

**Effects of habitat loss, fragmentation, and alteration on wild bees and
pollination services in fragmented Manitoba grasslands**

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ABSTRACT

Using bee sampling and cultivated plants, I investigated if habitat loss, habitat fragmentation, and introduced vegetation affect bee abundance and pollination services in fragmented Manitoba grasslands. I ran mixed-effects models analyzing effects of habitat loss using local and landscape scale variables, effects of habitat fragmentation using proximity to habitat edges, and effects of introduced vegetation using canopy cover and open flowers. I found that decreases in landscape-scale habitat resulted in declines in bee abundance and pollination services. Litter depth was also important, with negative effects on ground-nesting bees. Proximity to road edges negatively affected social bees. Introduced vegetation produced mixed effects, with positive effects of introduced canopy cover on bee abundance, but also positive effects of greater percentages of native flowers. My results indicate that habitat loss, and fragmentation have negative impacts on bee abundance in northern prairies, and must be incorporated in management for bee conservation.

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1. INTRODUCTION

1.1 Background

The grasslands of the Prairies ecozone are subject to considerable anthropogenic disturbance, leading to habitat loss and habitat fragmentation. The northern extent of the Prairies, the Aspen Parkland ecoregion, has less than 25% of its original grasslands remaining (Samson et al. 2004) and grassland remnants in this region are subject to ongoing anthropogenic disturbance, such as the introduction of alien species, fire suppression, and conversion to agricultural land (Ricketts 1999). In Manitoba and other parts of the northeastern prairies, the Aspen Parkland consists of remnant grasslands within a mosaic of different land-use types. Exploring habitat loss, fragmentation, and alteration are therefore important when considering how to best conserve and manage these northeastern prairie grasslands.

Pollination services provided by insects are key ecosystem functions that contribute to the reproductive success of the majority of wild and domestic flowering plants. Pollination services are important not only for food production from crops, but also for ecological resilience and ecosystem functioning. Bees (Order *Hymenoptera*, Superfamily *Apoidea*, series *Anthophila*) are the most important animal pollinators for plant reproductive success. Bees can vary widely with regards to body size, floral preference, sociality, and nesting requirements, and they require habitats that provide both floral and nesting resources. Given the importance of insect pollination services and recent declines in both wild and domestic bees, it is essential to understand the effect that habitat loss and habitat fragmentation have on bees and on pollination services (Winfree et al. 2011, Senapathi et al. 2017,).

Recent research in a variety of temperate ecosystems has shown that habitat loss is a major driver of declines in wild bee populations (Winfree et al. 2011). Depending on bee species,

they can be affected by habitat loss at both small, local scales, and at larger, landscape scales. Habitat loss has also been shown to affect pollination services to both wild and domestic plant species (Potts et al. 2010, Ricketts et al. 2008). Habitat fragmentation often accompanies habitat loss but has its own ecological effects. Fragmentation can be distinguished from habitat loss by looking at edge effects, which are the changes that occur at the boundary between two habitat types (Ries et al. 2004). Habitat fragmentation has been shown to affect bee abundance and diversity in agroecosystems and forested areas, but edge effects can vary by bee species traits, such as sociality and nesting requirements (Kremen et al. 2007, Williams et al. 2010). Edge effects have been shown to reduce pollination service to some domestic crops and habitat fragmentation is known to negatively affect some plant populations' reproductive success over time (Aguilar et al. 2006). Introduced plant species can also have mixed effects on pollinator populations and pollination services. Introduced flowers can provide novel resources to pollinators, but can also shift interactions between bees and host plants, resulting in declines in some pollinator species (Aizen et al. 2008, Stout and Morales 2009). Introduced flowers can also compete with or facilitate reproduction of native flowering species, depending on a range of factors (Bjerknes et al. 2007, Cavalliero et al. 2011).

1.2 Problem Statement and Research Objectives

Bee populations and pollination services by insects are often overlooked in Canadian grassland conservation. Little research has been conducted on bees or pollination services in the Canadian Prairies ecozone (Sheffield et al. 2014). Habitat conservation for animals often focuses well-studied birds or mammals; this approach does not ensure habitat conservation for grassland pollinators, since the scale of resource and habitat needs is often very different (Arenz and Joern 1996). Since edge effects on bees and pollination services have been found in croplands and

edges in fragmented grasslands are known to impact plants, birds, and other invertebrates (Koper et al. 2010, Ries and Debinski 2001, Sliwinski and Koper 2012), it is appropriate to extend this work to look at edge effects on bees and pollination services in these grasslands. Likewise, introduced species have effects on other grassland animals, including grassland birds (Wilson and Belcher 1989) and terrestrial insects (Haynes and Cronin 2003), as well as on native grassland plant species (Bakker and Wilson 2001, Fink and Wilson 2011, Larson et al. 2006). More information is needed on bee populations and pollination services in this region in order to make informed decisions and assessments of management approaches.

Identifying the scale of the effects of habitat loss and fragmentation is important to helping managers plan conservation activities at the most appropriate spatial scale. Understanding the strength and distance of edge effects can also help identify whether small grassland patches have “core” areas or if they are effectively all edge habitat (Fagan et al. 1999). Similarly, managers can benefit from understanding the scale of impacts of grassland habitat loss on bees and pollination services. Identifying habitat responses by different types of bees can help managers identify which species or groups are affected by management decisions or ongoing habitat changes.

Many studies look at habitat effects on species or groups of species, and there is limited research on whether these effects result in changes to ecosystem processes, such as pollination services. Existing research in this area has looked primarily at landscape variables such as amount of natural habitat in a landscape and the spatial arrangement of floral resources, and most of this research has been conducted in cropland (Viana et al. 2012). Few studies have explored edge effects, and few have focused on pollination services within grassland patches. Since effects of habitat loss and fragmentation, and of introduced species can differ by pollinator species and

by landscape context, it cannot be assumed that effects seen in other ecosystems will translate directly to northern prairie grasslands. Informed management of grassland pollination service may also benefit the agricultural landscapes surrounding grassland patches, as non-intensively managed grasslands are important as pollinator sources for domestic food and forage crops (Albrecht et al. 2007, Kremen et al. 2004).

Given the anthropogenic pressures on northern grasslands, and the need for information that is specific to bees and pollination services in this region, the objectives of this thesis were to:

- 1) Determine if habitat loss affects wild bee abundance or pollination services in fragmented northern Prairies grasslands.
 - a. Determine if habitat loss has effects at both local and landscape spatial scales.
 - b. Determine if habitat loss has differing effects based on bee sociality or nesting location.
- 2) Determine if habitat fragmentation affects wild bee abundance or pollination services in fragmented northern Prairies grasslands.
 - a. Determine if road edges have effects on bee abundance or pollination services.
 - b. Determine if treed edges have effects on bee abundance or pollination services
 - c. Determine if edge effects vary based on bee sociality or nesting location.
- 3) Determine if introduced plant species affect wild bee abundance or pollination services in fragmented northern Prairies grasslands.
 - a. Determine if canopy cover of introduced vegetative species has effects on bee abundance or pollination services.
 - b. Determine if abundance of introduced flowers has effects of bee abundance or pollination services.

- c. Determine if effects of introduced species vary based on bee sociality or nesting location.

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2. LITERATURE REVIEW

2.1 Pollination and Pollinators

2.1.1 Pollination services

Pollination services refer to the transfer of pollen by animals among flowering plants. Pollination services involve a mobile transfer of genetic material, which is key to plant species persistence and ecosystem resilience (Lundberg and Moberg 2003). This ecosystem function directly contributes to the reproductive success of approximately 90% of the world's flowering plants (Nabhan and Buchmann 1997). Pollination services are particularly important to the reproduction of self-incompatible (non-self-fertilizing) flowering species. Pollen limitation is the reduction in plant reproductive success that can result from inadequate quality or quantity of pollen being transferred to the stigma of a flower (Ashman et al. 2004). Pollen limitation is estimated to be present in at least 60% of flowering plants (Burd 1994) and when pollination limitation is chronic, it can result in ecological consequences including shifts in plant community composition (Ashman et al. 2004).

Pollination communities are structured as webs of interacting plants and pollinators. These webs have been shown to be nested and asymmetric, meaning that specialist species usually interact with generalists, instead of tightly-paired specialist-specialist relationships (Bascompte et al. 2003). It is thus appropriate to investigate pollinator communities as a whole or by looking at larger functional groups (Memmot 1999). Generally, flowering plants exhibit a suite of floral traits (pollination syndrome) that is associated with functional groups of pollinators (Fenster et al. 2004). For this reason researchers often group pollinators by body size (Albrecht et al. 2009), mouthparts size (Fontaine et al. 2006), or sociality (Steffan-Dewenter et

al. 2002) since these traits have been shown to be related to pollinator flower-visiting behaviour and pollen transfer.

Insects provide the majority of pollination services, and as discussed below, bees are generally the most effective and important pollinators (Neff and Simpson 1993, Willmer et al. 2017). Other important groups of pollinators in North America include flies, moths and butterflies, wasps, ants, and beetles. The effectiveness of an insect pollinator depends on both the frequency of visits and the effectiveness of a species as a pollen vector (Fenster et al. 2004, King et al. 2013). Experimental studies show that diversity of pollinator functional groups enhances the reproductive success of plants (Fontaine et al. 2006). Loss of functional groups can impact genetic linkages between plants, as well as ecosystem productivity (Lundberg and Moberg 2003). The loss of pollinators is hypothesized to be an important factor in pollen limitation, and declines in pollinator richness and abundance have been repeatedly correlated to reductions in plant seed set or fruit set (Albrecht et al. 2009, Garibaldi et al. 2011, Steffan-Dewenter and Tschamntke 1999).

2.1.2 Bee Pollinators

Bees are important and effective pollinators due to their life history traits. Bees are obligate florivores in both larval and adult stages (Winfree et al. 2011), with the females of the majority of bee species actively collecting pollen from flowers to feed or provision their offspring and adult bees also feeding on floral nectar (Michener 2007). These resource needs mean that bees, particularly adult females, are frequent floral visitors that carry relatively large pollen loads on their bodies. Recent research has shown that bees are more effective pollinators in comparison to other insects due to both the frequency of their floral visits and amount of pollen deposited onto floral stigmas (Willmer et al. 2017). Wild bees have been found to be more

effective pollinators than managed honey bees for both wild flowering plants and many flowering crops (Garibaldi et al. 2013, Willmer et al. 2017).

The effectiveness and ecological role of pollinating bees varies by species. There are approximately 800 bee species identified in Canada, with 387 bee species known in the grasslands of the Prairies ecozone (Sheffield et al. 2014). These species vary widely with regards to their floral specialization, body size and shape, nesting biology, sociality, foraging behaviour, and seasonal emergence patterns (Michener 2007, Sheffield et al. 2014.). The majority of bees nest underground, particularly in the Prairies ecozone (Sheffield et al. 2014), but many species nest above ground, using cavities found in vegetation or rocks. Some bees require pre-formed holes or cavities, while others will excavate their own nests. Similarly, some bees bring vegetation into nests to form cells, while others do not. Thus, nesting site and resource needs can vary widely by bee species. Sociality also varies: the majority of bees are solitary, but many species are social with varying degrees of nest sharing and sometimes division of reproductive and foraging behaviours (Michener 2007). Bee species vary in their floral foraging preferences. Polylectic bees will take pollen from a variety of floral species and families, while others rely on a family of flowers, or even a very few closely related species (Michener 2007). Bee populations in northern temperate areas often have seasonal emergence patterns, with adult bees being active at different points in the season, varying by species. Some species, such as most bumblebees, are active throughout the non-winter seasons, while others may only emerge for a few weeks at a time. (Patenaude 2007).

