interlake Plain (308 ± 142 individuals/site), and Lake of the Woods (194 ± 85 individuals/site), and the greatest average number of species per site in Aspen Parkland (50 ± 10 species/site), followed by Interlake Plain (43 ± 10 species/site), Lake of the Woods (42 ± 12 species/site), and Lake Manitoba Plain (40 ± 12 species/site). Although I caught the greatest number of bees in Lake Manitoba Plain, this ecoregion tended to have the lowest number of species on average. Communities in each ecoregion were distinct (Table 3) despite some overlap in ordination space (Fig. 4). Aspen Parkland had smaller community dispersion than Lake Manitoba Plain or Interlake Plain, but not Lake of the Woods (Table 4). Community dispersions between Lake Manitoba Plain, Interlake Plain, and Lake of the Woods were not different from one another. Indicator species analysis revealed that sand-nesting species (e.g. *Lasioglossum pruinosum*) were associated with the Aspen Parkland while wood-nesting species (e.g. *L. nigroviride*, *L. cressonii*, *L. oblongum*) were associated with Lake of the Woods and Interlake Plain (Table S3).

Summer-long community composition changed with disturbed land cover (Table 3). Urban area explained the greatest proportion of variation in composition, followed by forb crop and cereal crop cover. Common species associated with disturbed cover were *Melissodes agilis* with forb crop cover and *Lasioglossum zonulus* with cereal crop cover (Fig. 3). No common species were associated with urban area.

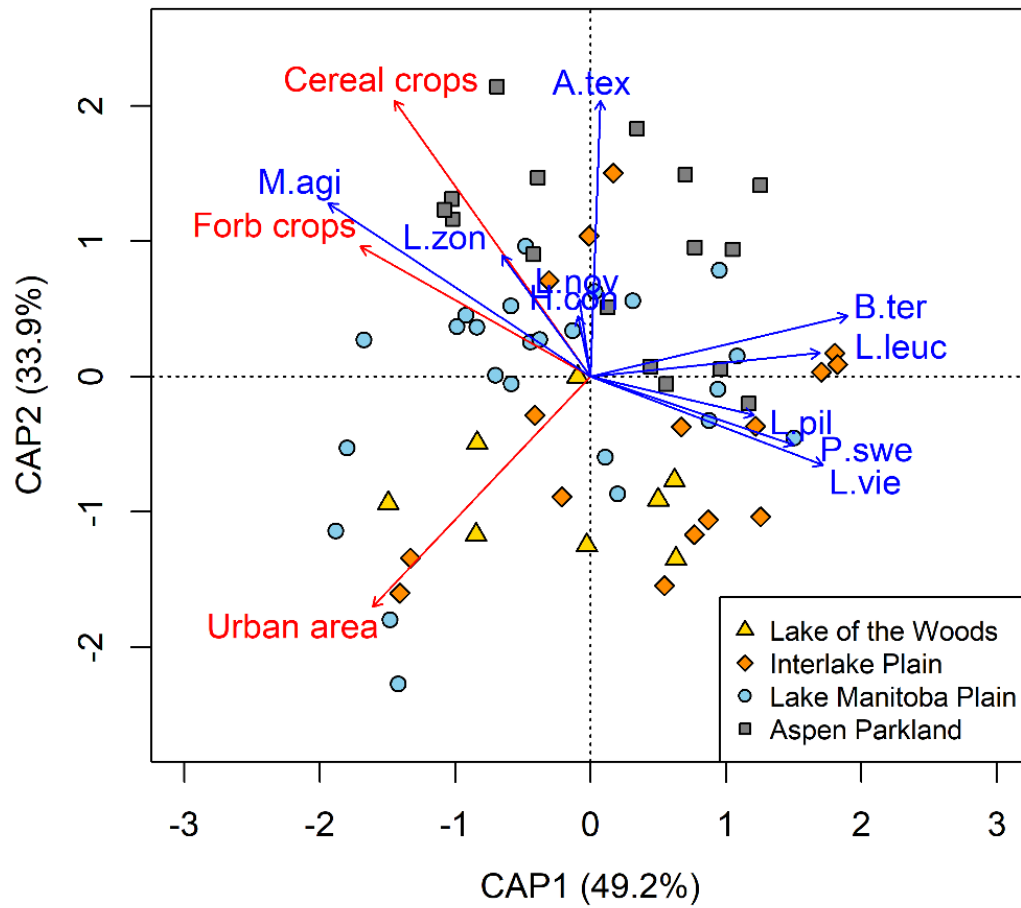


Fig. 4. Ordination of a dbRDA using Bray-Curtis dissimilarity of wild bee communities at all sites ($n=64$), grouped by ecoregion. Points represent summer-long communities. Sites were also constrained by their dissimilarities in disturbed land cover (forb crop cover, cereal crop cover, urban area). Red arrows are land cover in a 1000 m buffer. Blue arrows are the top-ten most abundant species. L.zon=*Lasioglossum zonulus*, L.pil=*Lasioglossum pilosum*, A.tex=*Agapostemon texanus*, L.nov=*Lasioglossum novascotiae*, M.agi=*Melissodes agilis*, H.con=*Halictus confusus*, L.leuc=*Lasioglossum leucocomus*, B.ter=*Bombus ternarius*, P.swe=*Perdita swenki*, L.vie=*Lasioglossum vierecki*.

Table 3. Landscape-level model results on community composition by ecoregion. Community Bray-Curtis dissimilarities were assessed using perMANOVA followed by a multiple pairwise comparison test. Landscape variables were calculated in a 1000 m buffer. Significant p-values are shown in bold ($\alpha=0.05$).

Predictor	d.f.	Sum of squares	R²	F	p
Cereal crop cover	1	0.432	0.025	1.929	0.0150
Forb crop cover	1	0.497	0.028	2.221	0.0100
Urban area	1	0.831	0.048	3.713	0.0010
Ecoregion	3	2.379	0.136	3.544	0.0010
Residual	57	12.75	0.731		
Total	63	17.45	1.000		
Ecoregion pairs:					
Aspen Parkland vs. Interlake Plain	1	1.056	0.131	4.517	0.001
Aspen Parkland vs. Lake Manitoba Plain	1	1.183	0.117	5.030	0.001
Aspen Parkland vs. Lake of the woods	1	1.218	0.202	5.574	0.001
Interlake Plain vs. Lake Manitoba Plain	1	0.751	0.070	2.869	0.002
Interlake Plain vs. Lake of the Woods	1	0.473	0.075	1.789	0.026
Lake Manitoba Plain vs. Lake of the Woods	1	0.646	0.077	2.505	0.002

Table 4. Bee community dispersion per ecoregion, assessed using perMANOVA followed by a multiple pairwise comparison test. Significant p-values are shown in bold ($\alpha=0.05$).

Predictor	d.f.	Sum of squares	F	p
Dispersion	3	0.046	4.088	0.0110
Residuals	60	0.227		
Ecoregion pairs:	d.f.	Difference	±95CI	p
Aspen Parkland vs. Interlake Plain	1	-0.067	0.057	0.0157
Aspen Parkland vs. Lake Manitoba Plain	1	-0.061	0.052	0.0169
Aspen Parkland vs. Lake of the woods	1	-0.040	0.070	0.4374
Interlake Plain vs. Lake Manitoba Plain	1	0.006	0.052	0.9885
Interlake Plain vs. Lake of the Woods	1	0.027	0.070	0.7442
Lake Manitoba Plain vs. Lake of the Woods	1	0.021	0.066	0.8459

Effect of landscape disturbance on bee abundance and diversity

Bee communities were influenced by landscape disturbance at scales of either 750 m (abundance, functional dispersion) or 1000 m (richness) (Table 5). Cereal crop cover reduced bee abundance (Fig. 5A) and richness (Fig. 5B) across all sites, suggesting that areas with greater cereal crop cover support fewer bees and have a less diverse bee community than areas with less cereal crops. The effects of forb crop cover were somewhat moderated by ecoregion (Table S4). Where it had an effect, forb crop cover usually reduced bee abundance (Fig. 6A-D) and richness (Fig. 7A-D), although effects were opposite in Lake of the Woods compared to other ecoregions. Greater crop cover (regardless of crop type) therefore reduces bee abundance and richness in most areas.

Effects of SHDI and edge density on bee abundance and richness were also moderated by ecoregion (Table S4). In ecoregions besides Lake of the Woods, an increase in SHDI usually had a positive effect on bee abundance (Fig. 6E-H) and richness (Fig. 7E-H), suggesting that areas with greater land cover diversity support greater abundances and more diverse communities of wild bees compared to areas with lower land cover diversity. Edge density had the opposite effects on abundance and richness in most ecoregions, such that an increase in edge density reduced bee abundance (Fig. 6I-L) and richness (Fig. 7I-L). This could indicate that areas with a more fields and thus a greater number of field edges supports fewer bees and bee species. However, functional dispersion of bee communities decreased with land cover diversity (Fig. 5C) and increased with edge density (Fig. 5D) regardless of ecoregion, which suggests that smaller field sizes improves trait accumulation better than land cover diversity.

Forb and cereal crop cover unimodally influenced SHDI (forb: $\beta=-1.9683$, $SE=0.3625$, $t=-5.43$, $p<0.0001$; cereal: $\beta=-0.8735$, $SE=0.3678$, $t=-2.38$, $p=0.0182$) (Fig. 8A-B) and negatively affected edge density (forb: $\beta=-0.7106$, $SE=0.1687$, $t=-4.21$, $p<0.0001$; cereal: $\beta=-1.7473$, $SE=0.2071$, $t=-8.44$, $p<0.0001$) (Fig. 8C-D). For SHDI, a value of 1.5 was the same for both 0% and 70% crop cover, indicating that it cannot adequately distinguish between levels of disturbance. Values of both SHDI and edge density thus depend on landscape context, which could have contributed to variation in bee responses due to ecoregion since some ecoregions (especially Aspen Parkland) were heavily dominated by agriculture compared to others.

Table 5. Global landscape-level model results on bee communities. Site was included as a random effect (n=64). Models were calculated at seven buffer sizes, but only the buffer size with the lowest AIC_c scores are reported. Significant p-values are shown in bold ($\alpha=0.05$). All variables had variance inflation factors ≤ 4 .

	Abundance				Rarefied richness				Functional dispersion			
Buffer size (m)	750				1000				750			
Pseudo-R _M ²	0.056				0.302				0.253			
Pseudo-R _C ²	0.088				0.328				0.321			
Predictor	ln(β)	SE	z	p	β	SE	z	p	β	SE	z	p
Intercept	4.2653	0.2255	18.91	<0.0001	9.9452	1.2026	8.27	<0.0001	0.2270	0.0193	11.76	<0.0001
Year	0.0163	0.0618	0.26	0.7925	1.0256	0.2950	3.48	0.0005	0.0093	0.0053	1.77	0.0774
Julian day	-0.0793	0.0409	-1.94	0.0529	0.3518	0.2185	1.61	0.1074	0.0264	0.0036	7.38	<0.0001
Julian day ²	0.0658	0.0439	1.50	0.1342	0.3958	0.2355	1.68	0.0928	0.0097	0.0039	2.53	0.0114
Julian day ³	0.1975	0.0399	4.96	<0.0001	1.1212	0.2161	5.19	<0.0001	-0.0092	0.0036	-2.59	0.0097
Latitude	0.0216	0.0559	0.39	0.6996	-1.4251	0.2570	-5.55	<0.0001	-0.0043	0.0046	-0.93	0.3537
Longitude	-0.1471	0.0571	-2.57	0.0100	-0.6284	0.2626	-2.39	0.0167	0.0146	0.0048	3.07	0.0022
PC1	-0.0399	0.0490	-0.81	0.4159	0.1840	0.2671	0.69	0.4908	0.0054	0.0044	1.25	0.2116
PC2	0.0370	0.0486	0.76	0.4468	-0.3864	0.2561	-1.51	0.1314	0.0001	0.0040	0.02	0.9823
Trap number	-0.0161	0.0432	-0.37	0.7099	0.1477	0.2221	0.67	0.5060	0.0048	0.0037	1.31	0.1913
Minutes	0.0422	0.0406	1.04	0.2981	0.2936	0.2299	1.28	0.2016	0.0051	0.0038	1.34	0.1791
Cereal crop cover (%)	-0.0122	0.0047	-2.58	0.0100	-0.0917	0.0247	-3.72	0.0002	0.0004	0.0004	1.07	0.2849
Forb crop cover (%)	-0.0069	0.0040	-1.74	0.0815	-0.0044	0.0187	-0.23	0.8151	0.0006	0.0003	1.81	0.0697
Urban area (%)	-0.0049	0.0041	-1.18	0.2398	-0.0158	0.0203	-0.78	0.4361	0.0003	0.0003	0.88	0.3776
SHDI	0.4888	0.2118	2.31	0.0210	2.4901	0.9736	2.56	0.0105	-0.0433	0.0175	-2.47	0.0134
Edge density (m/ha)	-0.0039	0.0014	-2.76	0.0058	0.0015	0.0067	0.23	0.8202	0.0003	0.0001	2.73	0.0064

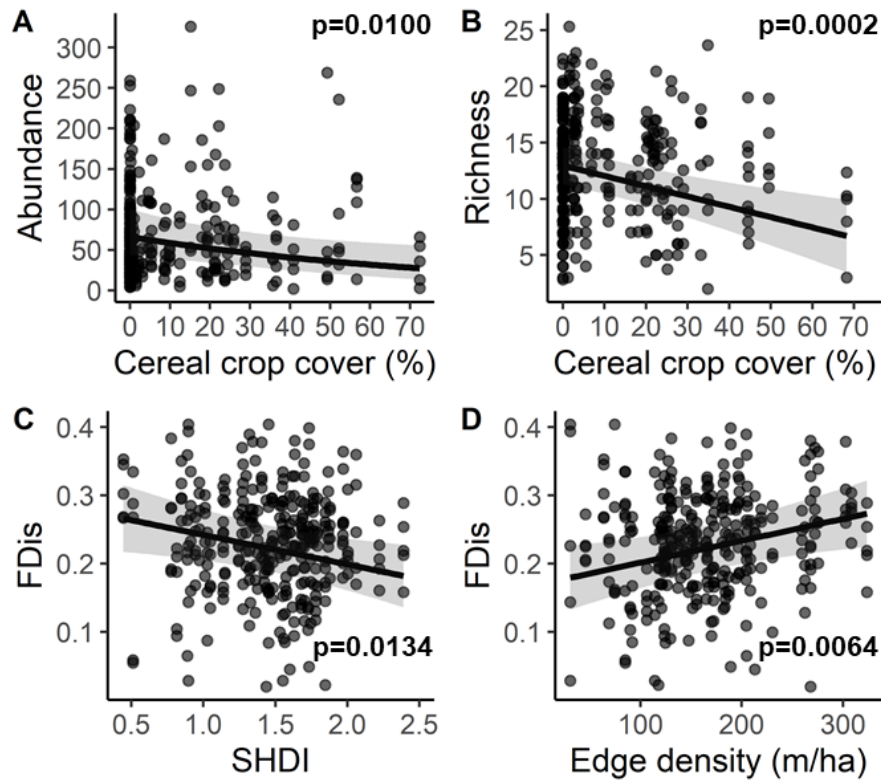


Fig. 5. Effects of (A-B) cereal crop cover, (C) Shannon's landscape diversity index, and (D) edge density on wild bee abundance, rarefied species richness, and functional dispersion across all ecoregions. Landscapes were calculated in a 750 m buffer (abundance, functional dispersion) or 1000 m buffer (richness). Points represent observed values per sampling event. Regression lines represent predicted values from GLMM. Shaded areas around regression lines are 95% confidence intervals.

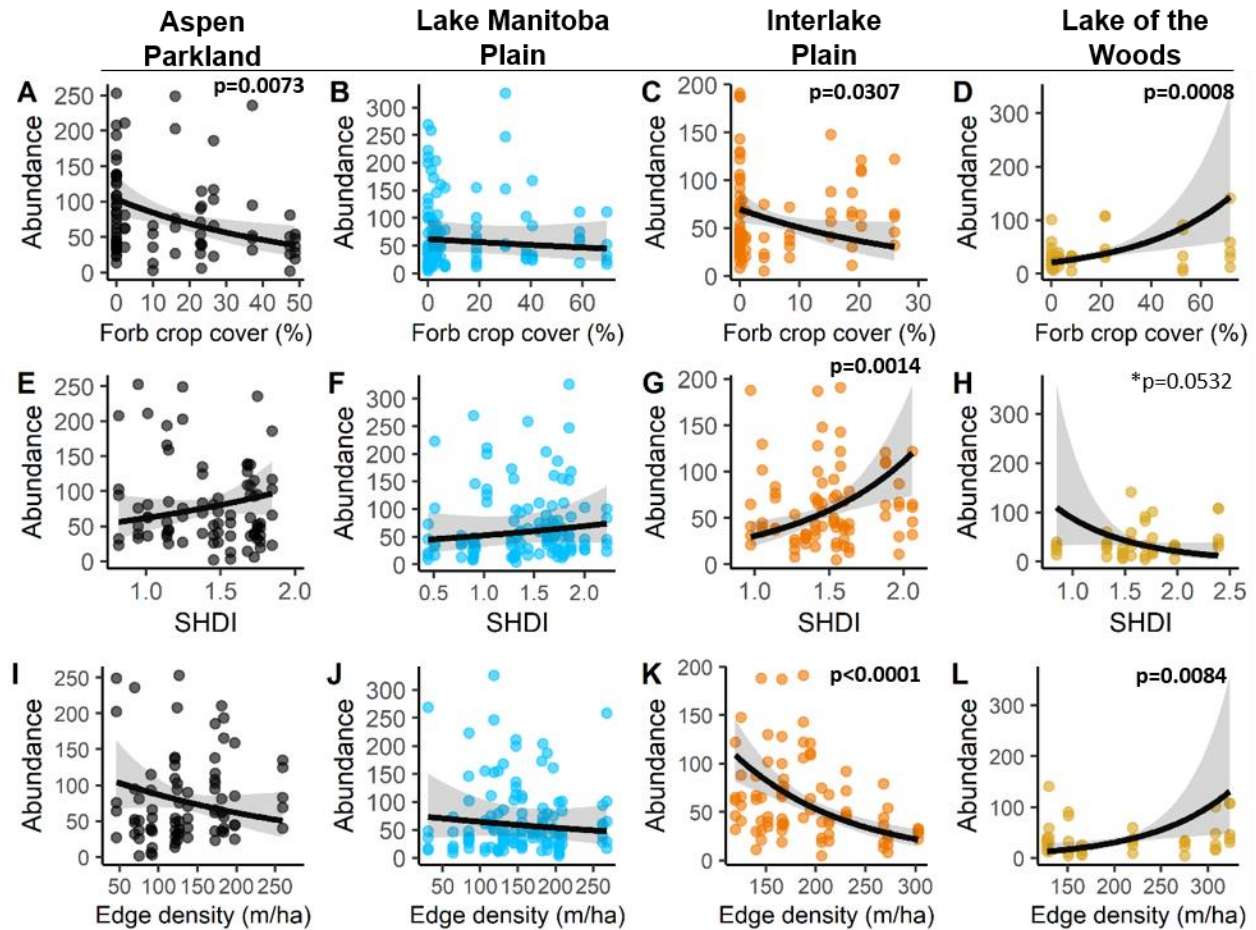


Fig. 6. Ecoregion-dependent effects of landscape disturbance on wild bee abundance. Points represent observations per sampling event. Regression lines represent predicted values from GLMM. Shaded areas around regression lines are 95% confidence intervals. Significant effects are shown with bolded p-values; marginal effect ($p < 0.1$) shown with an asterisk (*). All landscape values were calculated in a 750 m buffer.