The following examples illustrate the variation in bee nesting biology and life cycles found in the Canadian prairies. *Hoplitis pilosifrons* are small solitary bees that nest in cavities above ground. Individual females have been observed excavating pith from *Helianthus* stems,

then provisioning pollen into the hollowed out stem before laying an egg. The females then cut and bring leaf material to the stem to partition one cell from the next, before gathering more pollen and laying another egg. Thus eggs are individually provisioned with pollen, then left by the female, protected in the hollow stem (Michener 1955). The eggs hatch and larvae feed on the provisioned pollen, before pupating and exiting the nest as adults the following spring. Another solitary bee, *Andrena carlini*, nests in burrows in the soil. Females excavate these burrows, which contain cells where the female provisions individual eggs with pollen before sealing the cell. Eggs are often laid 10-25cm below ground (Schrader and Laberge 1978). *Lasioglossum zephyrum* are small social bees that also nest in soils. Nests are begun in the spring by a single mated female who lays several eggs and provisions the larvae with pollen. This first generation reaches maturity after several weeks, and new females stay at their natal nest, enlarging it by creating new cells, and some mate and lay new eggs. The population of the nests peaks in mid-late summer, and mated adult females pass the winter in their natal nests before founding new seasonal colonies the following spring (Batra 1964). *Bombus griseocollis* are social bumblebees that usually nest above ground in clumps of vegetation. A nest is founded by a mated female (queen) that overwinters and emerges in the spring. Initially, the queen forages and provisions larvae, but as the colony grows and more adult bees reach maturity, other bees perform many of the tasks such as foraging, guarding, and nursing (Cameron 1989). In late summer, the colony raises new queens, which mate and overwinter.

Bee populations can be particularly vulnerable to anthropogenic disturbance due to their habitat needs and biological traits. As central-place foragers, the majority of bee species move frequently from nesting sites to foraging sites, which may or may not occupy the same physical space. Pollen-collecting bees therefore require multiple “partial habitats” which can provide both

nesting sites and resources, as well as adequate floral food sources within a species' foraging range (Westrich 1996). The spatial scale of habitat needs can vary based on bee foraging ranges, with smaller bees often foraging only a few hundred meters from nest sites, while larger bees may forage up to a few kilometers from their nests (Greenleaf et al. 2007, Zurbuchen et al. 2010). As well, bees' foraging behaviours require them to have capacities for learning, navigation, and memory; such processes can be disrupted by disturbances that introduce nutrient deficiencies, pesticides, or pathogens (Klein et al. 2017).

Recent recorded declines of honey bees and bumblebees, and possible declines of other wild bee populations have led to increased attention to bee pollination services. Worldwide honey bee declines have been demonstrated for both wild and feral colonies (National Research Council 2007). Many species of North American bumblebee populations have declined rapidly in both range and abundance in the past decade (Cameron et al. 2011, Williams and Osborne 2009). Other North American wild bee species are not well-monitored and there is little direct data on their populations (Winfree 2010), but indirect evidence from studies on habitat loss and agricultural intensification point to declining populations, especially for pollen specialists and habitat specialists (Potts et al. 2010). Recent habitat modeling in the United States predicts declines in wild bee populations, particularly in areas where natural habitat has been converted to cropland (Koh et al. 2016). Habitat loss and habitat fragmentation have been identified as the primary anthropogenic causes of decline in wild bee abundance and richness (Winfree et al. 2009). Population trends and habitat effects for most bees in the Canadian portion of the Prairies ecozone are not well understood, as few surveys have been conducted and there is little baseline data to measure changes against (Sheffield et al. 2014). Monitoring bees in any ecosystem can be

difficult, as populations often fluctuate from year to year (Roubik 2001, Turnock et al. 2007, Williams et al. 2001), and species identification can be difficult and time-consuming.

2.2 Northern Prairies Landscape Context

The northern prairies of North America have been subject to a high degree of habitat loss. Historically, this loss has been mainly due to conversion of natural grassland areas to annual cropland: approximately 70% of Canada's native vegetation in the Prairies ecozone was converted to cropland by the 1990s (ESTR Secretariat 2014). Despite these habitat losses, there is relatively little prairie land under permanent protection: the ecozone is characterized by 79% of the land in private ownership, and only 2% of the land in protected areas (Riley et al. 2007). As of 2003, approximately 1% of Prairies ecozone was under some form of conservation management in Manitoba (compared with 2% in Alberta, and 9% in Saskatchewan (Gauthier and Wiken 2003).

The Aspen Parkland ecoregion is the northernmost extent of the Prairies ecozone in North America. The landscape can be characterized as a mosaic of grassland, cropland, forest and wetland (Manitoba Conservation 2005), and an estimated 87% of the Aspen Parkland is under private ownership, with less than 2% in protected areas (Riley et al. 2007). The grasslands of the Aspen Parkland have been subject to some of the greatest habitat loss in the Prairies ecozone: it is estimated that 75% of the original Aspen Parkland grasslands have been lost over the last two centuries (Samson et al. 2004). Although habitat loss appears to leveled off in some areas of the Prairies ecozone, the Aspen Parkland is experiencing ongoing losses, with an estimated 15% of remaining native grasslands in the Aspen Parkland ecoregion lost between 1985 and 2001 (Watmough and Schmoll 2007).

In addition to habitat losses, the Prairies ecozone is subject to high rates of habitat fragmentation, particularly in areas with higher human population density (Riley et al. 2007). In northern areas of the Prairies ecozone, such as the Aspen Parkland, fire suppression and bison extirpation have led to increasing woody encroachment on remaining grassland areas (Shorthouse 2010). Additionally, linear anthropogenic developments, particularly roads, have contributed to fragmentation of the landscape, especially in areas where soils and climate are conducive to agricultural crops (Willms et al. 2011). As such, habitat fragmentation of Aspen Parkland grasslands is severe and many patches are described as effectively isolated (Ricketts 1999).

Many Eurasian plant species were introduced deliberately and accidentally to the Prairies ecozone following European colonization. In the Aspen Parklands ecoregion, an estimated 10-15% of all vascular plant species are introduced (Ricketts 1999). Most of the Aspen Parklands grasslands, including prairie remnants, have introduced forage grasses such as smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), and crested wheatgrass (*Agropyron cristatum*) (Smith et al. 1998, Willms et al. 2011), and the degree of invasion of these grasses increases in eastern parts of the ecoregion (ESTR 2014). These species spread rhizomatously, in contrast to the tufted perennial growth of the majority of native grass species, and often outcompete native species (Wilson 1989, Fink and Wilson 2011). Introduced forb species include Canada thistle (*Cirsium arvense*), dandelion (*Taraxacum officinale*), common tansy (*Tanacetum vulgare*), and forage legumes such as alfalfa (*Medicago sativa*), clovers (*Trifolium* spp.) and sweet clovers (*Melilotus* spp.) (Beacom 1991, EDDMapS 2017, Smith et al. 1998)

2.3 Habitat Loss and Habitat Fragmentation

Early landscape ecology considered habitats to be embedded in a hostile matrix (non-habitat) with little or no resources, but more recent work recognizes that the matrix can influence species and ecosystem processes within focal patches, and can provide supplementary or complementary resources, and influence connectivity among habitat patches (Jules and Shahani 2003). Landscape ecology, therefore, focuses on understanding how organisms use resources and interact in spatially heterogeneous mosaics, and on the causes and consequences of spatial patterns at different scales (Turner 2005). Patterns of habitat loss and fragmentation are a key part of these landscape dynamics, which have significant effects on bees and pollination services (Winfrey et al. 2011).

Anthropogenic impacts on landscapes can generally be separated into impacts of habitat loss and impacts of habitat fragmentation, although the two often occur simultaneously and research does not properly separate the two (Fahrig 2003). Habitat loss is the reduction of a focal habitat type or set of resources as it relates to a species or guild, while habitat fragmentation can be defined as the breaking up of habitat types within a landscape (Fahrig 2003). The two processes often happen at the same time on a landscape, but can have different ecological effects. Edge effects are an important consideration in fragmented landscapes, as these effects can be used to separate the effects of habitat loss from those of habitat fragmentation, since effects of edges can be measured separately from metrics of habitat loss (Fahrig 2003). Edges are the boundary between different habitat patch types and have been shown to affect species abundances and richness (Ries et al. 2004).

2.4 Effects of habitat loss on bees and pollination services

2.4.1 Effects on bees

As noted above, anthropogenic habitat loss is one of the main drivers of declines in bees and other insect pollinators. Some anthropogenic disturbance can lead to increases in bee diversity since low to moderate disturbance may result in increased habitat diversity on a landscape (Michener 2007, Potts et al. 2010). However, disturbance that creates habitat loss and simplified landscapes, such as agricultural intensification, has been shown to result in overall declines in abundance and diversity of wild pollinators, including bees (Mogren et al. 2016, Senapathi et al. 2017). In anthropogenically impacted landscapes, agricultural intensification and land-use changes are associated with declines in pollinator abundance and diversity (Potts et al. 2010). One reason for this is that habitat loss often accompanies intensification, particularly the loss of previously uncropped areas, such as field margins, hedgerows, and other small natural habitats (Kremen et al. 2002). Thus, the intensity of change and the landscape context of habitat changes are important considerations (Le Feon et al. 2010).

The scale of habitat loss is also an important consideration, as bees have been shown to respond to small, local scale habitat changes, as well as larger, landscape scale changes (Kennedy et al. 2013, Kremen et al. 2007, Schuepp et al. 2013). Most bees forage at distances less than their maximum capabilities, so the local scale of habitat loss often means within ranges of 100-300m (Zurbuchen et al. 2010). On a larger scale, bees have also been repeatedly shown to respond to habitat loss at scales of 500m-2000m (Jauker et al. 2009, Steffan-Dewenter et al. 2002, Taki et al. 2007, Viana et al. 2012, Watson et al. 2011). Habitat at both local and landscape spatial scales can be significant simultaneously, but with differing effects, so it is important to

investigate multiple spatial scales when seeking to understand effects on bee populations (Grass et al. 2016, Hines and Hendrix 2005, Kennedy et al. 2013).

Habitat loss can mean that bees are no longer able to use an area at all, but it can result from a partial loss of some resources. For example, conversion of a natural area to annual cropland may still preserve some floral resources in the form of mass-flowering crops (Robson 2014), but may remove below-ground nesting habitat if fields are regularly tilled (Williams et al. 2010). Thus, effects of habitat loss and the spatial scale of these effects varies with different species' traits and resource needs.

Loss of floral resources appears to be the biggest driver of effects of habitat loss on overall bee abundance and diversity (Winfree et al. 2011). Floral specialization has a role in bee species' responses to habitat loss, with specialist bees showing greater sensitivity to habitat loss, likely due to their inability to switch food sources if habitat loss results in declines or disappearance of preferred floral resources (Winfree et al. 2011). In the Canadian Prairies ecozone, it is possible that specialist species have already declined historically, but the lack of baseline data in this region makes it difficult to assess if this has been the case (Sheffield et al. 2014). Bee body size can also affect the scale at which bees are affected by habitat loss, with larger bees showing less sensitivity at smaller spatial scales (Steffan-Dewenter and Tschamtkke 1999). This may be because they are able to interact with the landscape at a different scale than smaller bees due to their greater foraging distances (Osborne et al. 1999).

Nesting biology also determines how a bee will respond to different types of habitat loss: below-ground nesting bees are more sensitive to tilling, while above-ground nesting bees appear to respond more to removal of vegetative habitat (Williams et al. 2010). Sociality can also come into play, as social bees have also been shown to be respond more strongly to landscape scales

than solitary bees, regardless of body size, indicating that they may perceive the landscape differently (Kennedy et al. 2013). Social bees may also be more susceptible to landscape-scale habitat loss than solitary bees (Bommarco et al. 2010), but the mechanisms for this are not entirely clear, and these effects may change with landscape context (Steffan-Dewenter et al. 2002).

2.4.2 Effects on Pollination Services

Habitat loss can affect pollination services differently than bee populations. Pollen limitation is a primary cause of reduced plant reproduction and persistence, so factors that lead to pollen limitation are important considerations. Pollination services can be affected by changes in pollinator abundance, but variables such as frequency of pollinator visits, length of visits, and effectiveness of a pollinator species for a particular plant species are also important (Bernhardt 2005, Willmer 2017). Habitat loss can result in fewer flowers of the same species in an area, meaning that there are reduced amounts of conspecific (same-species) pollen being transferred by pollinators, leading to less effective pollinator visits and reduced reproductive success (Ashman et al. 2004). Habitat loss that results in lower floral densities in an area can also cause reduced visits by pollinating insects (Hegland and Boeke 2006), which may shift their foraging behaviour to larger or more resource-dense habitat patches, leading to reduced pollinator visit frequency for plants in low-density patches (Dauber et al. 2010).

2.5 Effects of habitat fragmentation on bees and pollination services

Edge effects on a species or an ecosystem process can be positive, negative, or neutral, depending on species responses and the quality of resources provided by adjacent habitats (Ries et al. 2004). Like the effects of habitat loss, edge effects on bees and pollination services will

vary by bee and plant taxa, as well as with the landscape context and qualities of different habitat types.

2.5.1 Effects on Bees

Edge effects can affect bees due to changes in plant communities at or near edges (Koper et al. 2010), which can lead to changes in floral resources availability and changes in vegetation structure. Increases or decreases in floral resources can lead to increases or decreases in bee abundance and diversity, depending on the floral preferences of individual species and the community composition of pollinating bees (Potts et al. 2003). Pollinator diet selection could also be affected by changes in vegetation composition or floral abundance at edges, causing behavioural shifts in foraging patterns (Slaa and Biesmeijer 2005). Such dietary and foraging changes have been shown to vary by bee functional group (Jha and Vandermeer 2009). Vegetation structure can affect pollinators if it produces physical barriers or conduits to foraging. Although bumblebees and honey bees have been shown to forage both through and around wooded patches (Krewenka et al. 2011, Kreyer et al. 2004), woody edges may have edge effects on abundance or richness since vegetation structure can affect nesting locations and flight patterns. Bare ground and roads have been shown to act as foraging barriers for bumblebees (Bhattacharya et al. 2003). It is possible that smaller bees with shorter flight distances may be more sensitive to changes in vegetation structure at or near edges, but this mechanism has not been investigated. It has been hypothesized that pollinator behaviour could change at edges due to shifts in predation risk, changes in the profitability of gap-crossing, or if edges act as corridors between partial habitats (Hadley and Betts 2012).

Edge effects that alter nesting resources can impact pollinator reproductive success and local abundance (Williams et al. 2010). Changes in plant communities can lead to shifts in

nesting resources, such as access to soils, litter depth or the number of woody stems (Coffin 2007). In agricultural areas, management practices, such as pesticide application, may lead to changes in nesting success near crop edges (Chacoff and Aizen 2005, Whitehorn et al. 2012). Road edge effects on soils, including changes to slope, compaction, or drainage (Trombulak and Frissell 2000) can also affect nesting locations, leading to changes in bee abundance and persistence (Sardinas and Kremen 2013). Roads and paved areas can also affect nest density for some ground-nesting bees (Jha and Kremen 2013).

Edges in grasslands affect a range of invertebrates including butterflies (Ries and Debinski 2001, Schultze and Crone 2001), leafhoppers (Haynes and Cronin 2006), and beetles (Collinge and Palmer 2002), and studies have recently begun to demonstrate edge effects on pollinators and pollination services. In remnant habitats, non-ant hymenoptera abundance show positive correlations with edge in scrub habitat in California (Bolger et al. 2000). Distance to different land cover type affects hymenoptera abundance in grassland-agricultural mosaic landscapes in Norway (Hirsch and Wolters 2003). Experimental data using small patches shows that insect pollinators are influenced by edge type, which in turn impacts the number of floral visits and seed set of red clover (Diekotter et al. 2007).

Evidence of edge effects on bee populations has mostly been gathered from studies in agricultural systems. In a variety of crops, bee abundance and diversity have been shown to decline at 50m to 500m from natural habitat edges (Bailey et al. 2014, Chacoff and Aizen 2006, Hirsch and Wolters 2003, Saunders and Luck 2014, Steffan-Dewenter and Tschardtke 1999). Like the effects of habitat loss, effects of fragmentation appear to vary by species and by type of bee, with the scale of edge effects varying by bee body size or genera (Bailey et al. 2014, Steffan-Dewenter and Tschardtke 1999).

2.5.2 Effects on Pollination Services

Research on habitat fragmentation is often species-focused, but landscape effects on pollination services and pollination communities have attracted recent attention (Viana et al. 2012). Due to concerns about crop pollination, the majority of this work has investigated effects in agroecosystems or in agricultural mosaic landscapes, although some have focused on wild plants. A review incorporating a wide range of regions and plant families found that there is a general large, negative effect of habitat fragmentation on pollination and plant reproduction (Aguilar et al. 2006). The authors found that reproductive system was the most important plant characteristic for predicting plant sensitivity to fragmentation, with self-incompatible species demonstrating the strongest response. The authors suggest that this is mainly due to pollination limitation. Another review identifies pollen limitation as the major driver behind the effects of fragmentation, but points out that the mechanisms behind this limitation are not always well known, and that these fragmentation mechanisms are often confounded with habitat loss (Hadley and Betts 2012).

Edge effects have been shown to impact ecosystem processes, including pollination services, but edge effects on these processes are often not as well understood as effects on individual species or groups of species (Ries et al. 2004). Plant abundance can be affected by edge via impacts to community composition due to individual species' responses to edge effects. Previous research shows that grassland plant species responses to edge can vary by species and that distance to edge is a key variable in determining plant community composition (Koper et al. 2010). Changes in light or nutrient availability at or near edges can also impact the abundance of plant species (Ries et al. 2004). As with habitat loss, the presence of conspecific (same species) blooms affect both the number of pollinator visits and subsequent seed set: edge effects on plant

abundance can result in impacts to pollination services if there are reduced pollinator visits or less pollen to transfer. In fragmented landscapes, agricultural practices and the presence of roads can increase the presence of alien species (Gelbard and Belnap 2003, Trombulak and Frissell 2000) which often respond positively to edge in grassland remnants (Koper et al. 2010). Edges that consist of flowering crops change the composition of flower resources at an edge that can result in spillover effects at or near these edges (Gladbach et al. 2011). Alien plant species introduced at edges can interrupt native plant-pollinator interaction webs by outcompeting native plants for pollinators, particularly if they share similar flower morphology (Larson et al. 2006, Morales and Traveset 2009) or by enhancing floral resources for only a subset of local pollinators (Potts et al. 2010).

Edge effects on pollination services have been demonstrated, mainly in agricultural systems. The frequency of bee flower visits to flowering crops is negatively impacted by increasing distance to natural area edge for both honey bees (Kremen et al. 2004) and wild pollinators (Chacoff and Aizen 2006). Distance to natural areas reduces both temporal and spatial stability of pollination service in flowering crops (Garibaldi et al. 2011). Increasing distance to natural habitat has also been shown to reduce seed set in phytometers placed in intensively-used agricultural areas (Albrecht et al 2009, Schuepp et al. 2013, Steffan-Dewenter and Tscharncke 1999).

2.6 Effects of Introduced Species on Bees and Pollination Services

The effects of introduced plant species vary depending on the species and on the ecological context, so it can be difficult to draw general conclusions (Vila et al. 2011). Common effects are a decrease in abundance and diversity of native species, and alterations of nutrient cycles (Ibid.). In the Canadian Prairies, introduced grasses and *C. arvensis* (Canada thistle) have

been shown to outcompete native grasses and forbs, often resulting in decreased plant species diversity and evenness (Bakker and Wilson 2001, Fink and Wilson 2011, Hodgson 1968).

Smooth brome and crested wheatgrass have been shown to change nutrient ability and soil characteristics (Christian and Wilson 1999, Jordan et al. 2008). Smooth brome, crested wheatgrass, and *Melilotus officinalis* (yellow sweet-clover) can also act as facilitators for the growth of other plant species, including other introduced species (Jordan et al. 2008, Van Riper and Larson 2008). Introduced plant species can impact other trophic levels: introduced grasses can restrict movement of prairie insects (Haynes and Cronin 2003), and some species of grassland birds avoid areas with dense introduced cover (Wilson and Belcher 1989).

2.6.1 Effects on Bees

Limited research has been conducted on the effects of introduced plant species on bees and other insect pollinators. The studies which have been conducted have found that the effects vary depending on the introduced plant species and on the species of pollinator (Stout and Tiedeken 2017). Introduced plant species can have both direct and indirect effects on bees. Introduced flowering forbs can provide novel forage species for native bees, potentially shifting bee foraging behaviour and phenological patterns (Stout and Morales 2009). Introduced flower species can also provide different nutrient levels to visiting bees (Stout and Tiedeken 2016). These novel forage species introduce changes to plant-pollinator interaction webs such as changes to the type and frequency of interactions between plants and pollinator species (Aizen et al. 2008). Such changes can result in shifts over time in bee community composition and changes in the relative abundance of some bee species.

Introduced plant species can also indirectly affect bees and other insect pollinators by creating changes in species composition and abundance of available forage flowers. If invasive

species outcompete native forage flowers, this can result in shifts in floral communities, including changes to richness and abundance of forage species. As a group, bees may be more resistant to such changes in forage availability than other insect pollinators, possibly because many bee species have a wider diet breadth than other pollinator groups (Montero-Castano and Vila 2012). Specialist bee species are likely to be most affected by changes in forage availability, since they are less able to adapt to changes in floral resources (Biesmeijer et al., 2006, Stout and Morales 2009). Smaller bees, which have smaller foraging ranges, may also be more affected by such changes, as they may be unable to change their foraging behaviours to find new habitat patches with preferred forage flowers (Zurbuchen et al. 2010).

Bees may also be affected by introduced species via changes to non-forage resources, including nesting and over-wintering sites. Introduced species can compete with native vegetation, potentially resulting in a loss of nest sites for above-ground nesting bees, such as clumping native grass tussocks (Svensson et al 2000, Jordan et al. 2014). Evidence that introduced forage grasses can change soil conditions may mean that these species also alter conditions in nesting sites for below-ground nesting bees (Jordan et al. 2008). The vegetative structure of many introduced species is different than that of native species: the dense rhizomatous growth of grasses such as smooth brome and Kentucky bluegrass may result in less loose soil for below-ground bee nesting sites, as well as increased litter cover, blocking access to bare soils (Potts et al. 2005).

2.6.2 Effects on Pollination Services

If there are habitat effects on bees, as discussed above, these may result in changes to pollination services to flowering plants. Changes in pollinator abundance or diversity can affect the pollination services they deliver. Changes in overall pollination services are likely if there are

habitat shifts (such as nesting location availability) resulting in changes in bee abundance or diversity. Introduced plant species can also impact pollination services to native plant species by competing for pollinator visits, or by facilitating pollinator visits. Competition for pollination services occurs when introduced flowering species attract pollinators, reducing visits to and pollen transport from native flowers. Facilitation, on the other hand, occurs when the presence of a flowering introduced species increases the pollination and reproductive success of co-flowering native species. This can occur when an earlier-flowering species provides support for pollinators then visit native species later on, a process known as “sequential mutualism” (Waser and Real 1979), or when introduced flowers attract greater densities of pollinators that then visit co-flowering native species (Rathcke 1993). The concept of facilitation via pollinator support is well-supported in research (Rathcke 1993, Ghazoul 2006, Rodriguez 2006, Feldman et al. 2004), but there appears to be little research on the role of introduced species providing this type of facilitation for native species. It is a plausible hypothesis that this could occur, and there is evidence that weedy introduced species facilitate pollination services to later-flowering crops (Carvalhiero et al. 2011).

A meta-analysis found that introduced flowering species more often produce competitive effects on co-flowering native species, which received reduced numbers of pollinator visits and less conspecific pollen deposition (Bjerknes et al. 2007). Introduced flowering species have greater negative effects on pollination services to native co-flowering species when the species share floral symmetry or colour, and when there are greater relative abundances of the introduced species (Morales and Traveset 2009). While competition may occur on a small, local scale, it is possible that introduced flowering species may facilitate pollination services on a broader scale by increasing pollinator densities on a landscape (Westphal et al. 2003). Competitive and

facilitative effects of introduced flowering species have also been shown to vary seasonally and annually (Bjerknes et al. 2007, Larson et al 2006).

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3. EFFECTS OF HABITAT LOSS, HABITAT FRAGMENTATION, AND INTRODUCED PLANT SPECIES ON WILD BEES AND POLLINATION SERVICES IN NORTHERN PRAIRIE GRASSLANDS

Abstract

Habitat loss, habitat fragmentation, and introduced vegetation negatively affect bees and pollination services in many landscapes by altering resource availability and configuration. I investigated if these changes affect bee abundance and pollination services in fragmented Manitoba grasslands. I conducted bee sampling and used cultivated plants to measure pollination services in 2014 and 2015. Using mixed-effects models I analyzed effects of habitat loss at local and landscape scales, effects of habitat fragmentation using proximity to habitat edges, and effects of introduced vegetation using canopy cover and open flowers. I found that decreases in landscape-scale habitat resulted in declines in bee abundance and pollination services. Local litter depth was also predictive, with negative effects on ground-nesting bees. Proximity to road edges negatively affected social bees. Effects of introduced vegetation were mixed; I detected positive effects of both introduced canopy cover and greater percentages of native flowers on bee abundance. Effects of habitat on bee abundance and pollination services varied across different temporal periods, and were most consistent for social bees and ground-nesting bees. My results indicate that habitat loss and fragmentation both have negative impacts on bees in northern prairies, and that maintenance of intact habitats is important to promote bee conservation in this region.