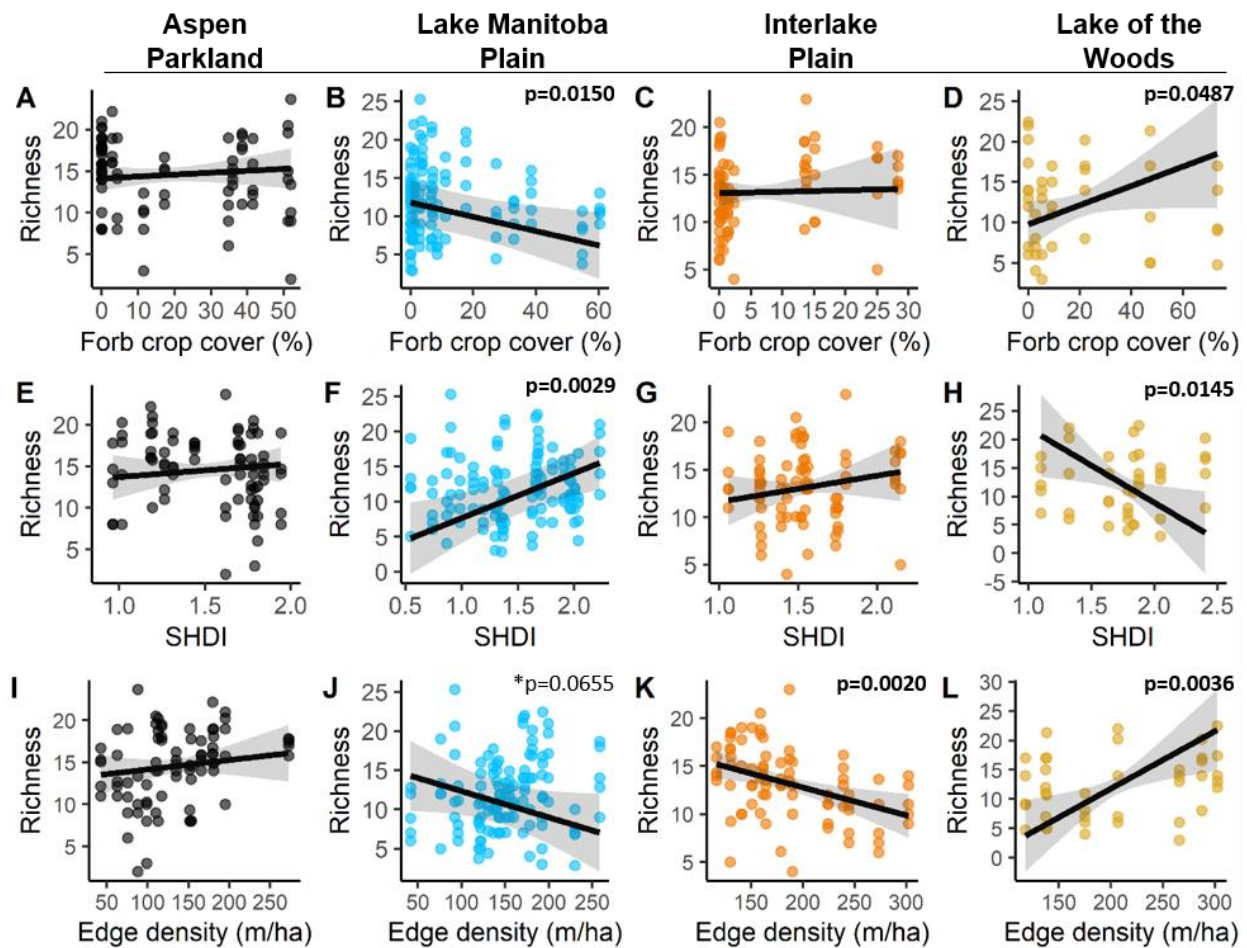


Fig. 7. Ecoregion-dependent effects of landscape disturbance on wild bee rarefied species richness. Points represent observations per sampling event. Regression lines represent predicted values from GLMM. Shaded areas around regression lines are 95% confidence intervals. Significant effects are shown with bolded p-values; marginal effect ($p < 0.1$) shown with an asterisk (*). All landscape values were calculated in a 1000 m buffer.

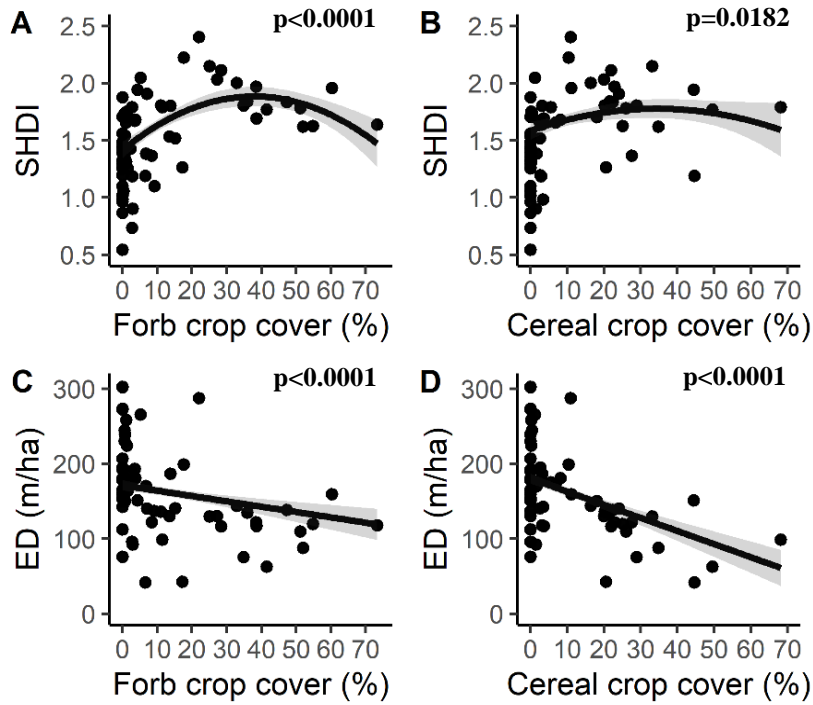


Fig. 8. Correlation between (A-B) SHDI and (C-D) ED with forb crop cover (left column) and cereal crop cover (right column) in a 1000 m buffer. Points represent sampling events. Shaded areas around regression lines are 95% confidence intervals.

Effects of local land cover

Across all sites, average grass cover was 62.9% (1.8–99.6%), average bare ground was 17.3% (0–83.1%), and average flower cover was 0.15% (0–0.79%). I found a total of 216 flowering plant species across all sites. Most species were native (184) compared to introduced (32). The mean total number of species (\pm SD) at any given site over the summer was 39 ± 12 species, and on any given sampling day was 12 ± 7 species. Flower richness at all sites was heavily dominated by native species ($80 \pm 8\%$ of all species). Flower richness did not influence flower cover (GLM, $t=0.664$, $p=0.508$), indicating that they were unrelated. Only variables relating to grass cover and flowers influenced bee communities (Table 6). Both flower cover and total flower richness reduced bee abundance (Fig. 9A-B). Introduced flower richness increased functional dispersion (Fig. 9D), but did not affect bee abundance or richness. Grass cover decreased bee richness (Fig. 9C). Grass cover increased linearly with urban area (Fig. 10), while flower cover and richness were not influenced by disturbed land cover.

Table 6. Local-level model results on bee communities caught in 2019. Significant p-values are shown in bold ($\alpha=0.05$). All variables had variance inflation factors ≤ 4 .

	Abundance				Rarefied richness				Functional dispersion			
Pseudo-R_M^2	0.095				0.317				0.341			
Pseudo-R_C^2	0.095				0.342				0.456			
Predictor	ln(β)	SE	z	p	β	SE	z	p	β	SE	z	p
Intercept	5.0597	0.3641	13.90	<0.0001	18.9316	2.3718	7.98	<0.0001	0.2356	0.0452	5.21	<0.0001
Julian day	-0.0181	0.0678	-0.27	0.7901	0.2269	0.3990	0.57	0.5695	0.0155	0.0070	2.20	0.0280
Julian day ²	-0.1959	0.0690	-2.84	0.0045	0.6007	0.4101	1.46	0.1430	0.0290	0.0071	4.10	<0.0001
Julian day ³	0.3639	0.0546	6.67	<0.0001	1.1507	0.3048	3.78	0.0002	-0.0111	0.0053	-2.07	0.0380
PC1	0.0236	0.0487	0.48	0.6286	0.2487	0.3014	0.83	0.4092	0.0073	0.0052	1.41	0.1593
PC2	-0.0294	0.0489	-0.60	0.5474	-0.0189	0.2864	-0.07	0.9473	0.0144	0.0050	2.86	0.0042
Trap number	-0.0859	0.0609	-1.41	0.1582	0.5766	0.3826	1.51	0.1318	0.0096	0.0062	1.54	0.1235
Minutes	-0.1380	0.0668	-2.07	0.0389	-0.6707	0.3716	-1.81	0.0711	0.0098	0.0065	1.51	0.1314
Latitude	-0.0026	0.0555	-0.05	0.9632	-1.4356	0.3260	-4.40	<0.0001	-0.0007	0.0070	-0.10	0.9222
Longitude	-0.0228	0.0554	-0.41	0.6803	-0.3872	0.3615	-1.07	0.2841	0.0062	0.0075	0.82	0.4102
Grass cover	-0.0039	0.0037	-1.07	0.2832	-0.0665	0.0247	-2.70	0.0070	-0.0005	0.0005	-1.03	0.3051
Bare ground	0.0024	0.0038	0.64	0.5251	-0.0387	0.0243	-1.59	0.1116	-0.0008	0.0005	-1.64	0.1009
Flower cover	-1.4491	0.2993	-4.84	<0.0001	-3.5209	1.8205	-1.93	0.0531	0.0439	0.0320	1.37	0.1695
Total flower richness	-0.0390	0.0115	-3.40	0.0007	0.0206	0.0719	0.29	0.7742	0.0013	0.0013	0.94	0.3476
Introduced flower richness	0.0048	0.0331	0.14	0.8851	0.1396	0.2053	0.68	0.4964	0.0078	0.0037	2.10	0.0355

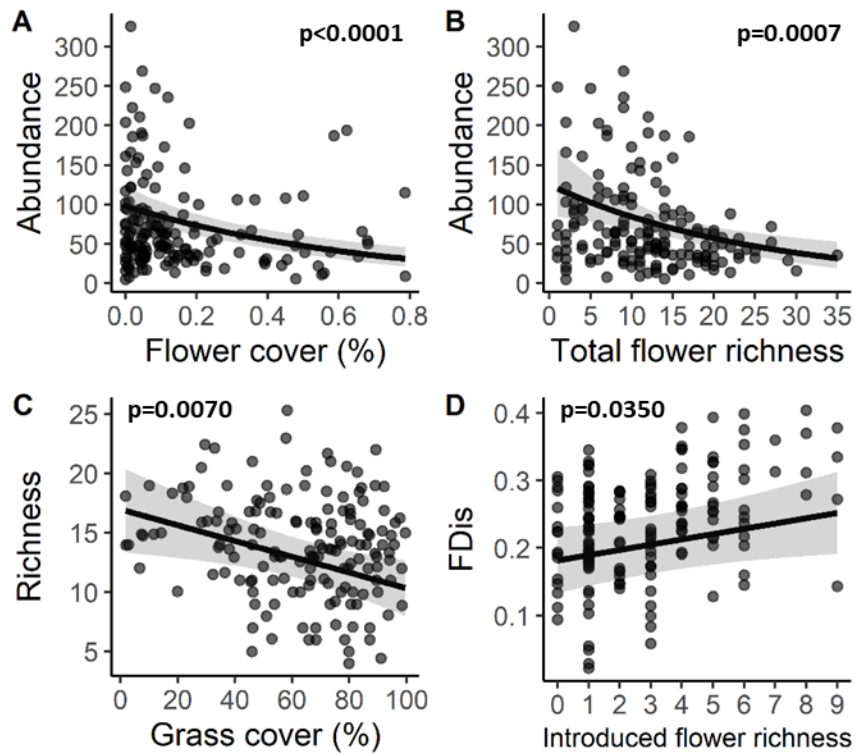


Fig. 9. Local effects on (A-B) abundance, (C) richness, and (C) functional dispersion (FDis) of wild bee communities. Points represent observed values per sampling event. Regression lines represent predicted values from GLMM. Shaded areas around regression lines are 95% confidence intervals. Local data were gathered in 2019 only.

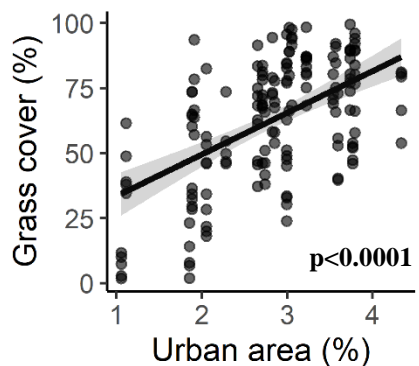


Fig. 10. Effect of urban area in a 1000 m buffer on local grass cover around traps in 2019. Points represent observed values per sampling event. Regression lines represent predicted values from linear regression. Shaded areas around regression lines are 95% confidence intervals.

Discussion

I found that habitat disturbance caused by human activities at both the local and landscape scales influenced bee communities across southern Manitoba. However, the type of disturbance and ecoregional context influenced how bee communities were affected.

Cereal crops had a negative effect on bee abundance and richness regardless of ecoregion. Cereal crops are resource-poor and are large sources of pesticides (Malaj et al. 2020), both of which could have contributed to less abundant and diverse communities of bees in this study. However, functional dispersion was unaffected by crop cover. Odanaka and Rehan (2019) found that functional diversity did not change despite changes to species richness and abundance under varying disturbance pressures and land management types, when using a similar but slightly different approach to calculate community trait differences. Some traits can make individual species more susceptible to habitat disturbance than others (Williams et al. 2010; Forrest et al. 2015; De Palma et al. 2015, 2016). However, traits defined as susceptible are not consistent across studies and can depend on the type of disturbance. The collection of functional traits in a community can also alter susceptibility to changes in community composition due to disturbance, such that communities may become functionally similar (i.e. are dominated by common, disturbance-tolerant traits) (Moretti et al. 2009). In this study, I found that cereal crop cover changed community composition. It could be that susceptible species were replaced with disturbance-tolerant species in areas with greater cereal crop cover, but that communities retained similar values of functional dispersion.

Canola and soybean were the most abundant forb crops across my sites and were in full bloom during my sampling period. Bees are known to visit both for pollen and nectar (de O. Milfont et al. 2013; Adamidis et al. 2019), and polylectic species are especially attracted to canola (Holzschuh et al. 2013). I expected forb crop cover to potentially benefit bees since they can be used as ephemeral resources by a large portion of the community, but found that the effects of forb crop cover depend on ecoregion. Pesticides are commonly used when growing canola and soybean and can persist in the environment in natural water features like wetlands (Malaj et al. 2020). This could have contributed to a decline in species richness in Lake Manitoba Plain, which is where most of my wetland-dominant sites were. Even though forb crop cover might be

beneficial to bees, they are a ‘boom-or-bust’ resource and any positive effect could be short lived if the crop is replaced by a less attractive crop the following year during yearly crop rotations.

Landscape diversity positive impacts on bee abundance and richness in this study, which aligned with my predictions. This suggests that more numerous and diverse patch types provides additional habitat for species to exploit. The exception to this trend was in Lake of the Woods where abundance and richness declined in response to landscape diversity. Landscape diversity estimates are known to depend on regional context (Martins et al. 2015; Martin et al. 2020), such that similar values of SHDI in landscapes dominated by one set of cover types are not biologically equivalent to landscapes with a different set of cover types (Martin et al. 2020). In this study, I noted that SHDI could be enhanced by increasing crop cover. Lake of the Woods is predominantly forest and has had far less land converted to crops compared to Aspen Parkland or Lake Manitoba Plain. Adding cropland in Lake of the Woods appears to have an adverse affect on bees, even though adding cropland increases landscape diversity. In addition, I found that wild bee species composition differed significantly between ecoregions, probably due to variability in vegetation and abiotic characteristics (soil type, moisture, average temperature, etc.). Differences in land cover as well as species composition likely explain why communities in Lake of the Woods responded differently to landscape diversity than communities in other ecoregions.

I predicted that functional dispersion would increase in response to increasing landscape diversity, but I found the opposite effect: functional dispersion declined as SHDI increased, the effect of which was independent of ecoregion. A decline in functional dispersion can indicate a loss of uncommon traits from the community. Since the functional dispersion index is an abundance-weighted metric (Laliberté and Legendre 2010), a decline can also indicate an increase in abundance of individuals with common traits without a loss of uncommon traits. My functional dispersion indices were negatively correlated with abundance, which suggests that at least the former is occurring. Although I found that more species-rich communities had slightly higher functional dispersion, the functional dispersion index is purportedly unaffected by species richness values because only trait abundance is taken into account (Laliberté and Legendre 2010). Diverse landscapes supported a greater abundance and richness bees in this study at the

cost of functional dispersion, but this may be an effect of increasing abundance of common traits in larger communities rather than the loss of uncommon traits.