3.1 Introduction

The grasslands of the North American northern prairies have undergone widespread changes since European settlement. These include extensive habitat loss, mainly due to conversion of native prairie to annual cropland, and habitat fragmentation due to anthropogenic activities, such as road construction and fire suppression leading to woody encroachment (Shorthouse 2010). These changes, along with anthropogenic introductions of Eurasian plant species, have resulted in loss and degradation of original northern prairie grassland ecosystems, with over 70% of Manitoba's original prairies now lost (Samson et al. 2004). Seventy-five percent of the original prairie grasslands in the northernmost part of the North American prairies, the Aspen Parkland ecoregion, have been lost over the past two centuries (Samson et al. 2004). Grassland loss and fragmentation is ongoing in these northern prairies; 15% of remaining native grasslands in the Aspen Parkland were lost between 1985 and 2001 (ESTR Secretariat 2014). Remaining Aspen Parkland grassland patches are highly fragmented and thus effectively isolated from other grasslands, and an estimated 10-15% of all plant species in the ecoregion are introduced (Ricketts 1999). Effects of northern prairie habitat loss and fragmentation, and of introduced species, have been demonstrated on many taxa, including birds (Sliwinski and Koper 2012, Wilson and Belcher 1989), invertebrates (Haynes and Cronin 2003, Ries and Debinski 2001), and plants (Koper et al. 2010).

These habitat changes to the northern prairies are likely to impact pollinators and pollination services to plants. Insects provide the majority of pollination services to flowering prairie plants, and thus are key to plant species persistence and ecosystem stability (Lundberg and Moberg 2003). Among insect pollinators, bees are the most important, providing more floral visits and better pollen deposition than other insects (Willmer et al. 2017), mainly due to their

pollen-collecting life history and morphology (Neff and Simpson 1993). Canada's prairies are home to some of the highest bee diversities in the country, with nearly half of all Canadian bee species found in this ecozone (Sheffield et al. 2014). However, effects of habitat loss, fragmentation, and alteration on bees and on pollination service in the Canadian prairies are poorly understood due to the fact that few pollination studies have been conducted in this region (Sheffield et al. 2014). Understanding the strength and scale of habitat effects can help grassland managers identify actions to maintain or enhance bee populations and pollination services in this heavily-impacted landscape.

In studies in non-prairie ecosystems, habitat loss has been shown to affect bees and pollination services in a variety of ways and at multiple spatial scales (Dauber et al. 2010, Hadley and Betts 2012, Kennedy et al. 2013). Habitat for pollinators is broadly based on the availability of floral resources: flower communities can determine diversity and composition of bee communities (Potts et al. 2003), and bee abundance in landscapes generally follows patterns of floral resource availability (Winfree et al. 2011). As central-place foragers, bees return to a "home-base" nesting location where they return between foraging bouts (Lonsdorf et al. 2009). Habitat for pollen-collecting bees, therefore, also requires nesting locations and resources within range of floral foraging locations (Westrich 1996). The availability of these floral and nesting habitat resources at a local scale is a driver of pollinator richness and abundance (Grass et al. 2016, Hines and Hendrix 2005, Orford et al. 2016, Williams et al. 2010). Many bees only forage a few hundred meters from their nest sites, so local habitat can be defined at that scale (Greenleaf et al. 2007, Zurburchen et al. 2010). Most bees in the Prairies ecozone nest below ground, preferring upland well-drained soils, but many nest above ground, using cavities in vegetation, rocks, or other available spaces (Sheffield et al. 2014). The availability of nesting resources is a

major predictor of bee community abundance and composition (Grundel et al. 2010, Kremen et al. 2007, Potts et al. 2005, Sardinas et al. 2017), and alterations to nest sites such as changes in vegetation litter depth or the number of woody stems often impacts pollinator reproductive success (Williams et al. 2010).

Bee populations and pollination services are also sensitive to larger-scale landscape effects. Landscape influences pollinator diversity by determining resource availability and connectivity among resources, and pollinator abundance by determining the amount of habitat that is available (Viana et al. 2012). Early landscape ecology considered habitats to be embedded in a hostile matrix (non-habitat) with little or no resources, but more recent work recognizes that the matrix can influence species and ecosystem processes within focal patches, and can provide supplementary or complementary resources, and influence connectivity among habitat patches (Jules and Shahani 2003). As mobile insects, bees make use of multiple “partial habitats”, often using different land cover types for foraging and nesting resources (Westrich et al.), so the distinction between matrix and habitat may not be easily determined. Despite the potential for bees’ use of multiple landscape cover types, bee abundance has been shown to decline with decreases in natural and semi-natural habitat, suggesting that anthropogenic land uses form a matrix that does not provide adequate resources for bees to persist over time (Kremen et al. 2007). Bee abundance has been consistently shown to be sensitive to the amount of natural and semi-natural habitat at landscape scales of 500m-2000m, with the exact scale of these effects varying by species (Steffan-Dewenter et al. 2002, Taki et al. 2007, Viana et al. 2012, Watson et al. 2011).

Landscape habitat effects on bees can vary with bee characteristics, notably body size (Steffan-Dewenter and Tschamntke 1999), and with bee behaviours, such as floral speciality

(Winfree et al. 2011). A review of bee responses to environmental disturbance found that sociality (social or solitary) and nesting location (above- or below-ground) were particularly predictive (Williams et al. 2010). Social bees were more sensitive to isolation from natural habitats than solitary bees, which may be due to social bees' season-long nesting needs, which may result in more sensitivity to landscape habitat loss (Ricketts et al. 2008, Williams et al. 2010). Social bees have often been shown to respond more strongly to landscape-scale variables than solitary bees, regardless of body size, indicating that they may perceive the landscape differently (Kennedy et al. 2013). Bee nesting location also affects which types of disturbance bees are more sensitive to: below-ground nesting bees are more sensitive to tilling, while above-ground nesting bees are more likely to respond to isolation from natural areas (Williams et al. 2010).

Habitat fragmentation often accompanies habitat loss, but is a separate process that can have unique ecological effects (Fahrig 2003). Many studies of landscape effects on pollination fail to effectively separate habitat loss and habitat fragmentation (Hadley and Betts 2012). One way to separate effects of fragmentation from effects of habitat loss is to evaluate effects of habitat edges, the ecological changes that occur at or near the boundary of different habitat types, because edge effects are one of the main effects of habitat fragmentation at a landscape scale and can be measured independently from habitat loss (Fahrig 2003). Edge effects on wild bee abundance and species diversity have been identified in agricultural crops at distances ranging from 50m to 500m from edges (Bailey et al. 2014, Chacoff and Aizen 2006, Hirsch and Wolters 2003, Saunders and Luck 2014, Steffan-Dewenter and Tscharnke 1999), but have rarely been considered beyond their impact on crop pollination (Hadley and Betts 2012). Like the effects of habitat loss, effects of fragmentation appear to vary by species and by type of bee, with the scale

of edge effects varying by bee body size or genera (Bailey et al. 2014, Steffan-Dewenter and Tschamntke 1999).

Along with habitat loss and fragmentation, the Canadian prairies are also heavily impacted by introduced plant species (Ricketts 1999). Introduced plant species affect bees in mixed ways depending on species and context (Stout and Tiedeken 2017). Direct effects of introduced flowering species include novel foraging resources, which can have different nutrient loads than native species, and this can result in shifts in bee foraging behaviours (Stout and Morales 2009, Stout and Tiedeken 2017). In the longer term, introduced flower species can alter plant-pollinator interactions, potentially affecting bee community composition and relative abundance of some species (Aizen et al. 2008). Bees with wider diet breadth may be more resistant to effects of introduced flowering species, since they can incorporate new species into their foraging patterns (Montero-Castano and Vila 2012). Bees may also be affected by non-forage introduced species that affect their nesting and over-wintering resources (Kremen et al. 2007). Introduced grasses that do not form tussocks may reduce nest-site availability for some above-ground nesting bees (Svensson et al. 2000, Jordan et al. 2014), and introduced grasses may also outcompete native vegetation with hollow stems that provide nest sites (Fink and Wilson 2011, Wilson 1989). Dense growth of introduced grasses and forbs may also reduce access to bare soils for ground-nesting bees (Potts et al. 2005). Thus introduced plant species may impact bee abundance in both direct and indirect ways, and such effects may vary with bee life-history traits.

While research on habitat loss, fragmentation, and alteration often focuses on effects on the abundance of a species or group of pollinators, pollination services to plants have been studied less frequently, and are not necessarily affected in the same way as insects (Taki and

Kevan 2007). Pollination services can be affected by changes in pollinator abundance, but variables such as frequency of pollinator visits, length of visits, and effectiveness of a pollinator species for a particular plant species are also important (Willmer 2017). Thus it is important to investigate pollination services separately from pollinator abundance or diversity. Currently, most knowledge on landscape effects on pollination services comes from agricultural studies. For example, the frequency of pollinator visits is enhanced by increased amounts of natural and semi-natural habitat on a landscape (Kohler et al. 2008, Kremen et al. 2004), and fruit or seed set increases for some pollinated crops when they are in landscapes with more natural areas (Klein et al. 2012, Morandin and Winston 2006), although the significance and strength of these effects on seed or fruit set vary by region and agricultural practice (Ricketts et al. 2008). Similarly, habitat fragmentation is known to affect pollination services for some plants. A broad review suggests that there is an overall large and negative effect of fragmentation on pollination and plant reproduction (Aguilar et al. 2006). Some studies on pollination services in agricultural crops have shown edge effects on seed and fruit set of a variety of domestic plants (Albrecht et al. 2007, Kohler et al. 2008, Schuepp et al. 2013, Steffan-Dewenter and Tschardt 1999).

The effects of introduced plant species on pollination services are often negative; a meta-analysis found that novel flowers often compete with native species resulting in reduced pollinator visits and less conspecific pollen deposition in many cases (Bjerknes et al. 2007). Overall, this can lower plant reproductive success, an effect that usually increases when introduced and native species share floral symmetry and colour (Morales and Traveset 2009). However, in some circumstances, introduced flowers can also facilitate pollination of native flowers by attracting greater densities of pollinators to a local area (Westphal et al. 2003). The

contrasting effects of competition and facilitation have been shown to vary seasonally and annually (Bjerknes et al. 2007, Larson et al. 2006).

My study objectives were to understand if landscape alterations impacting grasslands in the northern prairies, including habitat availability, habitat edges, and introduced plant species, affect bee pollinators and pollination services in Manitoba grasslands. I predicted that bee abundance would decrease with decreases in habitat on the landscape and with increases in amounts of introduced plant species. I also predicted that the strength of responses to specific habitat variables would vary with differing bee traits. I predicted that effects of habitat loss and of introduced species on pollination services would be similar to overall bee responses. I did not formulate predictions for bee or pollination services responses to habitat edges given the limited evidence for such effects in non-crop habitats.

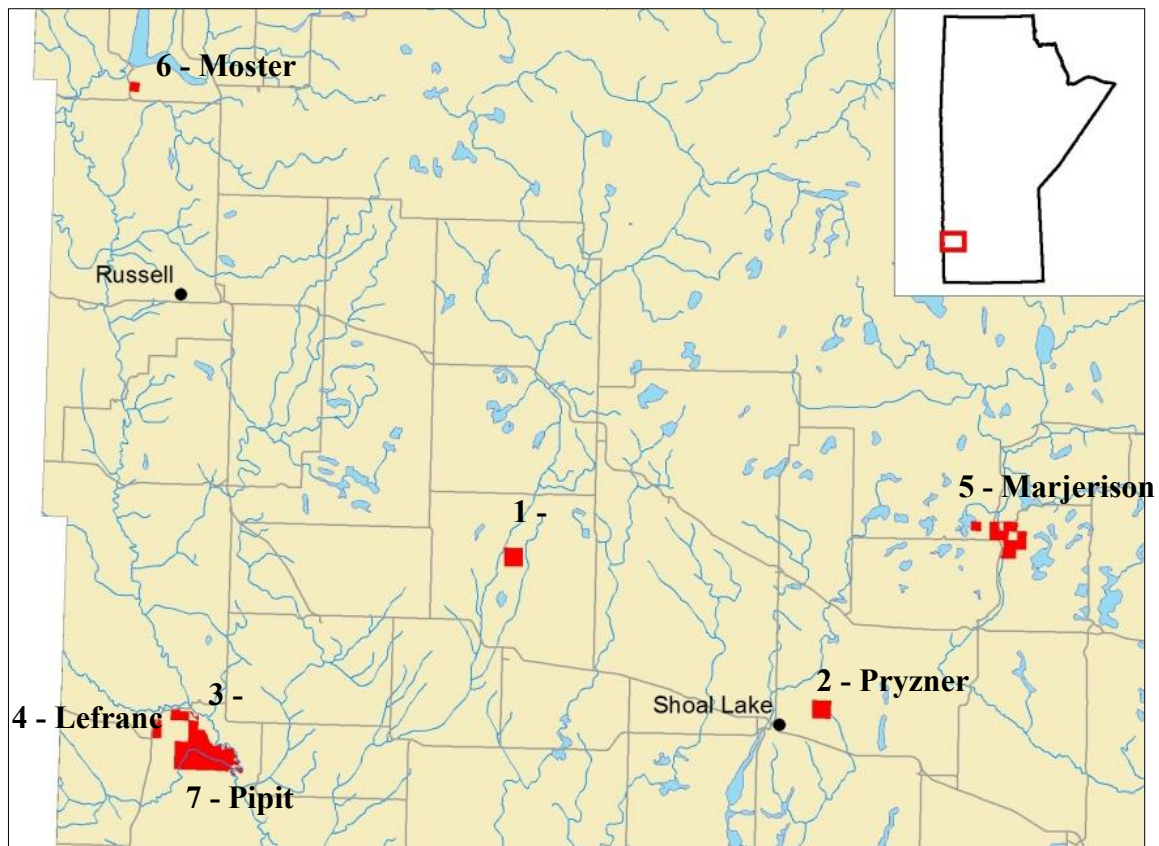
3.2 Methods

Study Region

My research took place on seven conservation properties in western Manitoba, Canada, in the Aspen Parkland ecoregion of the Prairies ecozone (Figure 1). These properties ranged in location from 100.1640°W to 101.2446°W and from 50.2502°N to 50.5641°N. The study region has lost the majority of its former grasslands to conversion to annual cropland, currently dominated by canola and wheat (Agriculture and Agri-Food Canada 2015). Most of the remaining grasslands are used for pasture or hay and often include introduced forage grasses such as smooth brome (*Bromus inermis*), Kentucky bluegrass (*Poa pratensis*), quackgrass (*Elymus repens*), and crested wheatgrass (*Agropyron cristatum*) (Willms et al. 2011). Prior to European settlement, the ecoregion was a mosaic of grasslands, dominated by slender wheatgrass

(*Elymus trachycaulus*), prairie junegrass (*Koeleria cristata*), rough hair grass (*Agrostis scabra*), needle-and-thread grass (*Hesperostipa comata*), and little bluestem (*Schizachyrium scoparium*), and deciduous forest, dominated by trembling aspen (*Populus tremuloides*) and Bur oak (*Quercus macrocarpa*) (Shorthouse 2010).

Figure 1: Map of study region showing study site locations



My study sites were chosen for the presence of grassland patches of sufficient size to allow placement of survey transects up to 150m away from habitat edges (Table 1). Four of the sites were native prairie remnants, while three had been seeded with introduced grasses more than ten years prior to this study. The sites were all managed with low-intensity livestock grazing, as is typical of the region. The average July temperature of the study ecoregion is

17.7°C and the average January temperature is -17.1°C. The mean annual precipitation for the ecoregion is 473.4 mm (Environment Canada 2010).

Table 1: Characteristics of western Manitoba grassland sites used as study locations

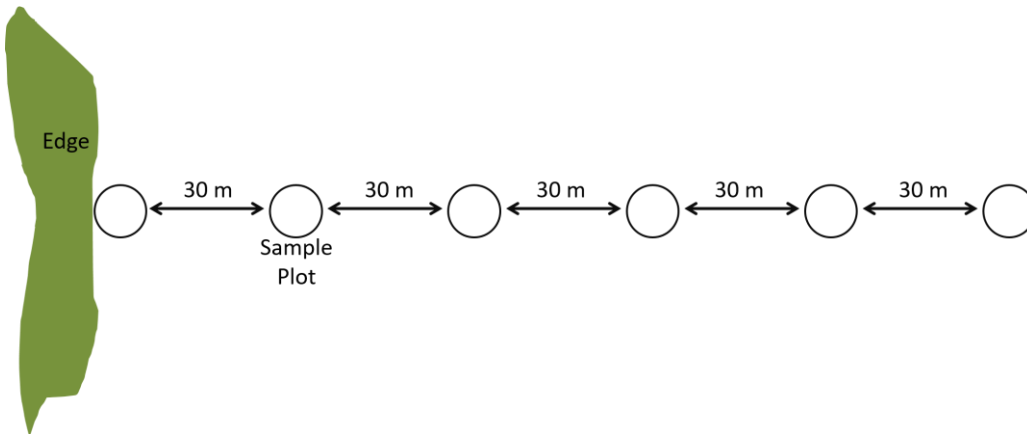
Site Number	Site Name	Owner	Grassland type	Soil type	Grassland patch size (ha)	Livestock Stocking Rate (AUM/ha)
1	Pedrick	MHHC	Tame grassland	Loam Till (Black Chernozem)	31.7	2013 - 0.264 2014 - 0.264 2015 - 0.264
2	Pryzner	MHHC	Prairie remnant	Loam Till (Black Chernozem)	180.2	2013 – 0 2014 - 0.230 2015 - 0.230
3	Fairgrounds	NCC	Prairie remnant	Loamy Till with water-worked surfaces	25.5	2013 - 0.336 2014 - 0.336 2015 - 0.336
4	LeFranc	NCC	Prairie remnant	Sand and Gravel	2.1	2013 - 0.700 2014 – 0 2015 - 0
5	Marjerison	NCC	Tame grassland	Loam Till (Dark Gray Chernozem)	22.6	2013 - 0.33 2014 - 0.336 2015 - 0.336
6	Moster	NCC	Prairie remnant	Sand and Gravel	42.4	2013 - 0.264 2014 - 0.268 2015 - 0.264
7	Pipit	NCC	Tame grassland	Sand and Gravel	146.1	2013 - 0.172 2014 - 0.179 2015 - 0.172

Experimental design

At each site, I conducted sampling at plots along 150 m transects that began at and ran perpendicular to either a treed edge or a road edge. I established sampling plots along each

transect every 30 metres from 0-150 m, for a total of six sample plots per transect (Figure 2) at 14 transects in my first two sampling rounds, and 16 transects in my third and final sampling round. I carried out three sampling rounds in 2014 and 2015. The first sampling period (Round 1) ran from June 5 to June 21 2014, the second (Round 2) ran from August 7 to August 21 2014, and the third (Round 3) ran from June 10 to July 2 2015. Bee data collection took place in all three rounds, and pollination service data collection took place in Round 1 and Round 3. In Round 1, average temperature was 13.2°C and average total precipitation was 60 mm, with a daily precipitation average of 3.8 mm in the study region. In Round 2, average temperature was 19.0°C and there was an average total of 50 mm of precipitation, with a daily precipitation average of 2.7 mm in the study region. In Round 3, average temperature was 16.4°C and there was an average total of 38 mm of precipitation, with a daily average precipitation of 1.7 mm in the study region (see Appendix 1 for weather details).

Figure 2: Example diagram of transects showing sampling design



Bee data collection

I sampled bee populations using pan bowl traps filled with one drop (approximately 1ml) of dish soap in approximately 300ml of water. Three bowl colours (blue, white, and yellow) were used to capture a greater range of bees since different taxa are attracted to different colours (Moreira et al. 2016). Although pan traps may under-sample certain taxa (Popic et al. 2013), they have been shown to provide efficient sampling coverage and reduce sampler bias, so I considered them appropriate for my comparative analyses (Westphal et al. 2008). Three traps, one of each colour, were placed within a square metre of each other on the ground at each sampling plot. Sampling occurred for two days over six-hour periods during each sampling round (once before pollination service sampling and once after) and bee abundance was calculated as the sum of the two sampling days. I conducted pollinator sampling when temperatures exceeded 18°C and when wind speeds did not exceed 20km/h. I collected trapped bees during the evening of each sampling day and stored them in 70% ethanol before pinning and identification. In Round 1, insects were sampled at 8 forest-edge transects and 3 road-edge transects. In Round 2, insects were sampled at 9 forest-edge transects and 5 road-edge transects. In Round 3, insects were sampled at 10 forest-edge transects and 6 road-edge transects (Table 2).

I first identified all bees to genus using Packer et al. (2007). I then identified them to species using a variety of North American identification keys. Dr. Cory Sheffield (Royal Saskatchewan Museum) assisted with identification of *Osmia*, *Melissodes*, *Andrena*, and *Hylaeus* genera, for which there are not up-to-date published identification keys. Dr. Sheffield and Dr. Jason Gibbs (University of Manitoba) provided verification of the other species identifications we had made using existing keys. I was unable to positively identify 92 adult female bees. These were grouped by morphology into 15 unknown species that were assigned morphospecies names

and used as such in analyses. According to available data (Sheffield et al. 2014), bees were defined by sociality (social or solitary), and by nest location (below-ground nesting or above-ground nesting). Analyses were conducted on the bees most likely to be effective pollinators, meaning that we excluded males and cleptoparasitic females since neither group actively gathers and carries pollen to feed or provision their offspring (Michener 2007).

Table 2: Characteristics of transects used for data collection

Site	Transect	Edge type	Round 1		Round 2	Round 3	
			Bee sampling	Seed set sampling	Bee sampling	Bee sampling	Seed set sampling
1	Ped1	Road	x	x	x	x	x
	Ped2	Road	x		x	x	
	Ped3	Road				x	
2	Pry1	Tree	x	x	x	x	x
	Pry2	Tree	x		x	x	
3	Fai1	Tree	x	x	x	x	x
	Fai2	Tree	x	x	x	x	x
	Fai3	Tree				x	
4	Lef1	Tree	x	x	x	x	
	Lef2	Road	x	x	x	x	x
5	Marj1	Road	x	x	x	x	x
	Marj2	Tree	x	x	x	x	x
6	Mos1	Road	x	x	x	x	x
	Mos2	Tree			x	x	x
7	Pip1	Tree	x	x	x	x	
	Pip2	Tree	x	x	x	x	x

Pollination Service Data Collection

To measure pollination services, I used the seed set of *Brassica rapa* L. (var. Ruvo) phytometers (greenhouse-grown plants) as a proxy measure (Woodcock 2012, Steffan-Dewenter et al. 2002). *Brassica rapa* is a hardy, fast-growing annual forb that produces large numbers of yellow flowers. The flowers are self-incompatible, and its heavy pollen is rarely carried by wind (Canadian Food Inspection Agency 1999), so seeds produced by *B. rapa* are the result of pollen transfer by insects. The species can be pollinated by a range of wild pollinators, including a

variety of bees and flies (Rader et al. 2013). In my first sample Round, I attempted to use a second phytometer species, *Raphanus sativus* L., but was unable to gather sufficient data using this species due to breakage of its trailing floral stems and because it was preferentially eaten by herbivores.