I found the opposite pattern between bee communities and fragmentation, such that landscapes with higher edge density supported fewer bees but had greater functional dispersion. Whereas land cover diversity benefits bee abundance and richness, fragmentation appears to benefit community functional dispersion regardless of a decrease in abundance and/or richness. Hass et al (2018) demonstrated that greater edge density obtained through smaller field sizes and maximal crop-crop borders can enhance bee abundance and diversity by connecting foraging areas in the landscape. Reduced field sizes may be one such way of enhancing edges within agricultural landscapes, but more work would be needed to understand if the effect of average field size is similar to the effect edge density on bees in my study system. My study suggests that land management strategies simultaneously enhancing edge density and land cover diversity can maximize bee abundance, richness, and functional traits.

Only one other study has examined the impact of landscape-level, human-driven disturbances on wild bee communities in Manitoba (Olynyk et al. 2021). Olynyk et al. (2021) showed that human activities causing grassland habitat loss, such as annual cropping and road development, decreased both social and below-ground nesting bee abundances. In this study, I did not find any strong evidence of an effect of urban area on whole bee communities. My estimate of urban area included both the gravel or concrete surfaces that make up roads and highways, as well as the semi-natural ditches and verges that run alongside them. Although the roads themselves remove habitat, ditches and verges can provide suitable habitat for wild bees because they can contain floral and nesting resources and can act as refugia in highly disturbed landscapes (Hopwood 2008; Cole et al. 2017), possibly explaining why I did not see a negative effect as predicted.

Local land cover influenced bee communities in this study, particularly variables relating to blooming flowers. Greater flower cover and richness are known to increase bee abundance and diversity through greater forage availability (Patenaude 2007; Hülsmann et al. 2015; Cole et al. 2017; Andrieu et al. 2018). However, I found that sites with greater flower cover or richness supported fewer bees than sites with minimal flower cover or richness, which is opposite to what I expected. Interestingly, flower cover was not related to flower diversity in this study.

Therefore, some sites with high flower cover could have been dominated by one or a few species. If these species are not attractive or beneficial to bees, then that particular site would support less bees even though it has high flower cover. Trap captures can also be problematic when relating bee communities to local flower variables since other studies have shown that pan traps (Cane et al. 2000) and blue vane traps (Gibbs et al. 2017b) may not accurately reflect the abundance or richness of bees visiting flowers. Diet specialist bees in particular are caught less frequently in traps than on their host flowers (Cane et al. 2000). My results suggest that greater flower cover and diversity does not necessarily equate to better resources for bees, but this trend may be influenced by catch method.

My study suggests that local flower richness benefits functional dispersion even when bee richness is unaffected. Greater trait diversity is favourable in agroecosystems, and has been shown to increase pollination services in caged systems (Fründ et al. 2013) and in pumpkin crops (Hoehn et al. 2008). I found that introduced plant species in particular promoted bee functional diversity, and did not negatively impact bee abundance or richness. Patenaude (2007) found that wild bee abundance and richness in the Manitoban mixed-grass prairie did not change in areas dominated by introduced plants. In Michigan, Carson et al. (2016) found that introduced spotted knapweed (*Centaurea stoebe*) attracts a wide range of bee species even in areas that are not dominated by knapweed. It is possible that introduced plants found in disturbed areas, such as alfalfa and sweetclover, are visited by bees in the absence of similar native varieties. In regards to physiological effects, one study found that introduced plants can be used by the generalist bumble bee *Bombus terrestris* without negative consequences to its populations (Drossart et al. 2017), but more studies are needed to fully understand the physiological effects of introduced plants on bees. These studies and mine suggest that introduced plants in field margins do not pose a threat to the persistence of bee communities in disturbed areas, while a monoculture of domesticated plants is more likely to cause negative effects on bee communities. A diverse plant community composed of both introduced and native plants can maintain bee abundance and diversity (Patenaude 2007; Carson et al. 2016).

I chose to sample in areas next to residual habitat in order to increase my odds of finding bees, since semi-natural habitats (including ditches and road verges) harbour bee communities (Lagerlöf et al. 1992; Kells et al. 2001). My abundance and diversity estimates are likely higher

than they would be if I had sampled in more disturbed areas (e.g., within crop fields). Even so, I was able to find bees in even the most degraded sites, suggesting that even small amounts of residual semi-natural habitat are critical for supporting wild bees.

Conclusion

Bee communities are responding to both local and landscape drivers in southern Manitoba, but responses are ecoregion-dependent. My results suggest that managing for smaller field sizes and increasing land cover diversity can support an abundant and diverse assemblage of wild bees with a wide array of functional traits. Bees in the Lake of the Woods ecoregion seem to respond differently to landscape disturbance compared to bees across other ecoregions, suggesting a need for ecoregion-specific conservation plans. Since introduced plants in field margins did not negatively affect bee abundance or richness and increased levels of functional dispersion, land managers should reconsider removing introduced plant species unless there is a plan to replace them with native species. In heavily disturbed landscapes, introduced plant species are often the only forage available to bees. Future research and management should occur at the local and landscape scales, since both are relevant to wild bees.

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Supplementary tables and figures

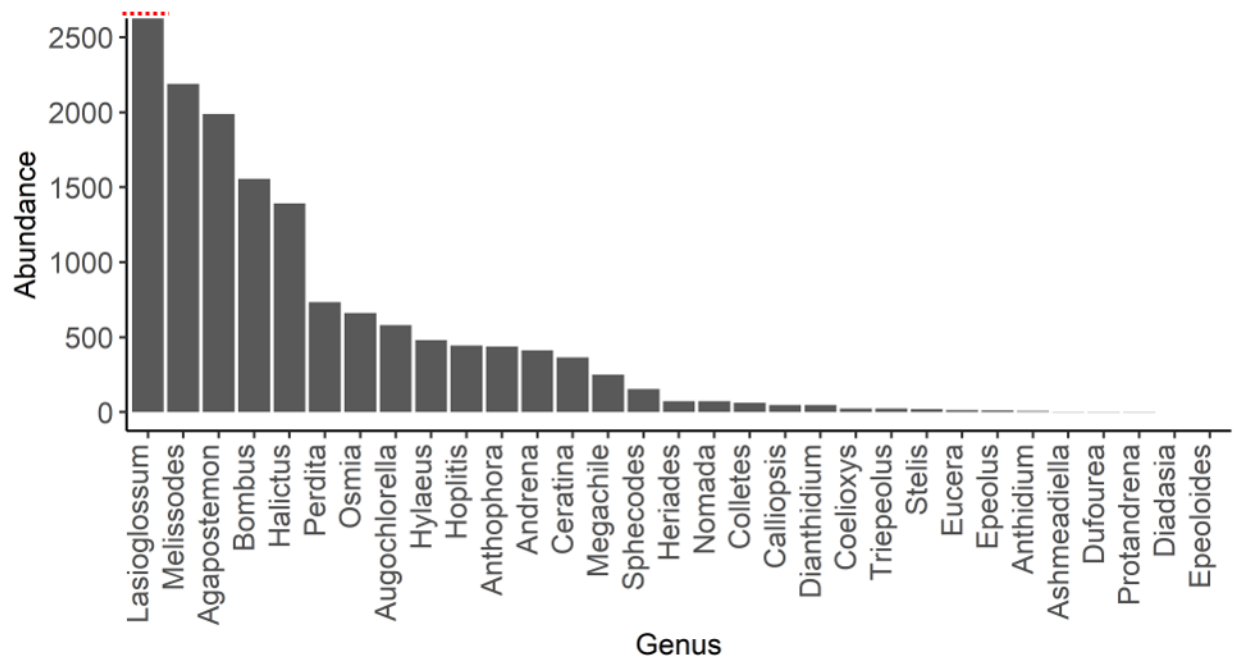


Fig. S1. Trap-collected bee abundance per genus across all sites (n=64). Total *Lasioglossum* abundance was 8952 (greater than plot margins). *Diadasia* and *Epeoloides* each had one individual.

Table S1. Site coordinates and dates sampled. Location names are based on the town, park or wildlife management area (WMA) they are near. Latitude and longitude are in decimal degrees. Site codes with a 1 were also aerial netted.

Site code	Latitude	Longitude	Dates sampled			
			May	June	July	August
2018						
Criddle/Vane Homestead Provincial Park						
AwP1D	49.716	-99.644	—	06, 28	17	07, 22
AwP1N	49.709	-99.603	—	06, 28	17	07, 22
AwP2D	49.665	-99.677	—	06, 28	17	07, 22
AwP2N	49.679	-99.600	—	06, 28	17	07, 22
Birds Hill Provincial Park						
BHP1D	50.042	-96.921	25	21	13	02, 18
BHP1N	50.011	-96.930	25	21	13	02, 18
BHP2D	50.062	-96.883	25	21	13	02, 18
BHP2N	50.033	-96.863	25	21	13	02, 18
Delta Marsh WMA						
DMP1D	50.152	-98.340	23	20	12, 30	20
DMP1N	50.176	-98.313	23	20	12, 30	20
DMP2D	50.137	-98.407	23	20	12, 30	20
DMP2N	50.170	-98.374	23	20	12, 30	20
Portage La Prairie						
PLPP1D	49.901	-98.343	—	04, 27	16	03, 21
PLPP1N	49.887	-98.297	—	04, 27	16	03, 21
PLPP2D	49.930	-98.262	—	04, 27	16	03, 21
PLPP2N	49.930	-98.330	—	04, 27	16	03, 21
Sandilands Provincial Forest						
SLP1D	49.676	-95.898	21	13	09, 24	13
SLP1N	49.635	-95.922	21	13	09, 24	13
SLP2D	49.712	-95.899	21	13	09, 24	13
SLP2N	49.694	-95.930	21	13	09, 24	13
Seven Sisters Falls						
SSP1D	50.095	-96.042	28	—	05, 23	08, 24
SSP1N	50.114	-96.026	28	—	05, 23	08, 24
SSP2D	50.090	-95.947	28	—	05, 23	08, 24
SSP2N	50.110	-95.887	28	—	05, 23	08, 24
Spruce Woods Provincial Park						
SWP1D	49.842	-99.251	—	09	06, 20	09, 29
SWP1N	49.730	-99.294	—	09	06, 20	09, 29
SWP2D	49.812	-99.303	—	09	06, 20	09, 29
SWP2N	49.709	-99.264	—	09	06, 20	09, 29
Winnipeg						
WinP1D	49.838	-97.299	22	15	10, 26	14
WinP1N	49.854	-97.246	22	15	10, 26	14
WinP2D	49.814	-97.254	22	15	10, 26	14
WinP2N	49.825	-97.225	22	15	10, 26	14

Table S1 cont'd

Site code	Latitude	Longitude	Dates sampled			
			May	June	July	August
2019						
Assiniboine Corridor WMA						
ACP1D	49.565	-99.325	30	26	19	09, 28
ACP1N	49.593	-99.346	30	26	19	09, 28
ACP2D	49.563	-99.394	30	26	19	09, 28
ACP2N	49.584	-99.392	30	26	19	09, 28
Mars Hill WMA						
MHP1D	50.251	-96.512	—	05, 24	23	13, 30
MHP1N	50.266	-96.568	—	05, 24	23	13, 30
MHP2D	50.239	-96.668	—	05, 24	23	13, 30
MHP2N	50.237	-96.613	—	05, 24	23	13, 30
Nourse						
NP1D	49.895	-96.430	29	20	16	08,20
NP1N	49.914	-96.433	29	20	16	08,20
NP2D	49.899	-96.394	29	20	16	08,20
NP2N	49.905	-96.361	29	20	16	08,20
Oak Hammock Marsh WMA						
OHMP1D	50.182	-97.161	28	18	12	07,19
OHMP1N	50.204	-97.161	28	18	12	07,19
OHMP2D	50.142	-97.184	28	18	12	07,19
OHMP2N	50.168	-97.131	28	18	12	07,19
Portage Sand Hills WMA						
PSHP1D	49.798	-98.165	21	14	05, 31	16
PSHP1N	49.799	-98.217	21	14	05, 31	16
PSHP2D	49.800	-98.324	21	14	05, 31	16
PSHP2N	49.798	-98.255	21	14	05, 31	16
Canadian Forces Base Shilo						
SHP1D	49.778	-99.689	23	12	10	04, 21
SHP1N	49.836	-99.584	23	12	10	04, 21
SHP2D	49.828	-99.689	23	12	10	04, 21
SHP2N	49.807	-99.511	23	12	10	04, 21
Senkiw						
SKP1D	49.237	-96.964	17	10	04, 29	15
SKP1N	49.207	-96.872	17	10	04, 29	15
SKP2D	49.238	-96.917	17	10	04, 29	15
SKP2N	49.209	-96.917	17	10	04, 29	15
Sandridge WMA						
SRP1D	50.566	-97.546	14	06, 27	24	14
SRP1N	50.610	-97.508	14	06, 27	24	14
SRP2D	50.551	-97.508	14	06, 27	24	14
SRP2N	50.581	-97.495	14	06, 27	24	14

Table S2. List of bee species sorted alphabetically by family, genus, subgenus, and species. Total number of species (excluding unknowns) is 273. Abundance by catch method are given. New records for Manitoba are in bold, and for Canada include an asterisk.

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
Andrenidae				1,093	103	192	1,388
<i>Andrena</i>	(<i>Andrena</i>)	<i>frigida</i>	Smith 1853	5	2	1	8
<i>Andrena</i>	(<i>Andrena</i>)	<i>thaspiae</i>	Graenicher 1903	10	4	7	21
<i>Andrena</i>	(<i>Callandrena s.l.</i>)	<i>asteris</i>	Robertson 1891	6	2	1	9
<i>Andrena</i>	(<i>Callandrena s.l.</i>)	<i>helianthi</i>	Robertson 1891	0	0	1	1
<i>Andrena</i>	(<i>Cnemidandrena</i>)	<i>canadensis</i>	Dalla Torre 1896	1	0	1	2
<i>Andrena</i>	(<i>Cnemidandrena</i>)	<i>chromotricha</i>	Cockerell 1899	0	2	0	2
<i>Andrena</i>	(<i>Cnemidandrena</i>)	<i>hirticincta</i>	Provancher 1888	0	0	3	3
<i>Andrena</i>	(<i>Euandrena</i>)	<i>algida</i>	Smith 1853	6	0	0	6
<i>Andrena</i>	(<i>Euandrena</i>)	<i>aff. nigrihirta</i>	(Ashmead 1890)	12	1	0	13
<i>Andrena</i>	(<i>Gonandrena</i>)	<i>persimulata</i>	Viereck 1917	2	1	5	8
<i>Andrena</i>	(<i>Holandrena</i>)	<i>cressonii cressonii</i>	Robertson 1891	1	0	0	1
<i>Andrena</i>	(<i>Larandrena</i>)	<i>miserabilis</i>	Cresson 1872	1	0	0	1
<i>Andrena</i>	(<i>Leucandrena</i>)	<i>barbilabris</i>	(Kirby 1802)	84	2	6	92
<i>Andrena</i>	(<i>Melandrena</i>)	<i>carlini</i>	Cockerell 1901	31	1	4	36
<i>Andrena</i>	(<i>Melandrena</i>)	<i>commoda</i>	Smith 1879	4	1	2	7
<i>Andrena</i>	(<i>Melandrena</i>)	<i>dunningi</i>	Cockerell 1898	3	0	5	8
<i>Andrena</i>	(<i>Melandrena</i>)	<i>erythrogaster</i>	(Ashmead 1890)	1	1	0	2
<i>Andrena</i>	(<i>Melandrena</i>)	<i>lupinorum</i>	Cockerell 1906	36	4	7	47
<i>Andrena</i>	(<i>Melandrena</i>)	<i>nivalis</i>	Smith 1853	3	0	4	7
<i>Andrena</i>	(<i>Melandrena</i>)	<i>regularis</i>	Malloch 1917	0	0	2	2
<i>Andrena</i>	(<i>Melandrena</i>)	<i>vicina</i>	Smith 1853	3	0	9	12
<i>Andrena</i>	(<i>Micrandrena</i>)	<i>melanochroa</i>	Cockerell 1898	1	0	1	2
<i>Andrena</i>	(<i>Micrandrena</i>)	<i>nubecula</i>	Smith 1853	0	0	1	1
<i>Andrena</i>	(<i>Micrandrena</i>)	<i>salictaria</i>	Robertson 1905	5	0	0	5
<i>Andrena</i>	(<i>Micrandrena</i>)	<i>ziziae</i>	Robertson 1891	3	0	27	30
<i>Andrena</i>	(<i>Parandrena</i>)	<i>andrenoides</i>	(Cresson 1878)	2	0	0	2
<i>Andrena</i>	(<i>Parandrena</i>)	<i>wellesleyana</i>	Robertson 1897	5	0	0	5
<i>Andrena</i>	(<i>Plastandrena</i>)	<i>crataegi</i>	Robertson 1893	0	0	2	2

Table S2 cont'd

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
<i>Andrena</i>	(<i>Plastandrena</i>)	<i>prunorum prunorum</i>	Cockerell 1896	12	5	0	17
<i>Andrena</i>	(<i>Callandrena</i> s.l.)	<i>placata</i>	Mitchell 1960	0	0	1	1
<i>Andrena</i>	(<i>Scrapteropsis</i>)	<i>alleghaniensis</i>	Viereck 1907	6	0	1	7
<i>Andrena</i>	(<i>Scrapteropsis</i>)	<i>imitatrix</i>	Cresson 1872	1	0	1	2
<i>Andrena</i>	(<i>Simandrena</i>)	<i>wheeleri</i>	Graenicher 1904	0	0	1	1
<i>Andrena</i>	(<i>Taeniandrena</i>)	<i>wilkella</i>	(Kirby 1802)	24	6	20	50
<i>Andrena</i>	(<i>Thysandrena</i>)	<i>medionitens</i>	Cockerell 1902	2	0	1	3
<i>Andrena</i>	(<i>Thysandrena</i>)	<i>w-scripta</i>	Viereck 1904	0	0	1	1
<i>Andrena</i>	(<i>Trachandrena</i>)	<i>cyanophila</i>	Cockerell 1906	75	13	0	88
<i>Andrena</i>	(<i>Trachandrena</i>)	<i>forbesii</i>	Robertson 1891	1	0	3	4
<i>Andrena</i>	(<i>Trachandrena</i>)	<i>hippotes</i>	Robertson 1895	0	0	5	5
<i>Andrena</i>	(<i>Trachandrena</i>)	<i>mariae</i>	Robertson 1891	4	2	0	6
<i>Andrena</i>	(<i>Trachandrena</i>)	<i>miranda</i>	Smith 1879	1	0	5	6
<i>Andrena</i>	(<i>Trachandrena</i>)	<i>sigmundi</i>	Cockerell 1902	13	0	1	14
<i>Calliopsis</i>	(<i>Calliopsis</i>)	<i>andreniformis</i>	Smith 1853	45	3	0	48
<i>Perdita</i>	(<i>Cockerellia</i>)	<i>albipennis canadensis</i>	Crawford 1912	18	9	0	27
<i>Perdita</i>	(<i>Perdita</i>)	<i>bruneri</i>	Cockerell 1897	5	4	1	10
<i>Perdita</i>	(<i>Perdita</i>)	<i>halictoides</i>	Smith 1853	21	0	0	21
<i>Perdita</i>	(<i>Perdita</i>)	<i>perpallida perpallida</i>	Cockerell 1901	7	1	7	15
<i>Perdita</i>	(<i>Perdita</i>)	<i>swenki</i>	Crawford 1915	632	37	50	719
<i>Protandrena</i>	(<i>Pterosarus</i>)	<i>aestivalis</i>	(Provancher 1882)	0	1	3	4
<i>Protandrena</i>	(<i>Pterosarus</i>)	<i>innuptus</i>	(Cockerell 1896)	1	0	0	1
<i>Protandrena</i>	(<i>Pterosarus</i>)	<i>simulans</i>	(Swenk & Cockerell 1907)	0	1	1	2
<i>Protandrena</i>	(<i>Pterosarus</i>)	sp.		0	0	1	1
Apidae				1,507	3,161	800	5,468
<i>Anthophora</i>	(<i>Clisodon</i>)	<i>terminalis</i>	Cresson 1869	65	338	7	410
<i>Anthophora</i>	(<i>Melea</i>)	<i>bomboides</i>	Kirby 1837	0	15	0	15
<i>Anthophora</i>	(<i>Melea</i>)	<i>occidentalis</i>	Cresson 1869	1	18	0	19
<i>Bombus</i>	(<i>Bombias</i>)	<i>nevadensis</i>	Cresson 1874	0	17	2	19
<i>Bombus</i>	(<i>Bombus</i>)	<i>terricola</i>	Kirby 1837	9	13	17	39