I seeded *B. rapa* phytometers in a greenhouse six to seven weeks before each sampling round. Prior to sampling, I housed the phytometers in screen-houses to expose them to outdoor weather conditions while preventing exposure of open flowers to pollinators. During sampling, I placed a single phytometer on the ground at each sample plot for exposure to insect pollinators. Bee sampling occurred at the same location both before and after phytometer sampling periods, but not during. In Round 1 the phytometer sampling period lasted five days, and in Round 3, the phytometer sampling period lasted seven days. I did not sample for pollination service in Round 2 due to high rates of phytometer herbivory, as well as severe stunting from aphids, which meant that I could not be confident that seed and fruit development were not affected. If grazing cattle were present at a study site during the sampling rounds, I used portable electric fencing to exclude them from the transect areas to reduce herbivory or trampling. After the sampling rounds, I returned phytometers to the greenhouse where the flowers matured and produced seeds. During the post-sampling periods, I treated the phytometers for aphids by manual removal and, after Round 3, using Intercept (a systemic herbicide). In Round 1 I conducted phytometer sampling at 8 tree-edge transects and 3 road-edge transects, and in Round 3 I conducted phytometer sampling at 6 tree-edge transects and 4 road-edge transects (Table 2).

The flowers of *B. rapa* open progressively from the base to tip of each raceme (flowering stalk), and at the beginning of each plant's sampling period, I placed small wires below any open flowers to mark which blooms were open at the beginning of the sampling period.

Following the sampling period, I placed a second wire above any open flowers on a raceme so we knew which had been open during the sampling period; I then recorded the total number of flowers that had been open on each plant during the sampling period. I collected the seeds from the phytometers as they matured: once the seedpods were dried but before they split open. I recorded how many of the flowers produced seed and calculated the percentage of pollinator-exposed flowers that had produced seed. I then counted the number of seeds produced from pollinator-exposed flowers and calculated the number of seeds per flower per plant.

Vegetation data collection

I collected vegetation data to measure floral and nesting habitat resources at a local scale. I conducted vegetation surveys at each plot along the sampling transects on each day that bees were sampled at a given transect. I collected vegetation structure and percent cover data within a 1-m quadrat that was placed directly adjacent to the insect traps. Within the quadrat I measured maximum litter depth and estimated percent cover of forbs, grass, and woody vegetation. The proportion of forb cover and grass cover consisting of introduced species were also estimated, as was an estimate of total cover of introduced species per quadrat.

I counted the number of flowering stems within a 5-m radius of each plot and identified these plants to species. I removed any flowering species that were exclusively wind-pollinated from the data set prior to analyses. The high variation in flowering stem counts among sites and sample rounds strongly skewed the flowering stem distribution, so I divided each flowering stem count by the maximum count of its respective round and used this proportion as an index in analyses.

Landcover data collection

In addition to local scale resources, I also sought information about effects of habitat structure at a landscape scale. Because I had only seven sites, I chose to calculate only one variable, percent of suitable bee habitat in the landscape matrix, to describe landscape habitat suitability, thus minimizing the risk of overparameterization of models. To create this matrix variable, I grouped land-cover types by the likelihood of perennial availability of both floral and nesting resources (Westrich 1996). While all land cover types may provide some resources to bees, anthropogenic land uses do not support the same abundance or diversity of bee populations (Kremen et al. 2007, Winfree et al. 2011). I gathered the land cover information surrounding each study site using Land Cover Landsat Thematic Mapper imagery from Manitoba Remote Sensing Centre (Manitoba Conservation 2006), which classifies land into seventeen land cover categories to a resolution of 30m. I ground-truthed these data to ensure that land cover classes had not changed within 1km of my study sites by the time of this study. Land cover types with low habitat availability, termed here as matrix habitat, were mainly annual cropland, along with roads, sand and gravel quarries, and open water. Using ArcMap software, I calculated the percentage of these different types of land cover within a 1km radius of each of the study sites. I then summed these percentages to create a total measure of matrix habitat within a 1km landscape radius (Table 3). This variable ranged from 2.6% to 40.9% of the surrounding landscape.

Table 3: Percentage cover of land cover classes within 1 km radius of each study site, grouped by suitability of habitat for bees

Land cover class	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7
Agricultural Cropland	30.5	27.1	0	0	23.3	2.6	0
Roads/Trails	3.7	1.2	4	3.8	3.6	2.1	2.6
Bare Rock/Gravel/Sand	0	0	0	0	0	0.6	0
Forage Crops	6.7	0	4.3	0	2.2	0	0
Water Bodies	0	3.4	1.4	0	6.5	0	0
Total matrix land cover	40.9	31.7	9.7	3.8	35.6	5.3	2.6
Marsh	3.5	16.2	0	0	7.4	0.6	0
Open Deciduous Forest/Shrub	0.6	0	18.7	11.3	0	0	25.1
Deciduous Forest	21.6	6.6	45.4	31.5	24.6	16.1	28.6
Grassland/Rangeland	33.5	45.6	26.1	53.4	32.5	78	43.8
Total habitat land cover	59.2	68.4	90.2	96.2	64.5	94.7	97.5

Statistical Analyses

I analyzed effects of habitat loss and fragmentation on bee abundance and pollination services using generalized linear mixed-effects models (GLMMs) and linear mixed-effects models (LMMs), respectively (Bolker et al. 2008) with the lme4 package (Bates et al. 2016) in program R (R Core Team 2016). I present all model results using an alpha value of 0.1 for significance in order to reduce the risk of a Type II error, which is a significant problem in conservation biology (McGarvey 2007), but present all p-values for evaluation. All models were assessed using residual plots and Cook's distance to identify outliers. I ran all models with and without any outliers, and only one showed a change in significance as a result of outliers. In that case, I show results with and without outliers. For all other models, only the results from the data set that included the outliers are presented, for conciseness. Prior to running my models, I ran

diagnostic tests including q-q plots and residuals plots to determine the distribution family that best fit my data, and to ensure that I met model assumptions.

All models included interaction terms between Round and each fixed effect to identify differences among sampling rounds as notable seasonal and annual shifts in bee communities have been found in prior studies in the northern prairies (Larson et al. 2006, Patenaude 2008, Semmler 2015). The models were assessed for collinearity among fixed effect variables and none were found. Preliminary analyses were conducted to determine which random variables should be included; AIC values showed that using site as a random variable resulted in improved model fit in comparison with models that used plot nested in site as random effects (Delta AIC ranged from 2-12). Therefore, for all models, site was used as a random variable to account for correlations among plots within sites. Sites were treated as a continuous variable, as their combinations of characteristics made it difficult to assign them to groupings that would allow for analysis by different “treatments” (Table 1). For all other analyses, I used a frequentist approach (Mundry 2011).

Bee abundance models

I ran GLMMs to evaluate effects of habitat structure on the following response variables: abundance of pollen-carrying female (PCF) bees, abundance of social PCF bees, abundance of solitary PCF bees, abundance of below-ground nesting PCF bees, and presence of above-ground nesting PCF bees. To understand effects of habitat loss, I ran models including the following fixed effects variables: plot litter depth and woody cover per plot as measures of local nesting resources, flowering stem abundance per plot and flowering stem species richness per plot as measures of local floral resources, and the amount of matrix habitat within a 1km radius as a measure of landscape-level habitat structure. I investigated effects of habitat edges by running

GLMMs using distance to tree edge and distance to road edge as fixed effects. I investigated effects of introduced plant species with GLMMs using introduced forb ground cover and introduced grass cover per plot, percentage of flowering stems that were native species per plot, and average introduced vegetation cover per site as fixed effects variables. All models were fitted using a negative binomial distribution to account for overdispersion in the count data (Zuur et al. 2009), except for occurrence of above-ground nesting bees, for which I had smaller sample sizes, and thus were analyzed using a binomial distribution.

Pollination services models

I ran LMMs to understand effects of habitat on pollination services by using log-transformed seed set per flower per phytometer as a response variable. I ran models for habitat loss effects, edge effects, and introduced vegetation effects using the same fixed effects variables as in the bee abundance models. I also investigated the effects of bee populations on pollination rates, by structuring models that included PCF bee abundance per plot, PCF bee species richness per plot, and PCF bee abundance per site as fixed effects variables. I included variables for both bee abundance per plot and per site to account for the potential effects of multiple scales on pollination services (Dauber et al. 2010). Bee abundance per site was adjusted to account for different sampling efforts (number of transects) for different sites by dividing the number of bees per site by the number of sample plots per site. I also ran models to investigate the effects of the abundance of the two most common bee genera in my study on pollination rates, using abundance of *Bombus* PCF bees per plot and the abundance of *Lasioglossum* PCF bees per plot as fixed effects.

3.3 Results

Bee Abundance

I collected 1,603 PCF bees consisting of eighty species or morphospecies (Appendix 2). Of these, 54.8% were below-ground nesting, 6.6% nested above ground, and nesting location for 28.6% were unknown. I found that 50.1% of the bees were social, 42.8% were solitary, and the sociality of the remaining 7.1% was unknown or variable. Bees in the genus *Lasioglossum* made up 54.0% of all the analyzed bees and genus *Bombus* (bumblebees) made up 17.8%. Four species made up 47.7% of total bee abundance: *Lasioglossum zonulum*, *Lasioglossum albipenne*, *Bombus rufocinctus* and *Lasioglossum succinipenne*.

Does bee abundance change with changes in local habitat availability?

My models included the local habitat variables litter depth, woody stem cover, flowering stem abundance, and flowering stem species richness (Table 4; see Appendices 4-9 for full results). Increasing litter depth resulted in decreased overall bee abundance in Round 1 ($\beta=-0.074$, $SE=0.04$, $p=0.061$) and Round 2 ($\beta=-0.115$, $SE=0.043$, $p=0.008$) (Figure 3). Increased litter depth also resulted in decreased social bee abundance in Round 2 ($\beta=-0.21$, $SE=0.07$, $p=0.002$) (Figure 4), and decreased abundances of solitary bees in Round 1 ($\beta=-0.12$, $SE=0.05$, $p=0.031$) and Round 3 ($\beta=-0.08$, $SE=0.04$, $p=.035$) (Figure 5). Litter depth was had the strongest and most consistend effect on below-ground nesting bee abundance, with increased litter depth resulting in decreased abundance in Rounds 1, 2, and 3 ($\beta=-0.09$ $SE=0.04$, $p=0.039$; $\beta=-0.13$, $SE=0.05$, $p=0.014$; $\beta=-0.06$, $SE=0.03$, $p=0.039$, respectively) (Figure 6). Above-ground nesting bee presence was not significantly affected by changes in litter depth ($p>0.19$). The percentage of woody cover at each plot had a positive effect on social bee abundance when I removed an

outlier data point in Round 1 ($\beta=0.03$, $SE=0.01$, $p=0.014$) and in Round 2 ($\beta=0.020$, $SE=0.010$, $p=0.055$) (Figure 7). With the outlier included, this effect was not significant in Round 1 ($p=0.33$). The outlier sample point had a woody cover percentage of 62.5, while the mean for Round 1 was 4.8% and the median was 0. Woody cover had no other significant effect on overall bee abundance or on abundance or presence of any subcategory of bees ($p>0.12$).

Table 4: Summary of effects of habitat variables on response variables. “+” indicates significant positive effect, “-“ indicates significant negative effect, and “/” indicates no significant effect.

	Litter depth			% woody cover			Flowering stem abundance			Flowering stem richness			% Matrix on landscape		
<i>Round</i>	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
<i>All bees</i>	-	-	/	/	/	/	/	-	/	/	/	/	-	/	/
<i>Social Bees</i>	/	-	/	+	+	/	/	-	/	/	/	/	-	-	-
<i>Solitary bees</i>	-	/	-	/	/	/	+	/	/	/	+	/	-	/	/
<i>Below-ground nesting bees</i>	-	-	-	/	/	/	/	/	/	/	/	+	-	-	-
<i>Above-ground nesting bees</i>	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
<i>Seed set</i>	/		-	/		/	/		/	/		/	/		-

Figures 3-6: Predicted effects of increasing litter depth on bee abundance.

Significant slopes marked with '*'. Shading represents 95% confidence intervals for each round.

Figure 3: Predicted effects of increasing litter depth on overall bee abundance.