Table S2 cont'd

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
<i>Bombus</i>	(<i>Cullumanobombus</i>)	<i>griseocollis</i>	(DeGeer 1773)	13	10	47	70
<i>Bombus</i>	(<i>Cullumanobombus</i>)	<i>rufocinctus</i>	Cresson 1863	157	194	128	479
<i>Bombus</i>	(<i>Psithyrus</i>)	<i>flavidus</i>	Eversmann 1852	0	0	1	1
<i>Bombus</i>	(<i>Psithyrus</i>)	<i>insularis</i>	(Smith 1861)	0	1	0	1
<i>Bombus</i>	(<i>Pyrobombus</i>)	<i>bimaculatus</i>	Cresson 1863	4	13	36	53
<i>Bombus</i>	(<i>Pyrobombus</i>)	<i>melanopygus</i>	Nylander 1848	0	1	0	1
<i>Bombus</i>	(<i>Pyrobombus</i>)	<i>perplexus</i>	Cresson 1863	1	2	8	11
<i>Bombus</i>	(<i>Pyrobombus</i>)	<i>sandersoni</i>	Franklin 1913	3	4	2	9
<i>Bombus</i>	(<i>Pyrobombus</i>)	<i>ternarius</i>	Say 1837	140	441	195	776
<i>Bombus</i>	(<i>Pyrobombus</i>)	<i>vagans vagans</i>	Smith 1854	69	97	79	245
<i>Bombus</i>	(<i>Subterraneobombus</i>)	<i>borealis</i>	Kirby 1837	51	307	44	402
<i>Bombus</i>	(<i>Thoracobombus</i>)	<i>fervidus</i>	(Fabricius 1798)	1	8	1	10
<i>Ceratina</i>	(<i>Zadontomerus</i>)	<i>calcarata</i>	Robertson 1900	40	5	34	79
<i>Ceratina</i>	(<i>Zadontomerus</i>)	<i>dupla</i>	Say 1837	14	11	5	30
<i>Ceratina</i>	(<i>Zadontomerus</i>)	<i>mikmaqi</i>	Rehan & Sheffield 2011	256	38	91	385
<i>Ceratina</i>	(<i>Zadontomerus</i>)	sp.		0	0	1	1
<i>Diadasia</i>	(<i>Coquillettapis</i>)	<i>australis australis</i>	(Cresson 1878)	0	1	0	1
<i>Epeoloides</i>		<i>pilosulus</i>	(Cresson 1878)	1	0	0	1
<i>Epeolus</i>		<i>americanus</i>	(Cresson 1878)	1	0	0	1
<i>Epeolus</i>		<i>gibbsi</i>	Onuferko 2018	1	0	0	1
<i>Epeolus</i>		<i>interruptus</i>	Robertson 1900	0	0	1	1
<i>Epeolus</i>		<i>minimus</i>	(Robertson 1902)	10	0	1	11
<i>Eucera</i>	(<i>Synhalonia</i>)	<i>atriventris</i>	(Smith 1854)	1	11	0	12
<i>Eucera</i>	(<i>Synhalonia</i>)	<i>chrysobotryae</i>*	(Cockerell 1908)	0	1	0	1
<i>Eucera</i>	(<i>Synhalonia</i>)	sp.	(Timberlake 1969)	0	1	0	1
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>agilis</i>	Cresson 1878	122	900	9	1,031
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>bidentis</i>	Cockerell 1914	0	1	0	1
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>confusus</i>	Cresson 1878	183	317	20	520
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>coreopsis</i>	Robertson 1905	32	14	7	53
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>denticulatus</i>	Smith 1854	0	1	0	1
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>druriellus</i>	(Kirby 1802)	89	30	7	126

Table S2 cont'd

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>illatus</i>	Lovell & Cockerell 1906	1	0	1	2
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>snowii</i>	Cresson 1872	2	1	0	3
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>subillatus</i>	LaBerge 1961	0	2	5	7
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>trinodis</i>	Robertson 1901	74	309	30	413
<i>Melissodes</i>	(<i>Eumelissodes</i>)	<i>wheeleri</i>	Cockerell 1906	76	15	2	93
<i>Melissodes</i>	(<i>Heliomelissodes</i>)	<i>rivalis</i>	Cresson 1872	5	14	0	19
<i>Nomada</i>		<i>fervida</i>	Swenk 1913	3	0	0	3
<i>Nomada</i>		cf. <i>armatella</i>	Cockerell 1903	1	0	0	1
<i>Nomada</i>		<i>articulata</i>	Smith 1854	10	1	1	12
<i>Nomada</i>		<i>australis</i>	Mitchell 1962	1	0	0	1
<i>Nomada</i>		cf. <i>bella</i>	Cresson 1863	2	0	0	2
<i>Nomada</i>		<i>crawfordi</i>*	Cockerell 1905	0	0	1	1
<i>Nomada</i>		<i>cuneata</i>	(Robertson 1903)	3	0	1	4
<i>Nomada</i>		<i>denticulata</i>	Robertson 1902	6	0	0	6
<i>Nomada</i>		<i>fuscicincta</i>*	Swenk 1915	5	0	7	12
<i>Nomada</i>		<i>imbricata</i>	Smith 1854	3	0	0	3
<i>Nomada</i>		<i>inepta</i>	Mitchell 1962	0	1	0	1
<i>Nomada</i>		<i>integerrima</i>	Dalla Torre 1896	9	0	0	9
<i>Nomada</i>		<i>lehighensis</i>	Cockerell 1903	1	0	1	2
<i>Nomada</i>		<i>lepida</i>	Cresson 1863	2	0	0	2
<i>Nomada</i>		<i>luteoloides</i>	Robertson 1895	1	0	0	1
<i>Nomada</i>		<i>maculata</i>	Cresson 1863	3	0	2	5
<i>Nomada</i>		<i>obliterata</i>	Cresson 1863	3	2	0	5
<i>Nomada</i>		<i>ovata</i>	(Robertson 1903)	3	0	0	3
<i>Nomada</i>		cf. <i>perplexa</i>	Cresson 1863	0	1	0	1
<i>Nomada</i>		<i>quadrimaculata</i>	Robertson 1903	1	0	0	1
<i>Nomada</i>		sp. 1		2	0	0	2
<i>Nomada</i>		sp. 2		1	0	0	1
<i>Nomada</i>		sp. 3		1	0	0	1
<i>Nomada</i>		sp. 4		1	0	0	1
<i>Nomada</i>		<i>sphaerogaster</i>*	Cockerell 1903	1	0	0	1

Table S2 cont'd

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
<i>Nomada</i>		<i>vincta</i>	Say 1837	4	0	0	4
<i>Triepeolus</i>		<i>helianthi</i>	(Robertson 1897)	2	3	1	6
<i>Triepeolus</i>		<i>obliteratus</i>	Graenicher 1911	13	0	3	16
<i>Triepeolus</i>		<i>occidentalis</i>	(Cresson 1878)	1	1	0	2
<i>Triepeolus</i>		<i>pectoralis</i>	(Robertson 1897)	1	0	0	1
<i>Triepeolus</i>		<i>subalpinus</i>	Cockerell 1910	0	1	1	2
<i>Triepeolus</i>		sp.		1	0	1	2
Colletidae				472	70	353	895
<i>Colletes</i>		<i>brevicornis</i>	Robertson 1897	3	1	3	7
<i>Colletes</i>		<i>consors mesocopus</i>	Cresson 1868	11	0	0	11
<i>Colletes</i>		<i>hyalinus hyalinus</i>	Provancher 1888	4	1	4	9
<i>Colletes</i>		<i>inaequalis</i>	Say 1837	30	2	4	36
<i>Colletes</i>		<i>kincaidii</i>	Cockerell 1898	8	2	9	19
<i>Colletes</i>		<i>simulans armatus</i>	Cresson 1868	0	0	3	3
<i>Colletes</i>		<i>susannae</i>	Swenk 1925	1	0	0	1
<i>Colletes</i>		<i>willistoni</i>	Robertson 1891	0	0	1	1
<i>Hylaeus</i>	(<i>Cephalylaeus</i>)	<i>basalis</i>	(Smith 1853)	3	0	0	3
<i>Hylaeus</i>	(<i>Hylaeus</i>)	<i>annulatus</i>	(Linnaeus 1758)	31	19	25	75
<i>Hylaeus</i>	(<i>Hylaeus</i>)	<i>mesillae cressoni</i>	(Cockerell 1907)	131	10	154	295
<i>Hylaeus</i>	(<i>Hylaeus</i>)	<i>rudbeckiae</i>	Cockerell & Casad 1895	1	0	0	1
<i>Hylaeus</i>	(<i>Hylaeus</i>)	<i>verticalis</i>	(Cresson 1869)	0	0	1	1
<i>Hylaeus</i>	(<i>Prosopis</i>)	<i>affinis</i>	(Smith 1853)	144	4	32	180
<i>Hylaeus</i>	(<i>Prosopis</i>)	cf. <i>gaigei</i>	(Cockerell 1916)	11	0	0	11
<i>Hylaeus</i>	(<i>Prosopis</i>)	<i>illinoisensis</i>	(Robertson 1896)	36	10	0	46
<i>Hylaeus</i>	(<i>Prosopis</i>)	<i>modestus modestus</i>	Say 1837	42	8	42	92
<i>Hylaeus</i>	(<i>Prosopis</i>)	<i>nelumbonis</i>	(Robertson 1890)	14	13	75	102
<i>Hylaeus</i>	(<i>Prosopis</i>)	sp. A		2	0	0	2
Halictidae				9,929	3,140	537	13,606
<i>Agapostemon</i>	(<i>Agapostemon</i>)	<i>sericeus</i>	(Forster 1771)	315	60	6	381
<i>Agapostemon</i>	(<i>Agapostemon</i>)	<i>splendens</i>	(Lepeletier 1841)	418	28	7	453

Table S2 cont'd

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
<i>Agapostemon</i>	(<i>Agapostemon</i>)	<i>texanus</i>	Cresson 1872	805	327	2	1,134
<i>Agapostemon</i>	(<i>Agapostemon</i>)	<i>virescens</i>	(Fabricius 1775)	30	6	0	36
<i>Augochlorella</i>		<i>aurata</i>	(Smith 1853)	554	25	62	641
<i>Dufourea</i>		<i>harveyi</i>	(Cockerell 1906)	1	0	0	1
<i>Dufourea</i>		<i>marginata marginata</i>	(Cresson 1878)	0	1	0	1
<i>Dufourea</i>		<i>maura</i>	(Cresson 1878)	1	0	0	1
<i>Halictus</i>	(<i>Nealictus</i>)	<i>parallelus</i>	Say 1837	6	28	1	35
<i>Halictus</i>	(<i>Protohalictus</i>)	<i>rubicundus</i>	(Christ 1791)	347	145	19	511
<i>Halictus</i>	(<i>Seladonia</i>)	<i>confusus confusus</i>	Smith 1853	835	31	72	938
<i>Lasioglossum</i>	(<i>Dialictus</i>)	cf. <i>abanci</i>	(Crawford 1932)	0	0	2	2
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>absimile</i>*	(Sandhouse 1924)	118	12	2	132
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>admirandum</i>	(Sandhouse 1924)	17	5	0	22
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>albipenne</i>	(Robertson 1890)	180	80	25	285
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>cressonii</i>	(Robertson 1890)	9	1	2	12
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>dreisbachi</i>	(Mitchell 1960)	2	0	0	2
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>ellisiae</i>	(Sandhouse 1924)	33	1	2	36
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>ephialtum</i>	Gibbs 2010	18	7	5	30
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>imitatum</i>	(Smith 1853)	3	0	0	3
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>laevissimum</i>	(Smith 1853)	30	11	9	50
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>leucocomus</i>	(Lovell 1908)	645	138	34	817
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>lineatulum</i>	(Crawford 1906)	50	14	23	87
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>michiganense</i>	(Mitchell 1960)	1	0	0	1
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>nigroviride</i>	(Graenicher 1911)	4	0	3	7
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>novascotiae</i>	(Mitchell 1960)	678	414	11	1,103
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>oblongum</i>	(Lovell 1905)	5	1	3	9
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>occidentale</i>	(Crawford 1902)	174	11	9	194
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>paradmirandum</i>	(Knerer & Atwood 1966)	5	0	0	5
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>perpunctatum</i>	(Ellis 1913)	362	78	34	474
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>pictum</i>	(Crawford 1902)	145	16	2	163
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>pilosum</i>	(Smith 1853)	975	242	26	1,243
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>planatum</i>	(Lovell 1905)	33	6	6	45

Table S2 cont'd

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>pruinatum</i>	(Robertson 1892)	130	45	0	175
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>sagax</i>	(Sandhouse 1924)	22	10	1	33
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>semicaeruleum</i>	(Cockerell 1895)	4	2	0	6
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>sheffieldi</i>	Gibbs 2010	8	2	0	10
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>subversans</i>	(Mitchell 1960)	4	0	0	4
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>subviridatum</i>	(Cockerell 1938)	8	3	1	12
<i>Lasioglossum</i>	(<i>Dialictus</i>)	cf. <i>succinipenne</i>	(Ellis 1913)	37	9	29	75
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>timothyi</i>	Gibbs 2010	18	5	2	25
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>versans</i>	(Lovell 1905)	28	1	1	30
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>versatum</i>	(Robertson 1902)	5	2	0	7
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>vierecki</i>	(Crawford 1904)	582	29	24	635
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>viridatum</i>	(Lovell 1905)	181	59	5	245
<i>Lasioglossum</i>	(<i>Dialictus</i>)	<i>zephyrus</i>	(Smith 1853)	9	3	1	13
<i>Lasioglossum</i>	(<i>Evylaeus</i>)	<i>cinctipes</i>	(Provancher 1888)	3	3	4	10
<i>Lasioglossum</i>	(<i>Hemihalictus</i>)	<i>foxii</i>	(Robertson 1895)	1	1	0	2
<i>Lasioglossum</i>	(<i>Hemihalictus</i>)	<i>inconditum</i>	(Cockerell 1916)	1	0	0	1
<i>Lasioglossum</i>	(<i>Hemihalictus</i>)	<i>macoupinense</i>	(Robertson 1895)	4	1	1	6
<i>Lasioglossum</i>	(<i>Hemihalictus</i>)	<i>nelumbonis</i>	(Robertson 1890)	1	0	0	1
<i>Lasioglossum</i>	(<i>Hemihalictus</i>)	<i>pectorale</i>	(Smith 1853)	85	2	9	96
<i>Lasioglossum</i>	(<i>Hemihalictus</i>)	<i>swenki</i>	(Crawford 1906)	4	0	0	4
<i>Lasioglossum</i>	(<i>Lasioglossum</i>)	<i>acuminatum</i>	McGinley 1986	10	1	1	12
<i>Lasioglossum</i>	(<i>Lasioglossum</i>)	<i>athabascense</i>	(Sandhouse 1933)	5	1	0	6
<i>Lasioglossum</i>	(<i>Lasioglossum</i>)	<i>coriaceum</i>	(Smith 1853)	83	20	4	107
<i>Lasioglossum</i>	(<i>Lasioglossum</i>)	<i>paraforbesii</i>	McGinley 1986	225	155	0	380
<i>Lasioglossum</i>	(<i>Leuchalictus</i>)	<i>leucozonium</i>	(Schrank 1781)	423	70	32	525
<i>Lasioglossum</i>	(<i>Leuchalictus</i>)	<i>zonulus</i>	(Smith 1848)	1,087	1,005	29	2,121
<i>Lasioglossum</i>	(<i>Sphecodogastra</i>)	<i>quebecense</i>	(Crawford 1907)	3	4	1	8
<i>Lasioglossum</i>	(<i>Sphecodogastra</i>)	<i>truncatum</i>	(Robertson 1901)	5	15	3	23
<i>Lasioglossum</i>	(<i>Dialictus</i>)	sp.		3	1	2	6
<i>Sphecodes</i>		<i>atlantis</i>	Mitchell 1956	10	1	5	16