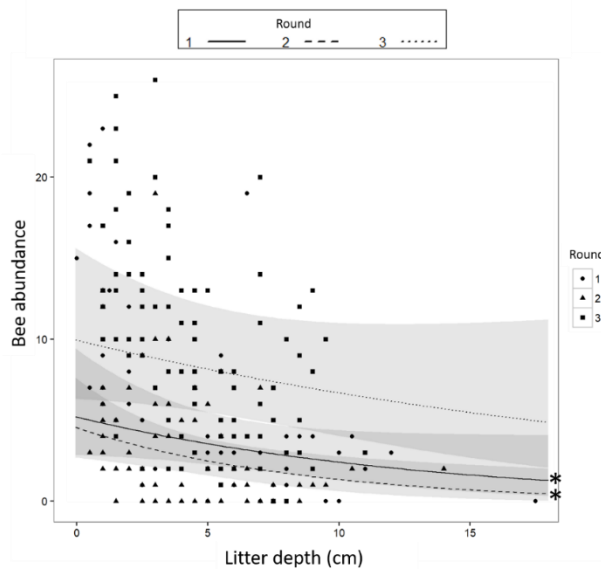


Figure 4: Predicted effects of increasing litter depth on social bee abundance

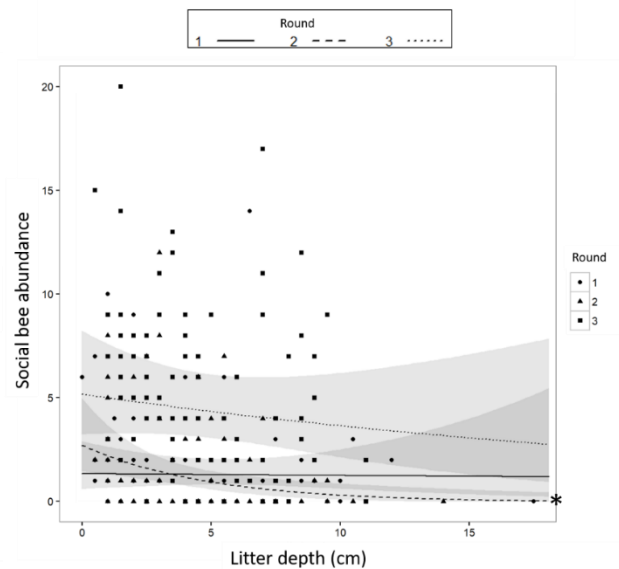


Figure 5: Predicted effects of increasing litter depth on solitary bee abundance.

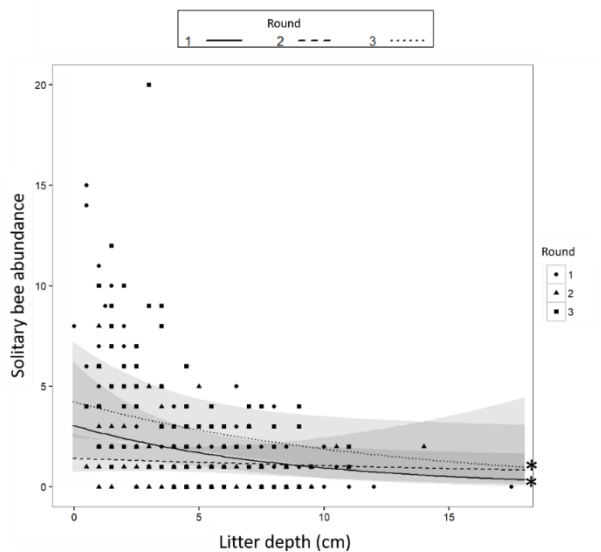


Figure 6: Predicted effects of increasing litter depth on below-ground nesting bee abundance.

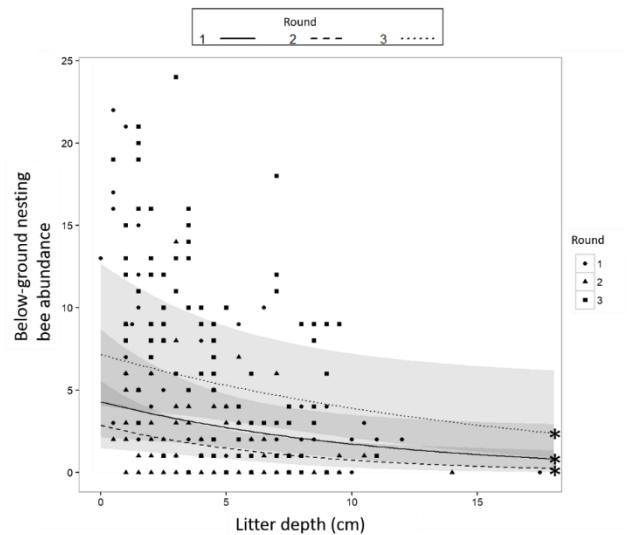
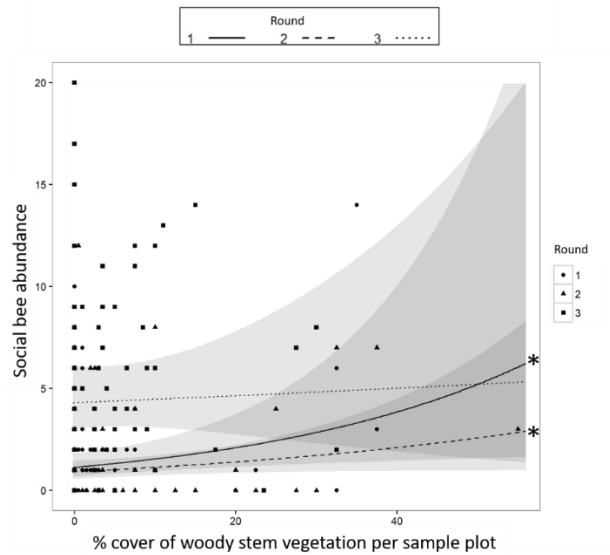


Figure 7: Predicted effects of % cover of woody stems on social bee abundance.

Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.



Floral resources showed little consistency across Rounds in their effects on bee abundance. The indexed amount of flowering stems had a significant negative impact on overall bee abundance in Round 2 ($\beta=-1.11$, $SE=0.49$, $p=0.022$), but no effect in Rounds 1 or 3 ($p>0.27$) (Figure 8). The indexed amount of flowering stems had a small significant negative effect on social bees in Round 2 ($\beta=-2.20$, $SE=0.84$, $p=0.009$) (Figure 9), a significant positive effect on solitary bees in Round 3 ($\beta=0.835$, $SE=0.422$, $p=0.048$) (Figure 10), and no effect in other Rounds or on other subcategories of bees ($p>0.14$). Species richness of flowering stems had a significant positive effect on solitary bee abundance in Round 2 ($\beta=0.084$, $SE=0.043$, $p=0.053$) (Figure 11), and on below-ground nesting bee abundance in Round 3 ($\beta=0.044$, $SE=0.024$, $p=0.064$) (Figure 12). Species richness of flowering stems showed no significant effect on overall bee abundance, social bee abundance or above-ground nesting bee presence ($p>0.101$).

Figures 8-10: Predicted effects of flowering stem abundance on bee abundance. Significant slopes marked with '*'. Shading represents 95% confidence intervals for each round.

Figure 8: Predicted effects of flowering stem abundance on overall bee abundance.

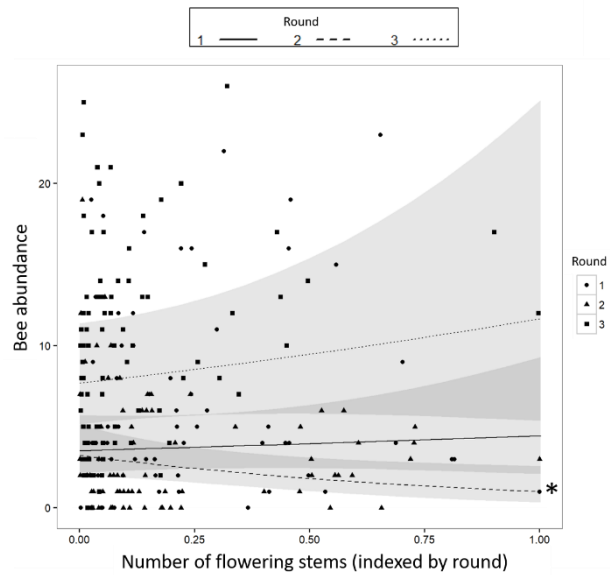


Figure 9: Predicted effects of flowering stem abundance on social bee abundance.

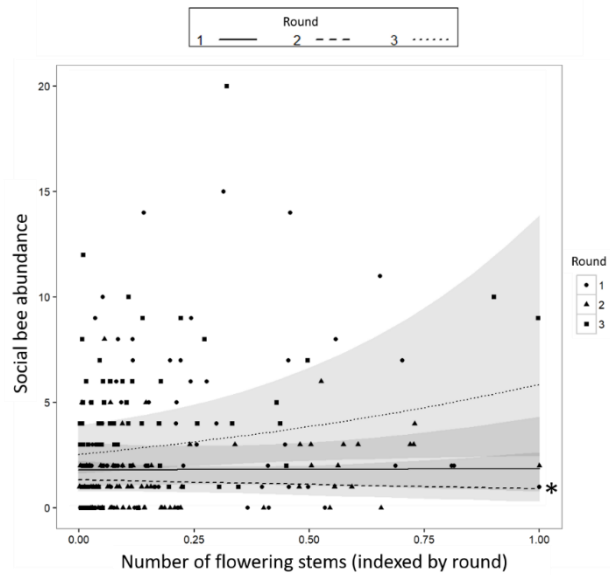
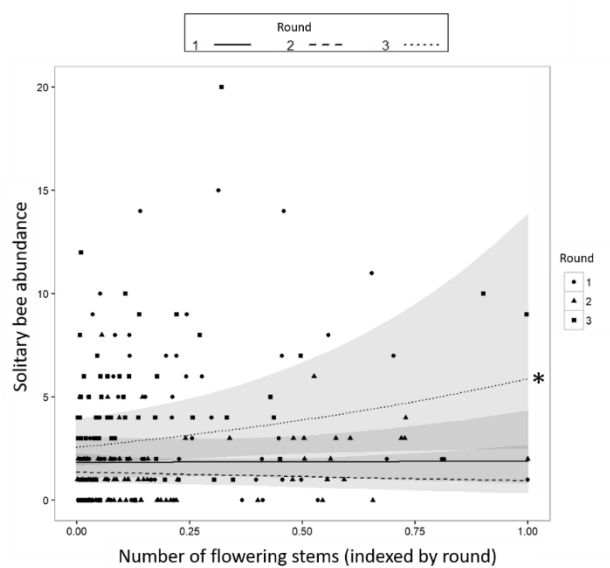


Figure 10: Predicted effects of flowering stem abundance on solitary bee abundance.



Figures 11-12: Predicted effects of flowering species richness on bee abundance. Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.

Figure 11: Predicted effects of flowering species richness on solitary bee abundance

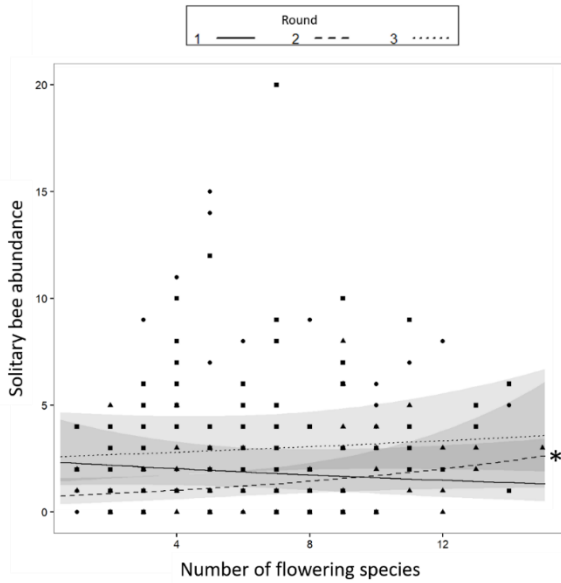
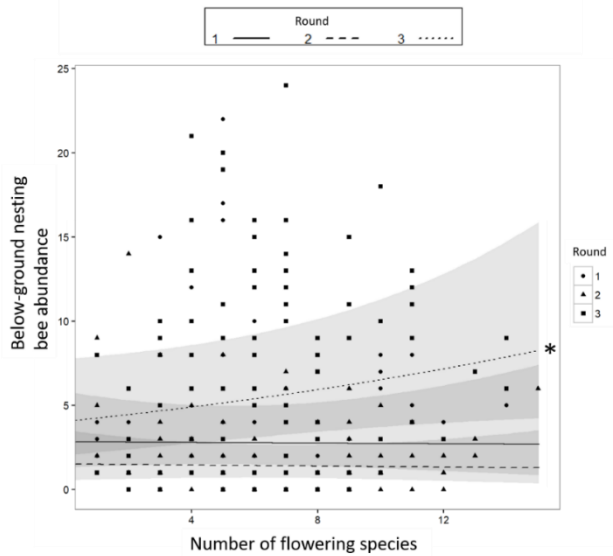


Figure 12: Predicted effects of flowering species richness on below-ground nesting bee abundance



Does bee abundance change with changes in landscape habitat availability?