Table S2 cont'd

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
<i>Sphecodes</i>		<i>banksii</i>	Lovell 1909	2	0	1	3
<i>Sphecodes</i>		<i>clematidis</i>	Robertson 1897	3	0	0	3
<i>Sphecodes</i>		<i>confertus</i>	Say 1837	8	0	0	8
<i>Sphecodes</i>		<i>coronus</i>	Mitchell 1956	49	0	0	49
<i>Sphecodes</i>		<i>cressonii</i>	(Robertson 1903)	13	1	2	16
<i>Sphecodes</i>		<i>davisii</i>	Robertson 1897	19	0	1	20
<i>Sphecodes</i>		<i>dichrous</i>	Smith 1853	0	0	1	1
<i>Sphecodes</i>		<i>illinoensis</i>	(Robertson 1903)	13	0	4	17
<i>Sphecodes</i>		<i>levis</i>	Lovell & Cockerell 1907	1	0	0	1
<i>Sphecodes</i>		<i>mandibularis</i>	Cresson 1872	3	0	0	3
<i>Sphecodes</i>		<i>minor</i>	Robertson 1898	3	0	0	3
<i>Sphecodes</i>		<i>pecosensis pecosensis</i>	Cockerell 1904	3	0	0	3
<i>Sphecodes</i>		<i>cf. pycnanthemii</i>	Robertson 1897	7	1	0	8
<i>Sphecodes</i>		<i>usp.</i>		17	0	6	23
Megachilidae				1,154	371	304	1,829
<i>Anthidium</i>	(<i>Anthidium</i>)	<i>clypeodentatum</i>	Swenk 1914	3	1	5	9
<i>Anthidium</i>	(<i>Anthidium</i>)	<i>tenuiflorae</i>	Cockerell 1907	2	1	1	4
<i>Ashmeadiella</i>	(<i>Ashmeadiella</i>)	<i>bucconis bucconis</i>	(Say 1837)	2	1	1	4
<i>Coelioxys</i>	(<i>Boreocoelioxys</i>)	<i>moestus</i>	Smith 1854	0	0	1	1
<i>Coelioxys</i>	(<i>Boreocoelioxys</i>)	<i>porterae</i>	Cockerell 1900	1	0	0	1
<i>Coelioxys</i>	(<i>Boreocoelioxys</i>)	<i>rufitarsis</i>	Smith 1854	15	1	17	33
<i>Coelioxys</i>	(<i>Coelioxys</i>)	<i>sodalis</i>	Cresson 1878	1	1	0	2
<i>Coelioxys</i>	(<i>Cyrtocoelioxys</i>)	<i>modestus</i>	Smith 1854	0	1	2	3
<i>Coelioxys</i>	(<i>Paracoelioxys</i>)	<i>funerarius</i>	Smith 1854	1	2	2	5
<i>Coelioxys</i>	(<i>Synocoelioxys</i>)	<i>alternatus</i>	Say 1837	0	0	2	2
<i>Dianthidium</i>	(<i>Dianthidium</i>)	<i>concinnum</i>	(Cresson 1872)	6	2	1	9
<i>Dianthidium</i>	(<i>Dianthidium</i>)	<i>pudicum pudicum</i>	(Cresson 1879)	7	3	0	10
<i>Dianthidium</i>	(<i>Dianthidium</i>)	<i>simile</i>	(Cresson 1864)	26	3	19	48
<i>Heriades</i>	(<i>Neotrypetes</i>)	<i>carinata</i>	Cresson 1864	27	41	34	102
<i>Heriades</i>	(<i>Neotrypetes</i>)	<i>variolosa variolosa</i>	(Cresson 1872)	4	0	9	13

Table S2 cont'd

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
<i>Hoplitis</i>	(<i>Alcidamea</i>)	<i>albifrons albifrons</i>	(Kirby 1837)	17	1	0	18
<i>Hoplitis</i>	(<i>Alcidamea</i>)	<i>pilosifrons</i>	(Cresson 1864)	207	81	23	311
<i>Hoplitis</i>	(<i>Alcidamea</i>)	<i>producta producta</i>	(Cresson 1864)	115	1	12	128
<i>Hoplitis</i>	(<i>Alcidamea</i>)	<i>spoliata</i>	(Provancher 1888)	22	0	1	23
<i>Megachile</i>	(<i>Chelostomoides</i>)	<i>campanulae</i>	(Robertson 1903)	3	0	3	6
<i>Megachile</i>	(<i>Eutricharaea</i>)	<i>rotundata</i>	(Fabricius 1787)	3	0	4	7
<i>Megachile</i>	(<i>Litomegachile</i>)	<i>brevis</i>	Say 1837	4	1	1	6
<i>Megachile</i>	(<i>Litomegachile</i>)	<i>mendica</i>	Cresson 1878	2	0	0	2
<i>Megachile</i>	(<i>Litomegachile</i>)	<i>texana</i>	Cresson 1878	7	1	01	89
<i>Megachile</i>	(<i>Megachile</i>)	<i>centuncularis</i>	(Linnaeus 1758)	1	0	1	2
<i>Megachile</i>	(<i>Megachile</i>)	<i>inermis</i>	Provancher 1888	49	18	42	109
<i>Megachile</i>	(<i>Megachile</i>)	<i>montivaga</i>	Cresson 1878	8	1	1	10
<i>Megachile</i>	(<i>Megachile</i>)	<i>relativa</i>	Cresson 1878	30	4	32	66
<i>Megachile</i>	(<i>Megachiloides</i>)	<i>dakotensis</i>*	Mitchell 1926	0	0	1	1
<i>Megachile</i>	(<i>Sayapis</i>)	<i>pugnata pugnata</i>	Say 1837	9	1	7	17
<i>Megachile</i>	(<i>Xanthosarus</i>)	<i>circumcincta</i>	(Kirby 1802)	1	0	0	1
<i>Megachile</i>	(<i>Xanthosarus</i>)	<i>frigida frigida</i>	Smith 1853	2	1	3	6
<i>Megachile</i>	(<i>Xanthosarus</i>)	<i>gemula gemula</i>	Cresson 1878	2	1	0	3
<i>Megachile</i>	(<i>Xanthosarus</i>)	<i>latimanus</i>	Say 1823	42	41	41	124
<i>Megachile</i>	(<i>Xanthosarus</i>)	<i>melanophaea melanophaea</i>	Smith 1853	5	12	7	24
<i>Megachile</i>	(<i>Xanthosarus</i>)	<i>perihirta</i>	Cockerell 1898	1	0	0	1
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>illinoensis</i>	Robertson 1897	13	0	0	13
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>atriventris</i>	Cresson 1864	73	36	7	116
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>bucephala</i>	Cresson 1864	71	13	1	85
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>distincta</i>	Cresson 1864	90	11	2	103
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>inermis</i>	(Zetterstedt 1838)	1	0	0	1
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>integra</i>	Cresson 1878	8	6	0	14
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>proxima</i>	Cresson 1864	28	1	0	29
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>simillima</i>	Smith 1853	167	29	11	207
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>subarctica</i>	Cockerell 1912	5	0	1	6
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>tarsata</i>	Provancher 1888	1	0	0	1

Table S2 cont'd

Genus	Subgenus	Species	Author	Pan	BVT	Net	Total
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>tersula</i>	Cockerell 1912	47	47	2	96
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>trevoris</i>	Cockerell 1897	1	2	0	3
<i>Osmia</i>	(<i>Melanosmia</i>)	<i>virga</i>	Sandhouse 1939	0	3	0	3
<i>Osmia</i>	(<i>Osmia</i>)	<i>lignaria lignaria</i>	Say 1837	1	0	0	1
<i>Osmia</i>	(<i>Melanosmia</i>)	sp.		4	2	0	6
<i>Stelis</i>	(<i>Stelis</i>)	<i>coarctatus</i>	Crawford 1916	0	0	1	1
<i>Stelis</i>	(<i>Stelis</i>)	<i>foederalis</i>	Smith 1854	1	0	0	1
<i>Stelis</i>	(<i>Stelis</i>)	<i>lateralis</i>	Cresson 1864	18	0	5	23
Melittidae				0	0	3	3
<i>Macropis</i>	(<i>Macropis</i>)	<i>nuda</i>	(Provancher 1882)	0	0	3	3
Grand Total				14,155	6,845	2,189	23,189
(% of total)				(61.1%)	(29.5%)	(9.4%)	(100%)

Table S3. Indicator species analysis. No indicator species were found for LMP or IP alone. AP = Aspen Parkland, LMP = Lake Manitoba Plain, IP = Interlake Plain, LOTW = Lake of the Woods.

Ecoregion	Indicator species	Ecoregions	Indicator species
AP	<i>Andrena barbilabris</i>	AP + IP	<i>Lasioglossum vierecki</i>
	<i>A. lupinorum</i>		<i>Melissodes druriellus</i>
	<i>A. nigrihirta</i>		<i>Sphecodes coronus</i>
	<i>A. prunorum prunorum</i>	AP + LOTW	<i>Lasioglossum cf. succinipenne</i>
	<i>Bombus griseocollis</i>		<i>Melissodes coreopsis</i>
	<i>Dianthidium concinnum</i>		<i>Nomada integerrima</i>
	<i>Halictus parallelus</i>	IP + LOTW	<i>Ceratina calcarata</i>
	<i>Lasioglossum paraforbesii</i>		<i>Dianthidium pudicum pudicum</i>
	<i>L. pictum</i>		<i>Lasioglossum cressonii</i>
	<i>L. pruinatum</i>		<i>L. oblongum</i>
	<i>Melissodes rivalis</i>		<i>L. quebecense</i>
	<i>Osmia distincta</i>		<i>L. versans</i>
	<i>O. illinoensis</i>	LMP + LOTW	<i>Lasioglossum absimile</i>
	<i>Perdita albipennis canadensis</i>	AP + IP + LMP	<i>Agapostemon sericeus</i>
	<i>P. bruneri</i>	AP + IP + LOTW	<i>Lasioglossum leucocomus</i>
LOTW	<i>Andrena commoda</i>		<i>L. lineatulum</i>
	<i>Eucera atriventris</i>		<i>Osmia bucephala</i>
	<i>Lasioglossum nigroviride</i>	IP + LMP + LOTW	<i>Augochlorella aurata</i>
	<i>L. subversans</i>		<i>Ceratina dupla</i>
	<i>L. versatum</i>		<i>C. mikmaqi</i>
	<i>L. zephyrus</i>		<i>Hyleaus affinis</i>
	<i>Melissodes subillatus</i>		<i>Lasioglossum viridatum</i>
	<i>Nomada oblitterata</i>		<i>Melissodes confusus</i>

Table S4. Ecoregion-landscape interaction models, showing significant non-landscape variables and interactions only. Site used as a random effect. Significant p-values are shown in bold ($\alpha=0.05$). Dashes (—) indicate that the variable was omitted from the model.

	Abundance				Richness				Functional dispersion			
Buffer size (m)	750				1000				750			
Pseudo- R_M^2	0.091				0.325				0.283			
Pseudo- R_C^2	0.098				0.334				0.312			
Variable	ln(β)	SE	z	p	β	SE	z	p	β	SE	z	p
Intercept	4.1693	0.5285	7.89	<0.0001	10.344	3.3552	3.08	0.0021	0.2110	0.0526	4.01	0.0001
Year	—	—	—	—	0.8768	0.3208	2.73	0.0063	—	—	—	—
Julian day	-0.1071	0.0388	-2.76	0.0058	0.3624	0.2120	1.71	0.0874	0.0268	0.0035	7.67	0.0001
Julian day ²	0.0797	0.0392	2.03	0.0421	0.3023	0.2100	1.44	0.1500	0.0079	0.0035	2.30	0.0215
Julian day ³	0.1846	0.0390	4.73	<0.0001	1.0371	0.2155	4.81	<0.0001	-0.0092	0.0036	-2.59	0.0097
Cereal crops*AP-IP	-0.0156	0.0139	-1.12	0.2638	0.0214	0.1002	0.21	0.8306	0.0009	0.0013	0.71	0.4780
Cereal crops*AP-LMP	0.0080	0.0103	0.77	0.4403	-0.0914	0.0669	-1.37	0.1716	-0.0008	0.0009	-0.84	0.3992
Cereal crops*AP-LOTW	0.0229	0.0381	0.60	0.5473	0.3998	0.1337	2.99	0.0028	0.0037	0.0035	1.07	0.2835
Cereal crops*LMP-IP	-0.0235	0.0146	-1.62	0.1057	0.1129	0.1054	1.07	0.2844	0.0017	0.0014	1.25	0.2121
Cereal crops*LMP-LOTW	0.0149	0.0383	0.39	0.6965	0.4912	0.1371	3.58	0.0003	0.0045	0.0035	1.29	0.1967
Cereal crops*IP-LOTW	0.0385	0.0394	0.98	0.3293	0.3783	0.1565	2.42	0.0156	0.0028	0.0036	0.78	0.4380
Forb crops*AP-IP	-0.0124	0.0207	-0.60	0.5485	0.0365	0.1227	0.30	0.7662	0.0021	0.0020	1.01	0.3118
Forb crops*AP-LMP	0.0154	0.0087	1.76	0.0781	-0.0987	0.0441	-2.24	0.0252	-0.0016	0.0008	-2.02	0.0437
Forb crops*AP-LOTW	0.0456	0.0115	3.97	<0.0001	0.0885	0.0604	1.47	0.1429	-0.0017	0.0010	-1.60	0.1089
Forb crops*LMP-IP	-0.0278	0.0199	-1.40	0.1626	0.1352	0.1210	1.12	0.2637	0.0037	0.0020	1.88	0.0607
Forb crops*LMP-LOTW	0.0302	0.0100	3.04	0.0024	0.1872	0.0571	3.28	0.0011	-0.0001	0.0009	-0.06	0.9524
Forb crops*IP-LOTW	0.0580	0.0212	2.73	0.0063	0.0520	0.1274	0.41	0.6831	-0.0037	0.0021	-1.80	0.0716
Urban area*AP-IP	-0.1290	0.1095	-1.18	0.2391	-0.7713	0.7009	-1.10	0.2711	-0.0005	0.0105	-0.05	0.9591
Urban area*AP-LMP	-0.1216	0.1091	-1.11	0.2649	-0.7454	0.6967	-1.07	0.2847	0.0002	0.0105	0.02	0.9810
Urban area*AP-LOTW	-0.0909	0.1349	-0.67	0.5003	-0.6358	0.8052	-0.79	0.4298	-0.0145	0.0128	-1.14	0.2558
Urban area*LMP-IP	-0.0073	0.0107	-0.68	0.4948	-0.0260	0.0714	-0.36	0.7161	-0.0008	0.0010	-0.78	0.4330
Urban area*LMP-LOTW	0.0307	0.0797	0.39	0.7001	0.1096	0.4053	0.27	0.7868	-0.0147	0.0073	-2.03	0.0425

Table S4 cont'd

Variable	ln(β)	SE	z	p	β	SE	z	p	β	SE	z	p
Urban area*IP-LOTW	0.0380	0.0803	0.47	0.6358	0.1356	0.4111	0.33	0.7416	-0.0140	0.0073	-1.91	0.0567
SHDI*AP-IP	0.5841	0.6661	0.88	0.3805	-1.6787	3.8976	-0.43	0.6667	-0.0397	0.0636	-0.62	0.5327
SHDI*AP-LMP	-0.1930	0.4842	-0.40	0.6903	5.1514	2.8192	1.83	0.0677	0.0529	0.0447	1.18	0.2371
SHDI*AP-LOTW	-1.7419	0.9187	-1.90	0.0579	-14.759	4.9599	-2.98	0.0029	0.0126	0.0826	0.15	0.8784
SHDI*LMP-IP	0.7771	0.5790	1.34	0.1795	-6.8301	3.4823	-1.96	0.0498	-0.0926	0.0562	-1.65	0.0994
SHDI*LMP-LOTW	-1.5489	0.8576	-1.81	0.0709	-19.910	4.6017	-4.33	<0.0001	-0.0403	0.0771	-0.52	0.6013
SHDI*IP-LOTW	-2.3260	0.9724	-2.39	0.0168	-13.080	5.3564	-2.44	0.0146	0.0523	0.0892	0.59	0.5575
ED*AP-IP	-0.0057	0.0032	-1.80	0.0716	-0.0374	0.0171	-2.19	0.0284	0.0004	0.0003	1.38	0.1677
ED*AP-LMP	0.0014	0.0031	0.45	0.6549	-0.0425	0.0177	-2.41	0.0161	-0.0005	0.0003	-1.85	0.0648
ED*AP-LOTW	0.0136	0.0054	2.50	0.0126	0.0858	0.0300	2.86	0.0042	-0.0003	0.0005	-0.52	0.6019
ED*LMP-IP	-0.0071	0.0029	-2.48	0.0131	0.0051	0.0174	0.29	0.7699	0.0010	0.0003	3.51	0.0005
ED*LMP-LOTW	0.0122	0.0053	2.31	0.0206	0.1283	0.0302	4.24	<0.0001	0.0003	0.0005	0.61	0.5449
ED*IP-LOTW	0.0193	0.0053	3.62	0.0003	0.1232	0.0295	4.17	<0.0001	-0.0007	0.0005	-1.42	0.1568

Table S5. Landscape-level model results on bee abundance by ecoregion. All variables calculated in a 750 m buffer. Site was used as a random effect. Significant p-values are shown in bold ($\alpha=0.05$). All variables had variance inflation factors ≤ 4 .

	Aspen Parkland				Lake Manitoba Plain				Interlake Plain				Lake of the Woods			
Pseudo-R²_M	0.042				0.034				0.053				0.085			
Pseudo-R²_C	0.042				0.059				0.053				0.085			
Variable	ln(β)	SE	z	p	ln(β)	SE	z	p	ln(β)	SE	z	p	ln(β)	SE	z	p
Intercept	4.2104	0.5165	8.15	<0.0001	4.2414	0.3452	12.29	<0.0001	4.2375	0.4452	9.52	<0.0001	2.7397	0.4222	6.49	<0.0001
Cereal crop cover (%)	-0.0112	0.0066	-1.69	0.0915	-0.0014	0.0097	-0.14	0.8880	-0.0257	0.0097	-2.64	0.0083	0.0236	0.0338	0.70	0.4855
Forb crop cover (%)	-0.0202	0.0075	-2.68	0.0073	-0.0048	0.0057	-0.84	0.4020	-0.0320	0.0148	-2.16	0.0307	0.0266	0.0080	3.35	0.0008
Urban area (%)	0.1300	0.1088	1.19	0.2322	-0.0090	0.0043	-2.12	0.0340	-0.0163	0.0080	-2.04	0.0418	0.0316	0.0722	0.44	0.6621
SHDI	0.5267	0.4162	1.27	0.2057	0.2794	0.3105	0.90	0.3680	1.2875	0.4034	3.19	0.0014	-1.4361	0.7427	-1.93	0.0532
ED	-0.0034	0.0023	-1.48	0.1400	-0.0018	0.0024	-0.76	0.4480	-0.0088	0.0016	-5.39	<0.0001	0.0117	0.0044	2.63	0.0084

Table S6. Landscape-level model results on bee richness by ecoregion. All variables calculated in a 750 m buffer. Site was used as a random effect. Significant p-values are shown in bold ($\alpha=0.05$). All variables had variance inflation factors ≤ 4 .

	Aspen Parkland				Lake Manitoba Plain				Interlake Plain				Lake of the Woods			
Pseudo-R²_M	0.234				0.174				0.252				0.220			
Pseudo-R²_C	0.234				0.315				0.252				0.220			
Variable	β	SE	z	p	β	SE	z	p	β	SE	z	p	β	SE	z	p
Intercept	10.3619	3.2773	3.16	0.0016	10.8659	2.3296	4.66	<0.0001	15.4648	3.2209	4.80	<0.0001	10.893	3.9574	2.75	0.0059
Cereal crop cover (%)	-0.1229	0.0404	-3.04	0.0023	-0.1986	0.0738	-2.69	0.0071	-0.1168	0.0759	-1.54	0.1240	0.2604	0.1560	1.67	0.0950
Forb crop cover (%)	0.0229	0.0337	0.68	0.4966	-0.0935	0.0384	-2.43	0.0150	0.0159	0.0974	0.16	0.8700	0.1196	0.0607	1.97	0.0487
Urban area (%)	0.8937	0.6795	1.32	0.1884	-0.0065	0.0279	-0.23	0.8168	-0.1209	0.0525	-2.30	0.0210	0.1389	0.4991	0.28	0.7807
SHDI	1.5956	2.2954	0.70	0.4870	6.4140	2.1521	2.98	0.0029	2.7663	2.5510	1.08	0.2780	-13.0841	5.3507	-2.45	0.0145
ED	0.0112	0.0118	0.94	0.3447	-0.0336	0.0182	-1.84	0.0655	-0.0291	0.0094	-3.09	0.0020	0.0978	0.0336	2.91	0.0036

Preface to Chapter Three

In Chapter Two, I examined how landscape disturbance influenced bee communities. I found negative effects of crop cover on bee abundance and richness, and positive effects of land cover diversity on bee abundance and richness and edge density on functional dispersion. Bees are important pollinators of flowering plants and flowers are the primary source of nutrition for adult bees and their young. The interactions between bees and plants in the community creates a functional network that maintains ecosystem functioning. I wanted to investigate if changes to bee diversity found in Chapter Two translate to changes in bee-plant interactions. Changes to bee abundance and richness may change the structure and stability of network interactions. To address this question, I conducted a parallel study in which I netted bees from flowers at a subset of sites that were sampled with traps in Chapter Two. By associating host plant data with bee collections, I was able to build plant-bee networks and test for effects of landscape-level drivers on these interactions. Knowing the landscape-level drivers of both bee communities and networks can inform landscape management practices to preserve both wild bee populations and plant-bee networks.

CHAPTER 3: FRAGMENTED AND DIVERSE LANDSCAPES ENHANCE PLANT-BEE NETWORK SIZE AND STABILITY

Abstract

Background. Plant-bee network complexity and interaction redundancy can stabilize networks, making them more resilient against species loss. Conversely, human driven landscape disturbance resulting in habitat loss and fragmentation can make networks smaller and more unstable, which could cause them to collapse. The goal of this study is to determine the effects of disturbance on network size, structure, and function to inform land management practices.

Methods. I constructed 32 plant-bee networks across southern Manitoba, Canada, by aerial netting bees while they were foraging on flowers. I modelled the effects of habitat disturbance on network size (total number of species), structure (nestedness, connectance, and modularity), and stability (extinction slopes of bees). I included several landscape-level drivers in my models

(cereal crop cover, forb crop cover, urban area, edge density, and Shannon's Landscape Diversity Index).

Results. Network size increased in response to increasing edge density, suggesting that smaller field sizes and more edge habitat promotes accumulation of plant and bee species participating in networks. Increasing edge density, as well as greater crop cover, resulted in networks that had fewer realized interactions, less interaction redundancy, and more potential breaking points across the network, which other studies suggest contribute to network collapse. However, I did not find any evidence to suggest that edge density negatively affected network stability. Instead, network stability was reduced by crop cover and enhanced by land cover diversity, indicating that diverse landscapes with smaller field sizes and more edge habitat can promote bigger and more stable networks.

Conclusion. Plant-bee network size, structure, and stability are being negatively affected by cropping in southern Manitoba but enhanced by land cover diversity and fragmentation. Land management policies should aim to both increase the number of field edges in the landscape and land cover diversity to support plant-bee networks in agro-ecosystems.

Introduction

Ecological networks describe the wealth and complexity of interactions between organisms in an ecosystem (Ings et al. 2009), and are vital to the organization and persistence of biodiversity itself (Bascompte and Jordano 2007). Although the majority of network research has involved food webs, the study of mutualistic networks has gained in popularity since the early 2000s (Ings et al. 2009). Mutualistic networks involve the co-existence of species that are beneficial to each other, such as plants and their pollinators (Bascompte and Jordano 2007). Plant-bee networks are bipartite maps of the interactions between wild bees and their host plants in a community, where wild bees are all non-*Apis* species. Wild bees benefit from these interactions by receiving floral rewards from their host plants, which are used to nourish themselves and to provision the nest for their offspring. Since most flowering plants depend on insect pollinators — especially wild bees — to carry out sexual reproduction (Ollerton et al. 2011), preserving biodiverse networks is essential for maintaining ecosystem functioning.

Habitat loss and fragmentation resulting from human activities like agriculture and urban expansion has directly caused species loss of bees and pollinator-dependent plants (Biesmeijer et al. 2006; Potts et al. 2010; Winfree 2010; Bartomeus et al. 2013). This has resulted in changes to the size and structure of networks (Kearns et al. 1998; Spiesman and Inouye 2013; Burkle et al. 2013). Typical metrics used to quantify network structure include connectance (proportion of realized interactions compared to the total possible number of interactions), nestedness (amount of resource overlap between generalist and specialist species), and modularity (number of potential “breaking points” across the network). As habitat loss and land-use intensity increase, networks tend to get smaller and less nested (Spiesman and Inouye 2013; Burkle et al. 2013; Moreira et al. 2015), which can sometimes cause network connectance and modularity to increase depending on the species that are lost (Spiesman and Inouye 2013). The loss of core, generalist species can have different effects on networks than the loss of peripheral, specialist species (Magrach et al. 2018).

In theory, changes to network size and structure can alter network stability. Simulated species extinction events suggests networks that are smaller and more modular, and have lower connectance and nestedness values, are less stable and more prone to secondary extinctions following species losses (Thébault and Fontaine 2010; Burkle et al. 2013; Evans et al. 2013; Lever et al. 2014; Moreira et al. 2015; Grass et al. 2018; Magrach et al. 2018). There are often interactions between elements of the network structure as well, such as an indirect effect of connectance on stability through its effects on modularity (Thébault and Fontaine 2010). Species loss can theoretically lead to network collapses (Memmott et al. 2004; Lever et al. 2014). Understanding how landscape disturbance influences network complexity and stability is key to preserving and promoting network function.

In this study, I assessed the effects of human-driven landscape disturbance on the size, structure, and stability of plant-bee networks in southern Manitoba. I predicted that networks would become smaller, have reduced interaction redundancy (i.e. are less nested), have a greater number of “breaking points” (i.e. are more modular), and have fewer realized interactions (i.e. lower connectance values) along increasing disturbance gradients, resulting in networks that are theoretically less stable and more susceptible to collapse or diminished ecosystem functioning.

The goal of this study is to inform sustainable land-development practices that will contribute to plant-bee network conservation.

Materials and methods

Study sites

I performed net surveys in the same area of southern Manitoba as Chapter two. I sampled at 16 sites in 2018 and 2019, for a total of 32 sites (see Table S1 from Chapter two). I randomly chose two of the four sites at each location to net within 100 m of the traps.

Sampling procedure

I actively caught wild bees from flowers while they were foraging by walking back-and-forth along a 50x2 m transect of high flower density for ten minutes (excluding handling time). I repeated this three times at different areas in the landscape for a total of 30 minutes of active netting per sampling event. I did not catch honey bees even if they were in the transect, and let them go if I caught one. I euthanized bees in a kill jar containing cyanide crystals and recorded the flowering species they were visiting. If the flowering species could not be identified in the field, they were pressed and identified in the lab to the lowest taxonomic rank possible using published keys (Scoggan 1957; Reaume 2009; Holm 2017). Photographs of plants were sometimes taken and posted to iNaturalist to facilitate identifications. Sites were sampled five times over the summer approximately three weeks apart. I randomly chose one of the two sites at each location to sample first. I sampled networks either in the morning (10:00–12:00) or afternoon (12:00–14:15) and then switched at the next round to minimize temporal bias. I only sampled on days that were forecasted to be $\geq 15^{\circ}\text{C}$ with light winds and no precipitation.

Bee identification

I used the same procedure for identifying bees to species/morphospecies outlined in Chapter two.

Network size and structure

I constructed summer-long plant-bee networks for each site in R (R Core Team 2018) using the bipartite package (Dormann et al. 2008). Network interactions were between each bee and the flower species that I caught it on while sampling. I included all non-*Apis* bees in the networks (i.e. females and males of both nest-constructing and cleptoparasitic species).

I estimated several network-level structural indices, including size, connectance, nestedness, and modularity (Table 7). Connectance was calculated as $C=L/IJ$, where L is the observed number of interactions, I is the number of plant species, and J is the number of bee species (Dormann et al. 2009). Connectance values range between 0 to 1, where higher values indicate greater network connectance. Nestedness was calculated using the nestedness metric based on overlap and decreasing fill (NODF), which is a modification of the typical nestedness value that accounts for overlap of interactions and decreasing fill in the species matrix (Almeida-Neto et al. 2008). NODF values range from 0 to 100 where 0 represents no nestedness (i.e. no overlap in species resource use) and 100 represents total nestedness (i.e. complete overlap in resource use). Modularity was estimated using the LPAwb+ algorithm derived by Beckett (2016), which weights all interactions by the number of times they appear in the web. Modularity scores range from 0 to 1 where higher values indicate greater modularity.

I also calculated web asymmetry for all sites to see if network size was changing due to unequal losses of bee versus plant species in response to disturbance. Web asymmetry was calculated as $W=(J-I)/(J+I)$ where J is the number of bee species and I is the number of plant species (Dormann et al. 2021). Dividing by the total number of species standardizes web asymmetry by network size. Positive values indicate bee-dominated networks and negative values indicate plant-dominated networks. To see if networks were gaining generalist interactions and losing specialist interactions in response to landscape disturbance, I calculated the mean number of links per species, which is the sum of all interactions in one trophic level divided by the number of species, $\bar{L}_x=L/(J+I)$ (Dormann et al. 2009). Greater average links per species indicates that the network contains more generalist species. I calculated the mean number of links per species for bees only.

Table 7. Network size and structural features used in this study.

Network feature	Description
Size	Total number of plant and bee species.
Mean number of links per bee species	Average number of interactions across all bee species. Used as an indicator of interaction generality.
Web asymmetry	Number of bee minus plant species in the network, weighted by network size.
Connectance	Degree to which all interactions occur
Nestedness	Amount of resource overlap across all bee and plant species.
Modularity	Amount of aggregation in the network of interacting sets of plant and bee species.
Stability	Ability of networks to resist extinction cascades following plant species loss.

Network stability

I assessed network stability by calculating the extinction slopes of bee species in response to random and least-to-most abundant plant species loss (repeated 500 times) using the bipartite package (Dormann et al. 2008). Abundance-based plant losses will always have most-linked plant species lost last, whereas random plant losses are equally likely to lose most and least-linked plants. Random plant extinctions therefore represent a “worst-case” scenario in which core species can be lost early on in the extinction sequence. I focused on the loss of plant rather than bee species because disturbance can directly alter plant communities and thus change the amount and type of plants available to bees (Potts et al. 2010). Loss of bees from my networks are less likely to impact plant survival because there are other insect visitors that can continue to visit flowers. The extinction slope is the exponent (a) of a power function ($y=1-x^a$) describing the secondary extinction sequence of bees (Dormann et al. 2009). Networks with larger extinction slopes are able to resist network collapse over a greater number of plant species losses and therefore have greater network stability.

Landscape data

I used the same method as outlined in Chapter 2 to collect landscape data. The variables I measured were forb crop cover, cereal crop cover, urban area, SHDI, and edge density in seven buffer sizes around the sites (500, 750, 1000, 1250, 1500, 1750, 2000 m radii).

Statistical analysis

All of my statistical analyses were performed in R (R Core Team 2018). I modelled the effects of landscape disturbance on network size, structure, and stability using either multiple linear regression or generalized linear models (GLM). I used the MASS package to compute GLMs (Venables and Ripley 2002). I fit my nestedness and modularity models to a Gaussian distribution, my size model to a negative binomial distribution, and my connectance model to a gamma distribution with a log-link function. In addition to my landscape variables, I included year, latitude, and longitude in all of my models. Latitude and longitude were scaled and centered around mean values. I used Akaike Information Criterion with a sample size correction (AIC_c) to choose the best fitting buffer size, which was the model with the lowest AIC_c score (Akaike 1973). I also compared models with and without location as a random effect, but the AIC_c scores were lower for the models without the random effect and thus had a better fit. This suggests a lack of similarity in network size or structure due to location, so I excluded it. I explored whether network size influenced the effects of landscape variables on connectance, nestedness, and modularity, by including interaction terms between size and landscape variables. I performed the interaction models separately for each network response variable. Model effects were considered significant if p-values were less than 0.05. I examined all model residuals using quantile-quantile and residual plots to evaluate model fit. I also used variance inflation factors to determine if predictor variables were strongly collinear. All values were at or below 5, indicating little to no collinearity between predictors (Craney and Surles 2002).

Results

Across all 32 networks, I found 2,189 interactions involving 172 bee species on 129 flowering plant species (Table S7). Of the plant species, 105 were native and 24 were introduced. The plants with the greatest average number of interactions were (mean percent in parentheses): *Melilotus albus* (10.5%), *Solidago canadensis* (6.6%), *Heterotheca villosa* (4.7%), *Cirsium arvense* (3.9%), and *S. rigida* (3.5%), and the bees with the greatest average number of interactions were: *Bombus ternarius* (8.0%), *Hylaeus mesillae cressoni* (5.8%), *B. rufocinctus* (5.6%), *Ceratina mikmaqi* (3.7%), and *Lasioglossum leucozonium* (3.4%).

Average (\pm SD) network size was 35 ± 12 species. All networks were dominated by bees (web asymmetry 1.85 ± 0.5) with an average of 22 bee species and 13 plant species, except for one site which had slightly more plant species (24) than bee species (21). Average network connectance was 0.15 ± 0.07 , average NODF was 17.63 ± 11.73 , and average modularity was 0.57 ± 0.12 . Network size strongly predicted network connectance and modularity, but was not a good predictor of nestedness (Table 8). Network connectance decreased with network size (Fig. 11A) and network modularity increased with network size (Fig. 11B) thus larger networks had lower connectance and greater modularity. Network nestedness was enhanced by bee species generalism, such that nestedness increased with the mean number of links per bee species (LM, $\beta=4.775$, $SE=1.352$, $t=3.531$, $p=0.0014$). Greater nestedness was therefore due in part to an increase in generalist species.

Table 8. Effects of network size on network structure. Connectance model was estimated using a GLM with a Gamma distribution and a log-link function. Modularity and NODF models were estimated using linear regression. Significant p-values are shown in bold ($\alpha=0.05$). *Estimates are in units of $\ln(y)$.

Response	Predictor	β	SE	t	p
Connectance*	Intercept	-0.9205	0.1175	-7.834	< 0.0001
	Network size	-0.0296	0.0032	-9.312	< 0.0001
Modularity	Intercept	0.4353	0.0628	6.932	< 0.0001
	Network size	0.0039	0.0017	2.324	0.0271
NODF	Intercept	25.640	6.5652	3.905	0.0005
	Network size	-0.2281	0.1776	-1.285	0.2088

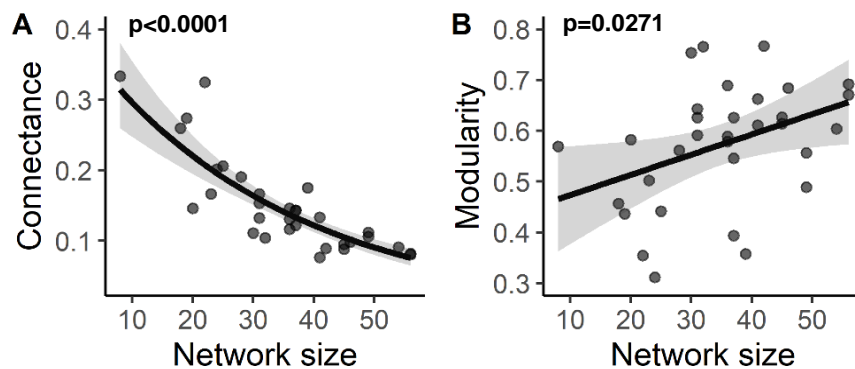


Fig. 11. Network size (total number of interacting species) predicts network (A) connectance and (B) modularity. Points represent observed values. Regression lines represent predicted values from linear models. Shaded areas are 95% confidence intervals. Network nestedness was not influenced by network size.

Networks responded most strongly to landscapes at the broadest scales, including 1750 m (modularity) and 2000 m (size, connectance, nestedness). Edge density and crop cover influenced network size and structure (Table 9) such that edge density increased network size and modularity, and decreased network connectance and nestedness (Fig. 12A, B, D, F), while cereal crop cover decreased connectance and increased modularity (Fig. 12C, G), and had a marginally positive effect on network size (Table 9). Forb crop cover decreased nestedness (Fig. 12E). I did not find any significant interactions between network size and landscape variables on connectance, nestedness, or modularity, indicating that both large and small networks behaved similarly to landscape disturbance. This also indicates that the effects of network size were independent of landscape composition. Web asymmetry was enhanced by SHDI in a 2000 m buffer (LM, $\beta=0.2318$, $SE=0.0918$, $t=2.53$, $p=0.0189$) (Table S8. Landscape-level model results on network web asymmetry and mean number of links per bee species. Both models were estimated using multiple linear regression. Significant p-values are shown in bold ($\alpha=0.05$). Table S8). Since greater values of web asymmetry are due to an increase in bee richness, local networks gained bee species with increasing landscape diversity. Bee species generalism was not influenced by landscape level factors (Table S8).

Table 9. Landscape-level model results on network size and structure. Size model was fit using a GLM with a negative binomial distribution. Connectance model was fit using a GLM with a log-link Gamma distribution. Modularity and NODF models were fit using multiple linear regression. Significant p-values are shown in bold ($\alpha=0.05$). *Estimates are in units of $\ln(y)$.

Response	Buffer (m)	R ² _{adj}	Predictor	β	SE	t	p
Network size*	2000	0.050	Intercept	3.0962	0.3571	8.67	<0.0001
			Year	0.2850	0.1076	2.65	0.0081
			Latitude	-0.0729	0.0499	-1.46	0.1440
			Longitude	0.1237	0.0563	2.20	0.0281
			Cereal crop cover (%)	0.0125	0.0072	1.73	0.0829
			Forb crop cover (%)	0.0062	0.0054	1.15	0.2501
			Urban area (%)	0.0040	0.0039	1.04	0.2998
			SHDI	-0.3165	0.2106	-1.50	0.1328
			Edge density (m/ha)	0.0040	0.0015	2.61	0.0090
Connectance*	2000	0.476	Intercept	-1.4379	0.4340	-3.31	0.0030
			Year	-0.4136	0.1289	-3.21	0.0039
			Latitude	0.1475	0.0624	2.37	0.0268
			Longitude	-0.1281	0.0687	-1.86	0.0753
			Cereal crop cover (%)	-0.0194	0.0087	-2.23	0.0357
			Forb crop cover (%)	-0.0116	0.0065	-1.79	0.0866
			Urban area (%)	-0.0028	0.0047	-0.59	0.5597
			SHDI	0.5282	0.2582	2.05	0.0524
			Edge density (m/ha)	-0.0054	0.0019	-2.94	0.0073
Nestedness	2000	0.364	Intercept	42.871	12.1714	3.52	0.0018
			Year	-7.9808	3.6146	-2.21	0.0375
			Latitude	5.1967	1.7492	2.97	0.0068
			Longitude	1.1557	1.9276	0.60	0.5547
			Cereal crop cover (%)	-0.3205	0.2444	-1.31	0.2027
			Forb crop cover (%)	-0.4365	0.1812	-2.41	0.0244
			Urban area (%)	-0.1261	0.1330	-0.95	0.3531
			SHDI	7.2394	7.2401	1.00	0.3278
			Edge density (m/ha)	-0.1513	0.0519	-2.92	0.0078
Modularity	1750	0.554	Intercept	0.3397	0.0947	3.59	0.0016
			Year	0.1141	0.0312	3.65	0.0013
			Latitude	-0.0668	0.0149	-4.49	0.0002
			Longitude	-0.0032	0.0162	-0.20	0.8424
			Cereal crop cover (%)	0.0067	0.0021	3.17	0.0043
			Forb crop cover (%)	0.0024	0.0014	1.67	0.1079
			Urban area (%)	0.0012	0.0011	1.04	0.3115
			SHDI	-0.0931	0.0604	-1.54	0.1369
			Edge density (m/ha)	0.0015	0.0005	3.24	0.0036

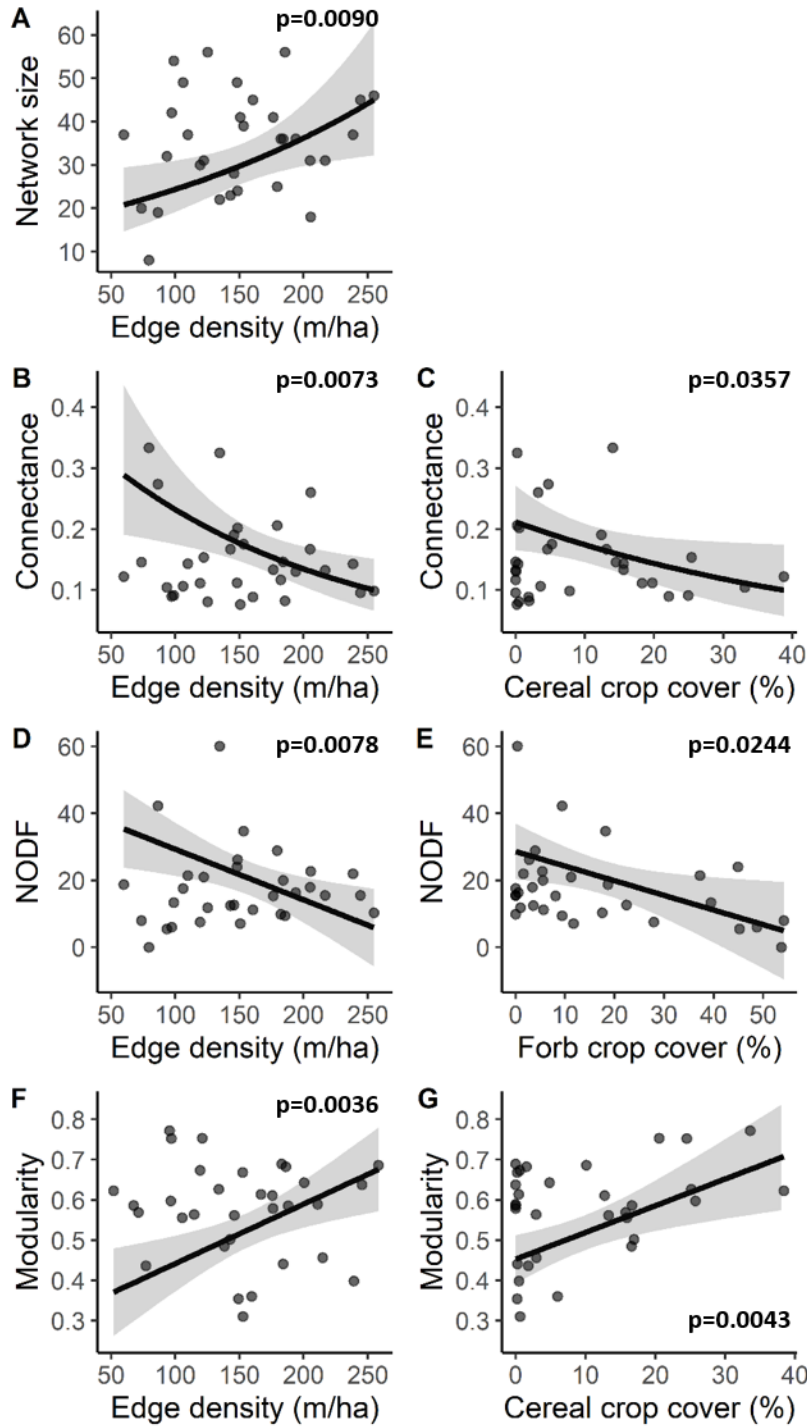


Fig. 12. Effects of edge density and crop cover on network (A) size, (B-C) connectance, (D-E) nestedness (NODF), and (F-G) modularity. Points represent observed values. Regression lines represent predicted values from GLMs. Shaded areas are 95% confidence intervals. Landscapes were calculated at the 1750 m scale for NODF and 2000 m scale for size, connectance, and modularity. Network size was not significantly influenced by forb or cereal crop cover.

Responses of network stability to landscape disturbance depended on the order of plant loss, since only extinction slopes based on random plant losses responded to disturbance while network stability calculated using abundance-based plant loss was unaffected by disturbance (Table 10). Because random plant extinctions are more likely to include the loss of core species compared to abundance-based extinctions, this indicates that stability under a worst-case extinction scenario was influenced by landscape disturbance. Landscape diversity increased network stability based on the positive influence of SHDI on extinction slopes (Fig. 13A). Forb crop cover decreased network stability based on decreasing extinction slopes in areas of greater forb crops (Fig. 13B). Network nestedness enhanced stability (Table 11), which was evident by an increase in extinction slopes following random plant loss with increasing levels of nestedness (Fig. 14). However, I did not find significant interaction terms between nestedness and landscape variables in my interaction models. This indicates that landscape diversity and forb crop cover influenced stability regardless of the level of network nestedness.

Table 10. Landscape-level model results on extinction slopes of bees following plant extinctions. Abundance-based extinctions occurred from least to most abundant plant species. Both models were estimated using multiple linear regression. Significant p-values are shown in bold ($\alpha=0.05$).

Response	Buffer (m)	R ² _{adj}	Predictor	β	SE	t	p
Extinction slope (Random plant extinctions)	2000	0.246	Intercept	1.9719	0.6150	3.21	0.0039
			Year	-0.4193	0.1827	-2.30	0.0311
			Latitude	0.1552	0.0884	1.76	0.0924
			Longitude	-0.1512	0.0974	-1.55	0.1342
			Cereal crop cover (%)	-0.0078	0.0123	-0.63	0.5340
			Forb crop cover (%)	-0.0244	0.0092	-2.66	0.0140
			Urban area (%)	-0.0020	0.0067	-0.30	0.7668
			SHDI	0.7917	0.3659	2.16	0.0411
			Edge density (m/ha)	-0.0025	0.0026	-0.96	0.3481
Extinction slope (Abundance-based plant extinctions)	2000	0.200	Intercept	4.7326	5.6078	0.84	< 0.0001
			Year	0.2024	1.6654	0.12	0.9043
			Latitude	2.3178	0.8059	2.88	0.0085
			Longitude	-0.4093	0.8881	-0.46	0.6493
			Cereal crop cover (%)	-0.0522	0.1126	-0.46	0.6471
			Forb crop cover (%)	-0.1486	0.0835	-1.78	0.0885
			Urban area (%)	-0.0279	0.0613	-0.46	0.6528
			SHDI	4.3085	3.3358	1.29	0.2093
			Edge density (m/ha)	-0.0185	0.0239	-0.77	0.4476

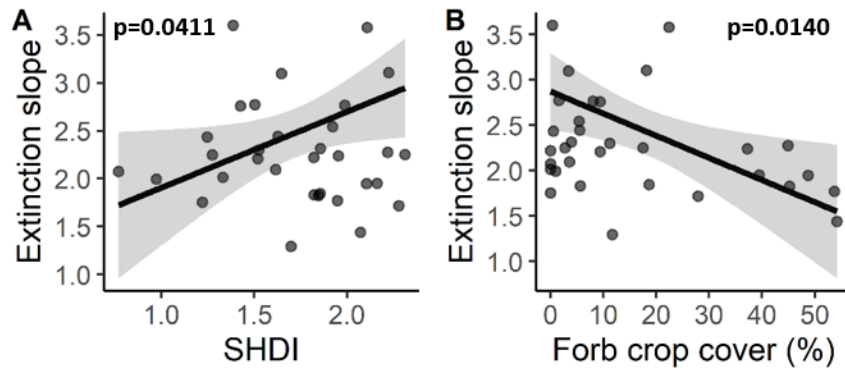


Fig. 13. Effects of (A) Shannon's Landscape Diversity Index, and (B) forb crop cover on extinction slopes of bees following random plant losses. Points represent observed values. Regression lines represent predicted values from multiple linear regression. Shaded areas are 95% confidence intervals.

Table 11. Effects of network structure on the extinction slopes of bees following random plant losses. Model was fit using multiple linear regression. Significant p-values are shown in bold ($\alpha=0.05$).

Response	Predictor	B	SE	t	p
Extinction slope	Intercept	1.4565	0.8285	1.76	0.0897
	Connectance	1.6099	1.4703	1.10	0.2829
	Modularity	0.1798	1.0597	0.17	0.8665
	NODF	0.0267	0.0100	2.68	0.0122

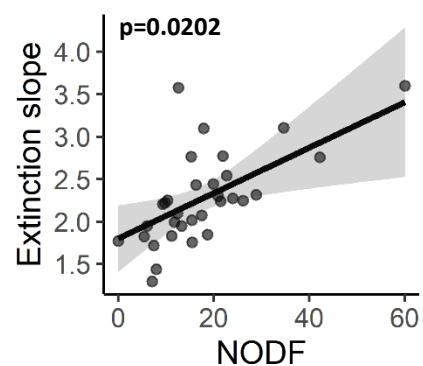


Fig. 14. Effect of increasing network nestedness (NODF) on extinction slopes of bees following random plant losses. Points represent observed values. Regression lines represent predicted values from linear regression. Shaded areas are 95% confidence intervals.

Discussion

Effects of landscapes on network size and structure

One of the most important finding in this study was landscape fragmentation through smaller field sizes and greater edge habitat supported larger networks. Other studies report a decrease in network size due to habitat loss (Spiesman and Inouye 2013; Burkle et al. 2013; Moreira et al. 2015; Magrach et al. 2018), but fragmentation effects on networks are poorly understood (Hadley and Betts 2012; Xiao et al. 2016). Grass et al. (2018) found that larger habitat patches supported larger networks, and Ferreira et al. (2020) found that patch isolation decreased network size and favoured generalism in forest-based networks. However, both studies confounded fragmentation with habitat loss (Fahrig 2003). In this study, I measured fragmentation as an increase in edge habitat, which is a measurement of fragmentation *per se* (McGarigal 2015). Edge habitats can contain greater plant diversity than surrounding land cover (Brudvig et al. 2009) and can provide corridors for bees to move along when foraging, essentially connecting foraging patches (Griffin and Haddad 2021). A greater number of nearby edge habitats adequately explained why I found more species and thus larger networks of plants and bees in fragmented landscapes. I suggest that land management policies should favour smaller field sizes in agro-ecosystems to support larger networks.

Another main finding in this study was that habitat loss due to crop cover and fragmentation both reduced network-level interaction redundancy. Forb crops like canola and soybean produce showy flowers with floral rewards that may have drawn generalist bees away from the semi-natural patches I was sampling in, which Magrach et al. (2018) showed can change network nestedness and other features of network structure during bloom periods. Effects of forb crops can be evident even post-bloom, suggesting more permanent changes to network structure when forb crops are planted (Magrach et al 2018). Permanent changes may be due to pesticide use, which are used extensively on some forb crops (e.g. canola is the second major source of pesticides across the prairies after wheat (Malaj et al. 2020)). Pesticides may directly kill bees, but they may also reduce the amount of forage available in the landscape by killing off weedy plant species. Although Moreira et al. (2015) found that land cover diversity increased network nestedness, I found that the amount of edge habitat was a better determiner of nestedness. Greater amounts of edge habitat in the landscape may diffuse the number of interacting bee

species in any specific area by connecting habitat patches (Griffin and Haddad 2021). The ability of bees to better access foraging resources could mean that our snapshot of networks during sampling had a greater number of species, but a lower number of interaction overlap between species.

I found a relationship between connectance and modularity with network size, such that larger networks were less connected and more modular. Size-structure relationships have been reported previously (Olesen et al. 2007; Spiesman and Inouye 2013). Modularity is known to increase with network size since larger networks have increased odds of finding interaction-dense areas compared to smaller ones (Olesen et al. 2007). Connectance has been reported to both increase and decrease with network size depending on the type of interactions lost with disturbance (generalist-specialist versus generalist-generalist, respectively (Soares et al. 2017)). A decline in connectance with size can also be caused by “forbidden links”, which are interactions between species that cannot occur due to separations through time or space (Bascompte et al. 2003). Since I sampled over multiple months, some interactions are biologically impossible due to non-overlapping bee-flight and flower-bloom phenologies, such as the spring flying *Colletes inaequalis* and late summer blooming golnderods. This probably contributed to decreasing the observed network-level resource use (i.e. connectance) in larger networks in my study. Even so, my average connectance value (0.15) was within the normal range of previous studies (0.11–0.18) (Landi et al. 2018). Despite the size-structure relationships in this study, I did not find any evidence to suggest that network size moderates the response of network connectance or modularity to landscape disturbance.

Since the mean number of links per bee or plant species was not influenced by landscape variables in this study, I conclude that the number of species acting as generalists or specialists did not change in response to landscape disturbance. This differs from other studies which have shown that habitat loss (Burkle et al. 2013; Redhead et al. 2018; Ferreira et al. 2020) and likely fragmentation (Henle et al. 2004) favours generalist species since they can host-switch when resources are lacking (Ferreira et al. 2020). This essentially re-wires the network without changing overall structure (Nielsen and Totland 2014). Because large-scale disturbance has been occurring in Manitoba for over a century and continues to increase (Scott 1996), it could also be that extinction-prone specialist species were already lost from disturbed areas before I sampled

them (Burkle et al. 2013).

Effects of landscapes on network stability

My study shows that networks are more stable in areas of higher land cover diversity and lower crop cover in this study, suggesting that a diverse assemblage of cover types can benefit networks in disturbed landscapes. My measurement of landscape diversity included crop cover, indicating that a diverse array of crop types along with semi natural areas can enhance stability. Supporting large, diverse networks that include native bees can enhance pollination to pollinator-dependent crops such as strawberry (Connelly et al. 2015) and apple orchards (Blitzer et al. 2016). Because my extinction slopes were based on random plant extinctions which can include the loss of core species, conserving compositionally diverse landscapes can promote network stability under worst-case extinction scenarios. Diverse landscapes are therefore integral to supporting network functionality. I suggest that land managers promote a diverse array of cover types in the landscape to enhance network stability, which includes diversifying semi natural patches as well as crop cover.

I additionally found that nestedness promoted network stability, such that highly nested networks were more stable than less nested networks. The nested structure of plant-pollinator networks confers stability through interaction redundancy, which maintains species inclusion in the network even when some are lost (Memmott et al. 2004). Nestedness is a key feature that prevents loss of bees following plant extinctions (Campbell et al. 2012; Lever et al. 2014) or loss of plants following bee extinctions (Memmott et al. 2004). Even though nestedness upholds network functionality during disturbance events, Campbell et al. (2012) and Ferreira et al. (2020) suggest that extreme cases of nestedness can promote an over-reliance on core species to maintain network stability, which puts networks at greater risk of collapsing if core species are lost. Connectance, modularity, and network size had little effect on network stability in this study compared to nestedness, although some studies suggest that increased connectance and decreased modularity can also stabilize networks (Thébault and Fontaine 2010; Magrach et al. 2018).

One limitation of using extinction slopes to estimate stability is that extinction events follow a rigid, consecutive pattern of species loss. This over-simplifies the effects of real world

disturbances, which can result in the loss of more than one species at once. Disturbances are not limited to just plants, either; some bee species are susceptible to disturbance and may be lost even though host plants survive (Burkle et al. 2013). Because they require a specialized diet, specialist species are almost always lost first in response to disturbance (Burkle et al. 2013; Ferreira et al. 2020). Extinction slopes also assume that network interactions are non-pliable, when in fact networks can re-organize themselves to a more stable state through host switching of generalist species (Spiesman and Inouye 2013; Grass et al. 2018). These assumptions mean that real world networks could respond in a much different way to plant extinctions compared to what mathematical models predict. Being able to manipulate extinctions in the field could tell us more about how networks respond to consecutive or simultaneous extinction events in the real world.

Conclusion

Network size, structure, and stability are changing along disturbance gradients in southern Manitoba. Networks were larger, less nested/connected, and more modular with increasing crop cover and fragmentation. Reduced nestedness in particular destabilizes networks more than changes to size, connectance, or modularity. Land management policies should focus on reducing field sizes to increase edge habitat and enhancing land cover diversity, which I showed can increase network size and promote stability under worst-case plant extinctions scenarios.

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Supplementary tables

Table S7. Flower species that bees were caught foraging on. Also shown are the raw number of interactions they were involved in across all networks, as well as the mean percentage of interactions per network. Sorted alphabetically by family (shown in bold) and species name. Species name, common name, and status were taken from the database of vascular plants of Canada (VASCAN).

					Interactions	
Species	Author	Common name	Status	#	Mean (%)	
Aceraceae						
<i>Acer</i> sp.		maple	Native	21	1.15	
Amaryllidaceae						
<i>Allium stellatum</i>	Fraser ex Ker Gawl.	autumn onion	Native	5	0.30	
Apiaceae						
<i>Sanicula marilandica</i>	L.	Maryland sanicle	Native	3	0.16	
<i>Zizia aptera</i>	(A. Gray) Fernald	heart-leaved alexanders	Native	50	2.52	
<i>Zizia aurea</i>	W.D.J. Koch	golden alexanders	Native	54	2.12	
Apocynaceae						
<i>Apocynum androsaemifolium</i>	L.	spreading dogbane	Native	15	0.83	
<i>Asclepias incarnata</i>	L.	swamp milkweed	Native	1	0.06	
<i>Asclepias ovalifolia</i>	Decne.	oval-leaved milkweed	Native	24	1.30	
<i>Asclepias speciosa</i>	Torr.	showy milkweed	Native	1	0.05	
<i>Asclepias syriaca</i>	L.	common milkweed	Native	1	0.05	
Asparagaceae						
<i>Maianthemum</i> sp.		Solomon's seal	Native	2	0.11	
Asteraceae						
<i>Achillea millefolium</i>	L.	common yarrow	Introduced	14	0.64	
<i>Agoseris glauca</i>	(Pursh) Raf.	pale agoseris	Native	1	0.05	
<i>Cirsium arvense</i>	(L.) Scop.	Canada thistle	Introduced	93	3.89	
<i>Cirsium flodmanii</i>	(Rydb.) Arthur	Flodman's thistle	Native	14	0.66	
<i>Crepis</i> sp.		hawksbeard	Native	7	1.45	
<i>Crepis tectorum</i>	L.	narrow-leaved hawksbeard	Introduced	28	1.96	

Table S7 cont'd

Species	Author	Common name	Status	Interactions	
				#	Mean (%)
<i>Doellingeria umbellata</i>	(Mill.) Nees	flat-top white aster	Native	5	0.12
<i>Echinacea purpurea</i>	(L.) Moench	purple coneflower	Native	2	0.27
<i>Erigeron annuus</i>	(L.) Pers.	annual fleabane	Native	3	0.14
<i>Erigeron glabellus</i>	Nutt.	streamside fleabane	Native	25	1.19
<i>Erigeron philadelphicus</i>	L.	Philadelphia fleabane	Native	8	0.54
<i>Erigeron strigosus</i>	Muhl. Ex Willd.	rough fleabane	Native	15	0.61
<i>Euthamia graminifolia</i>	(L.) Nutt.	grass-leaved goldenrod	Native	20	0.83
<i>Eutrochium purpureum</i>	(L.) E.E. Lamont	joe-pye weed	Native	4	0.10
<i>Gaillardia</i> sp.		blanketflower	Native	3	0.09
<i>Grindelia squarrosa</i>	(Pursh) Dunal	curly-cup gumweed	Native	3	0.11
<i>Helianthus decapetalus</i>	L.	pale sunflower	Native	15	0.92
<i>Helianthus maximiliani</i>	Schrad.	Maximilian sunflower	Native	16	0.89
<i>Helianthus pauciflorus</i>	Nutt.	stiff sunflower	Native	1	0.06
<i>Helianthus tuberosus</i>	L.	Jerusalem artichoke	Native	3	0.14
<i>Heliopsis helianthoides</i>	(L.) Sweet	false sunflower	Native	3	0.32
<i>Heterotheca villosa</i>	(Pursh) Shinnars	hairy goldenaster	Native	90	4.70
<i>Hieracium umbellatum</i>	L.	umbellate hawkweed	Native	7	0.11
<i>Liatris ligulistylis</i>	(A. Nelson) K. Schum.	meadow blazing-star	Native	1	0.05
<i>Liatris punctata</i>	Hook.	dotted blazing-star	Native	49	2.70
<i>Lygodesmia juncea</i>	(Pursh) D. Don ex Hook.	rush skeletonplant	Native	3	0.28
<i>Melilotus officinalis</i>	(L.) Lam.	yellow sweet-clover	Introduced	52	1.35
<i>Mulgedium oblongifolium</i>	(Nutt.) Reveal	blue lettuce	Native	18	2.08
<i>Nabalus albus</i>	(L.) Hook.	white rattlesnakeroot	Native	1	0.02
<i>Packera plattensis</i>	(Nutt.) W.A. Weber & Á. Löve	prairie groundsel	Native	11	0.73
<i>Rosa acicularis</i>	Lindl.	prickly rose	Native	3	0.28
<i>Rudbeckia hirta</i>	L.	black-eyed Susan	Native	7	0.23
<i>Senecio</i> sp.		ragwort	Native	1	0.05
<i>Solidago canadensis</i>	L.	Canada goldenrod	Native	149	6.61

Table S7 cont'd

Species	Author	Common name	Status	Interactions	
				#	Mean (%)
<i>Solidago gigantea</i>	Aiton	giant goldenrod	Native	7	0.28
<i>Solidago nemoralis</i>	Aiton	grey-stemmed goldenrod	Native	60	2.92
<i>Solidago ptarmicoides</i>	(Torr. & A. Gray) B. Boivin	upland white goldenrod	Native	3	0.15
<i>Solidago rigida</i>	L.	stiff goldenrod	Native	99	3.50
<i>Sonchus arvensis</i>	L.	field sow-thistle	Introduced	6	0.36
<i>Sonchus</i> sp.		sow-thistle	Introduced	68	2.02
<i>Symphyotrichum boreale</i>	(Torr. & A. Gray) A. Löve & D. Löve	rush aster	Native	2	0.07
<i>Symphyotrichum ciliolatum</i>	(Lindl.) A. Löve & D. Löve	Lindley's aster	Native	16	0.54
<i>Symphyotrichum ericoides</i>	(L.) G.L. Nesom	white heath aster	Native	7	0.28
<i>Symphyotrichum laeve</i>	(L.) Á. Löve & D. Löve	smooth aster	Native	34	1.63
<i>Symphyotrichum lanceolatum</i>	(Willd.) G.L. Nesom	white panicle aster	Native	16	0.53
<i>Symphyotrichum</i> sp.		aster	Native	3	0.08
<i>Tanacetum vulgare</i>	L.	common tansy	Introduced	23	0.61
<i>Taraxacum officinale</i>	F.H. Wigg.	common dandelion	Introduced	56	2.83
<i>Tragopogon dubius</i>	Scop.	yellow goatsbeard	Introduced	3	0.30
Boraginaceae					
<i>Lithospermum canescens</i>	(Michx.) Lehm.	hoary puccoon	Native	1	0.05
Brassicaceae					
<i>Brassica napus</i>	L.	rapeseed	Introduced	2	0.11
<i>Erysimum asperum</i>	(Nutt.) DC.	prairie rocket	Native	6	0.37
<i>Thlaspi arvense</i>	L.	field pennycress	Introduced	22	0.54
Campanulaceae					
<i>Campanula rotundifolia</i>	L.	harebell	Native	19	1.00
<i>Lobelia kalmii</i>	L.	Kalm's lobelia	Native	1	0.04
Caryophyllaceae					
<i>Cerastium arvense</i>	L.	field chickweed	Native	2	0.10
<i>Silene vulgaris</i>	(Moench) Garcke	bladder campion	Introduced	1	0.04
Convolvulaceae					

Table S7 cont'd

Species	Author	Common name	Status	Interactions	
				#	Mean (%)
<i>Calystegia sepium</i>	(L.) R. Br.	hedge false bindweed	Native	1	0.03
Cornaceae					
<i>Cornus sericea</i>	L.	red-osier dogwood	Native	9	0.33
Ericaceae					
<i>Arctostaphylos uva-ursi</i>	(L.) Spreng.	common bearberry	Native	13	0.70
Euphorbiaceae					
<i>Euphorbia esula</i>	L.	leafy spurge	Introduced	7	0.65
Fabaceae					
<i>Amorpha canescens</i>	Pursh	downy false indigo	Native	4	0.37
<i>Astragalus agrestis</i>	Douglas ex G. Don	field milk-vetch	Native	7	0.38
<i>Astragalus</i> sp.		milk-vetch	Native	54	1.92
<i>Caragana arborescens</i>	Lam.	Siberian pea shrub	Introduced	4	0.24
<i>Dalea candida</i>	Michx. ex Willd.	white prairie-clover	Native	15	0.75
<i>Dalea purpurea</i>	Vent.	purple prairie-clover	Native	42	1.72
<i>Desmodium canadense</i>	(L.) DC.	Canada tick-trefoil	Native	3	0.11
<i>Glycyrrhiza lepidota</i>	Pursh	wild licorice	Native	2	0.07
<i>Lathyrus ochroleucus</i>	Hook.	pale vetchling	Native	1	0.04
<i>Lathyrus palustris</i>	L.	marsh vetchling	Native	1	0.02
<i>Lathyrus venosus</i>	Muhl. ex Willd.	veiny vetchling	Native	1	0.05
<i>Lotus corniculatus</i>	L.	garden bird's-foot trefoil	Introduced	39	1.13
<i>Medicago sativa</i>	L.	alfalfa	Introduced	43	2.84
<i>Melilotus albus</i>	Medik.	white sweet-clover	Introduced	265	10.50
<i>Pedimelum argophyllum</i>	(Pursh) J.W. Grimes	silver-leaved Indian breadroot	Native	1	0.06
<i>Trifolium campestre</i>	Schreb.	low hop clover	Introduced	1	0.05
<i>Trifolium hybridum</i>	L.	alsike clover	Introduced	18	0.91
<i>Trifolium pratense</i>	L.	red clover	Introduced	10	0.44
<i>Trifolium repens</i>	L.	white clover	Introduced	29	1.07

Table S7 cont'd

				Interactions	
Species	Author	Common name	Status	#	Mean (%)
Iridaceae					
<i>Sisyrinchium montanum</i>	Greene	strict blue-eyed-grass	Native	2	0.08
Lamiaceae					
<i>Agastache foeniculum</i>	(Pursh) Kuntze	blue giant hyssop	Native	21	0.60
<i>Monarda fistulosa</i>	L.	wild bergamot	Native	38	1.33
<i>Physostegia virginiana</i>	(L.) Benth.	Virginia false dragonhead	Native	6	0.16
<i>Prunella vulgaris</i>	L.	common self-heal	Native	2	0.07
Oleaceae					
<i>Syringa</i> sp.		lilac	Introduced	13	0.71
Onagraceae					
<i>Chamaenerion angustifolium</i>	(L.) Scop.	fireweed	Native	3	0.11
<i>Oenothera flava</i>	(A. Nelson) Garrett	low yellow evening-primrose	Native	1	0.08
Orchidaceae					
<i>Cypripedium parviflorum</i>	Salisb.	yellow lady's-slipper	Native	1	0.05
Orobanchaceae					
<i>Pedicularis canadensis</i>	L.	Canada lousewort	Native	6	0.15
Plantaginaceae					
<i>Penstemon gracilis</i>	Nutt.	slender beardtongue	Native	2	0.09
<i>Penstemon</i> sp.		beardtongue	Native	2	0.07
Polygalaceae					
<i>Polygala senega</i>	L.	Seneca snakeroot	Native	3	0.21
Primulaceae					
<i>Lysimachia ciliata</i>	L.	fringed yellow loosestrife	Native	5	0.25
Ranunculaceae					
<i>Anemonastrum canadense</i>	(L.) Mosyakin	Canada anemone	Native	6	0.20
<i>Anemone cylindrica</i>	A. Gray	long-headed anemone	Native	1	0.04
<i>Ranunculus acris</i>	L.	common buttercup	Introduced	9	0.22
<i>Ranunculus hispidus</i>	Michx.	bristly buttercup	Native	2	0.05

Table S7 cont'd

				Interactions	
Species	Author	Common name	Status	#	Mean (%)
Rosaceae					
<i>Amelanchier</i> sp.		serviceberry	Native	7	0.38
<i>Crataegus</i> sp.		hawthorn	Native	3	0.08
<i>Dasiphora fruticosa</i>	(L.) Rydb.	shrubby cinquefoil	Native	26	1.35
<i>Dryocallis arguta</i>	(Pursh) Rydb.	tall wood beauty	Native	6	0.25
<i>Fragaria virginiana</i>	Duchesne	wild strawberry	Native	11	0.46
<i>Malus</i> sp.		apple	Introduced	1	0.03
<i>Potentilla anserina</i>	L.	silverweed	Native	20	1.22
<i>Potentilla norvegica</i>	L.	rough cinquefoil	Native	5	0.23
<i>Potentilla</i> sp.		cinquefoil	Native	12	0.50
<i>Prunus pensylvanica</i>	L. f.	pin cherry	Native	1	0.05
<i>Prunus pumila</i>	L.	sand cherry	Native	24	1.01
<i>Prunus</i> sp.		cherry	Native	8	0.45
<i>Prunus virginiana</i>	L.	chokecherry	Native	11	0.31
<i>Rosa arkansana</i>	Porter	prairie rose	Native	20	1.60
<i>Rubus idaeus</i>	L.	red raspberry	Native	1	0.04
<i>Spiraea alba</i>	Du roi	white meadowsweet	Native	11	0.40
Rubiaceae					
<i>Galium boreale</i>	L.	northern bedstraw	Native	1	0.06
Saliceae					
<i>Salix</i> sp.		willow	Native	6	0.29
Santalaceae					
<i>Comandra umbellata</i>	(L.) Nutt.	bastard toadflax	Native	12	0.85
Violaceae					
<i>Viola adunca</i>	Sm.	hooked violet	Native	1	0.02
Grand Total				2,189	

Table S8. Landscape-level model results on network web asymmetry and mean number of links per bee species. Both models were estimated using multiple linear regression. Significant p-values are shown in bold ($\alpha=0.05$).

Response	Buffer (m)	R ² _{adj}	Predictor	β	SE	t	p
Web asymmetry	2000	0.174	Intercept	0.0310	0.1543	0.20	0.8424
			Year	-0.0710	0.0458	-1.55	0.1346
			Latitude	-0.0258	0.0222	-1.16	0.2563
			Longitude	-0.0562	0.0244	-2.30	0.0309
			Cereal crop cover (%)	-0.0003	0.0031	-0.11	0.9135
			Forb crop cover (%)	-0.0046	0.0023	-2.00	0.0580
			Urban area (%)	0.0015	0.0017	0.91	0.3741
			SHDI	0.2318	0.0918	2.53	0.0189
			Edge density (m/ha)	-0.0004	0.0007	-0.54	0.5943
Mean number of links per bee species	2000	0.394	Intercept	3.5000	1.3480	2.60	0.0161
			Year	0.2391	0.4003	0.60	0.5561
			Latitude	0.7628	0.1937	3.94	0.0007
			Longitude	0.2745	0.2135	1.29	0.2112
			Cereal crop cover (%)	-0.0014	0.0271	-0.05	0.9596
			Forb crop cover (%)	-0.0024	0.0201	-0.12	0.9059
			Urban area (%)	-0.0067	0.0147	-0.46	0.6529
			SHDI	-0.6578	0.8018	-0.82	0.4204
			Edge density (m/ha)	0.0024	0.0057	0.42	0.6771

CONCLUSION AND IMPLICATION OF FINDINGS

In this study, I explored the effects of human-driven landscape disturbance on bee communities (Chapter two) and plant-bee networks (Chapter three) in southern Manitoba. My objectives were: (i) document bee diversity and contribute to species records at both the provincial and national level, (ii) discover which aspect of the changed landscape bee communities and networks respond to the most, and (iii) use these findings to inform land management practices for conserving bee communities and plant-bee networks.

I met my first objective by contributing sixty bee species records for the province, six of which were also new records for Canada. This study, as well as other concurrent studies and examination of historical material by taxonomists, has increased the number of known species in Manitoba to 380 (Gibbs et al. in press) compared to 264 reported in 2015 (Canadian Endangered Species Conservation Council 2016). This puts Manitoba in-line with the current number of species recorded in Alberta (~364) and Ontario (~429) (Royal Museum of Saskatchewan 2020). I want to highlight the importance of maintaining sampling efforts into the future so that researchers can uncover even more species diversity, as well as track population and range shifts over time in response to ongoing human disturbance.

I met my second objective by showing that both bee communities and plant-bee networks changed along disturbance gradients. Crop cover, edge density, and lands cover diversity drove changes in bee abundance, richness, functional dispersion, and community composition, as well as network size, structure, and stability. Networks responded to disturbance at a larger scale (1750–2000 m) than bee communities (750–1000 m). Burkle and Knight (2012) similarly found that networks work at a larger spatial scale compared to bee communities. Although I explored the effects of urban area, it did not strongly influence communities or networks. I found that some effects on bee communities were ecoregion-dependent, likely due to biotic (e.g., vegetation) and abiotic (e.g., soil type, precipitation, temperature) factors. Ecoregions had significantly different bee community compositions, which may have contributed to variability in effects by ecoregion. Bee communities were also influenced at the local scale by grass cover, flower cover, and flower richness, but results were often mixed and contradicted my expectations (such as a decrease in bee abundance in response to increasing flower cover and richness).

I used the results from my second objective to make recommendations for land management practices, which fulfilled my final objective. Habitat loss and fragmentation were found in a previous study to create bee abundance, diversity, and pollination services deficits in Manitoba (Olynyk et al. 2021). My study adds a layer of understanding to these patterns, and shows that regional context should be taken in to account before implementing land management practices. What benefits bees in one ecoregion may not benefit bees in another, simply because the landscapes and bee communities are different. Scale of effect should also be taken into account, since I found that bee populations responded at a smaller landscape scale than networks. Even though small plots of land can host a wide variety of species and are easier to conserve, conservation at a larger scale is needed to preserve broader ecosystem functions like plant-bee networks (Burkle and Knight 2012). At the local scale, I found that introduced plant species in field margins enhanced bee functional dispersion and did not reduce bee abundance or species richness, which challenges the practice of removing introduced plant species. In conclusion, I recommend that land management policies at the landscape scale promote greater numbers of field edges and increased land cover diversity to protect wild bee communities and plant-bee networks, especially in agriculturally dominated areas of Manitoba. I also recommend that land managers reconsider removing introduced plant species from field margins because they are often the only forage plants available to bees in highly disturbed landscapes, and they can attract bees with a wide array of functional traits.

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