Increasing amounts of matrix habitat within 1km of each site resulted in decreased overall bee abundance only in Round 1 ($\beta=-0.41$, $SE=0.016$, $p=0.012$) (Figure 13), but had stronger and more consistent effects for certain groups of bees (Table 5). Social bees were significantly negatively affected by increases in matrix habitat in all three Rounds ($\beta=-0.055$, $SE=0.019$, $p=0.003$; $\beta=-0.031$, $SE=0.014$, $p=0.028$; $\beta=-0.027$, $SE=0.012$, $p=0.022$, respectively) (Figure 14), as were below-ground nesting bees ($\beta=-0.041$, $SE=0.021$, $p=0.046$, $\beta=-0.036$, $SE=0.019$, $p=0.064$; $\beta=-0.033$, $SE=0.018$, $p=0.075$) (Figure 16). Solitary bees were significantly negatively affected by increases in matrix habitat in Round 1 ($\beta=-0.048$, $SE=0.019$, $p=0.012$) (Figure 15), and above-ground nesting bees were not significantly affected ($p>0.6$).

Figures 13-16: Predicted effects of increasing landscape matrix habitat (1km radius) on bee abundance. Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.

Figure 13: Predicted effects of increasing landscape matrix habitat (1km radius) on overall bee abundance.

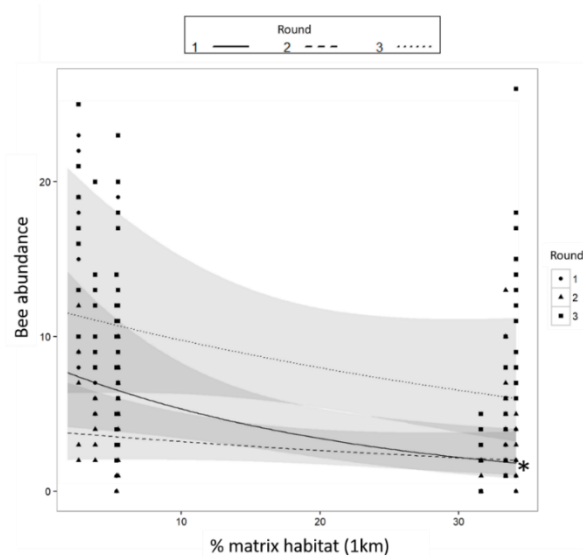


Figure 14: Predicted effects of increasing landscape matrix habitat (1km radius) on social bee abundance.

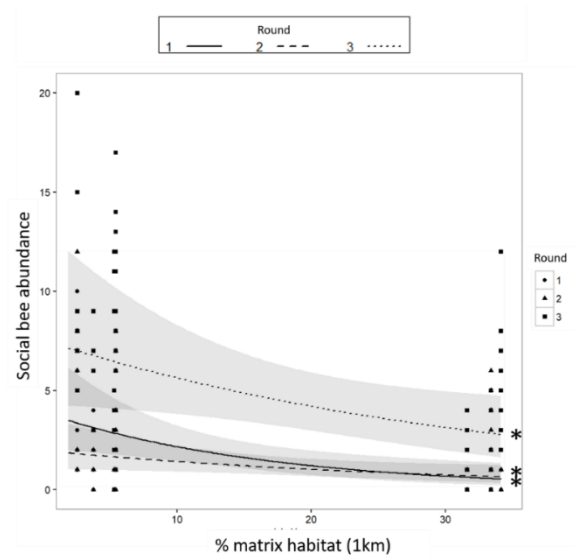


Figure 15: Predicted effects of increasing landscape matrix habitat (1km radius) on solitary bee abundance.

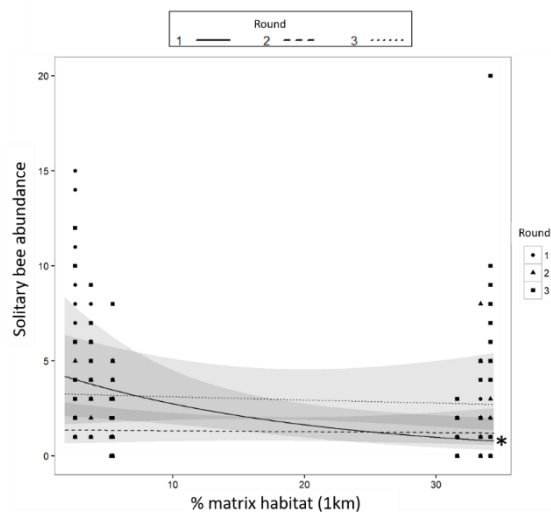


Figure 16: Predicted effects of increasing landscape matrix habitat (1km radius) on below-ground nesting bee abundance.

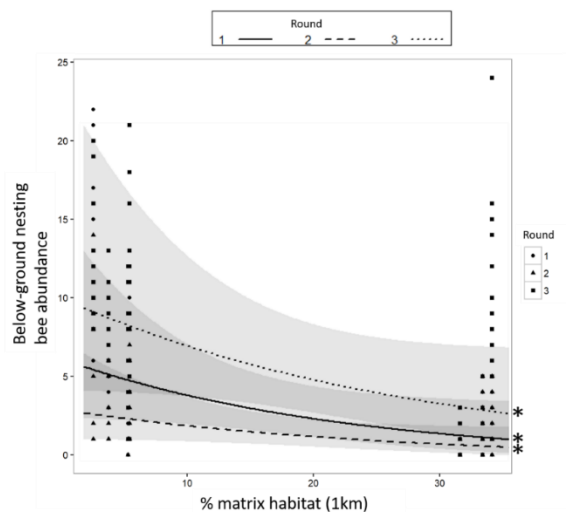


Table 5: Effects of surrounding landscape matrix on bee abundances. Values shown are derived from full habitat models (see Appendices 3-8 for full model results). Significant values marked with bolding.

	Round 1			Round 2			Round 3		
	Beta	SE	p	Beta	SE	p	Beta	SE	p
<i>All Bees</i>									
matrix1km	-0.041	0.016	0.012	-0.018	0.014	0.200	-0.019	0.014	0.174
matrix1km:round1	-	-	-	-0.023	0.012	0.052	-0.023	0.011	0.037
matrix1km:round2	0.023	0.012	0.052	-	-	-	0.000	0.008	0.973
matrix1km:round3	0.023	0.011	0.037	0.000	0.008	0.973	-	-	-
<i>Social Bees</i>									
matrix1km	-0.055	0.019	0.003	-0.031	0.014	0.028	-0.027	0.012	0.022
matrix1km:round1	-	-	-	-0.024	0.018	0.179	-0.028	0.016	0.090
matrix1km:round2	0.024	0.018	0.179	-	-	-	-0.003	0.011	0.763
matrix1km:round3	0.028	0.016	0.090	0.003	0.011	0.763	-	-	-
<i>Solitary Bees</i>									
matrix1km	-0.048	0.019	0.012	-0.004	0.016	0.826	-0.005	0.015	0.731
matrix1km:round1	-	-	-	-0.045	0.015	0.004	-0.043	0.014	0.002
matrix1km:round2	0.045	0.015	0.004	-	-	-	0.002	0.010	0.870
matrix1km:round3	0.043	0.014	0.002	-0.002	0.010	0.870	-	-	-
<i>Below-ground nesting bees</i>									
matrix1km	-0.041	0.021	0.046	-0.036	0.019	0.064	-0.033	0.018	0.075
matrix1km:round1	-	-	-	-0.006	0.014	0.667	-0.009	0.012	0.450
matrix1km:round2	0.006	0.014	0.667	-	-	-	-0.003	0.009	0.744
matrix1km:round3	0.009	0.012	0.450	0.003	0.009	0.744	-	-	-
<i>Above-ground nesting bees</i>									
matrix1km	-0.092	0.178	0.604	-0.009	0.027	0.740	0.010	0.027	0.705
matrix1km:round1	-	-	-	-0.083	0.177	0.640	-0.103	0.178	0.563
matrix1km:round2	0.083	0.178	0.640	-	-	-	-0.019	0.028	0.502
matrix1km:round3	0.103	0.178	0.563	0.019	0.028	0.502	-	-	-

Does bee abundance change with proximity to tree or road edges?

Generally speaking, bee abundance showed either a negative or a non-significant response to increasing distance from treed edges (Table 6). Distance to tree edge had a small negative effect on overall bee abundance in Round 1 ($\beta=-2.08$, $SE=.92$, $p=.024$) (Figure 17). This effect appears to have been driven by solitary and ground-nesting bees, as similar effects were found in Round 1 for solitary bees ($\beta=-4.34$, $SE=1.17$, $p<0.001$) (Figure 18) and below-ground

nesting bees ($\beta=-2.36$, $SE=0.96$, $p=0.014$) (Figure 19). For other bee types and all other Rounds, there was no significant effect of distance to tree edge ($p>0.17$).

Overall bee abundance increased with increasing distance to road edge in Rounds 1 ($\beta=0.48$, $SE=0.24$, $p=0.044$) and Round 2 ($\beta=0.40$, $SE=0.27$, $p=0.092$) (Figure 20). Social bee abundance showed a strong response, increasing with increasing distance to road edge in all three Rounds ($\beta=0.92$, $SE=0.29$, $p=0.002$; $\beta=1.05$, $SE=0.29$, $p=0.0004$; $\beta=0.51$, $SE=0.27$, $p=0.064$, respectively) (Figure 21), but proximity to road edge did not show a significant effect on solitary bees ($p>0.28$). Below-ground nesting bees also increased in abundance further from road edge in Round 1 ($\beta=0.56$, $SE=0.25$, $p=0.028$) and Round 2 ($\beta=0.49$, $SE=0.26$, $p=0.054$), but the effect size was smaller than that for social bees (Figure 22). Above-ground nesting bee presence did not change with proximity to road edge ($p>0.22$).

Table 6: Summary of effects of edge effect variables on response variables. “+” indicates significant positive effect, “-” indicates significant negative effect, and “/” indicates no significant effect.

	Distance to tree edge			Distance to road edge		
	Round 1	Round 2	Round 3	Round 1	Round 2	Round 3
All bees	-	/	/	+	+	/
Social Bees	/	/	/	+	+	+
Solitary bees	-	/	/	/	/	/
Below-ground nesting bees	-	/	/	+	+	/
Above-ground nesting bees	/	/	/	/	/	/
Seed set	/		-	/		/

Figures 17-19: Predicted effects of increasing distance to tree edges on bee abundance. Significant slopes marked with a '*'. Shading represents 95% confidence intervals for each round.

Figure 17: Predicted effects of increasing distance to tree edges on overall bee abundance.

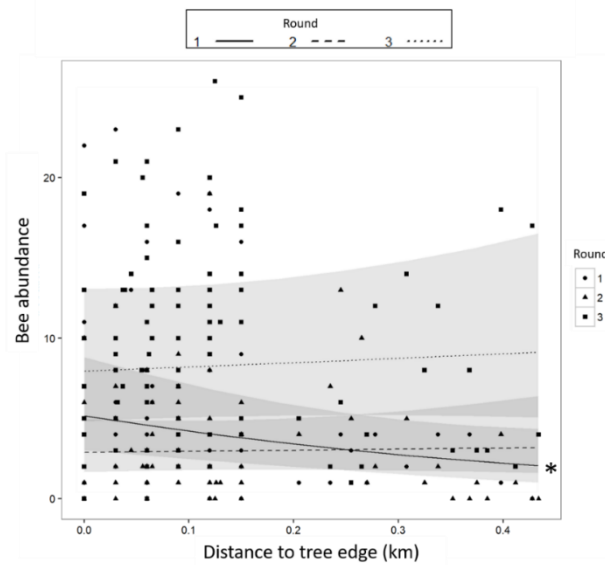


Figure 18: Predicted effects of increasing distance to tree edges on solitary bee abundance.

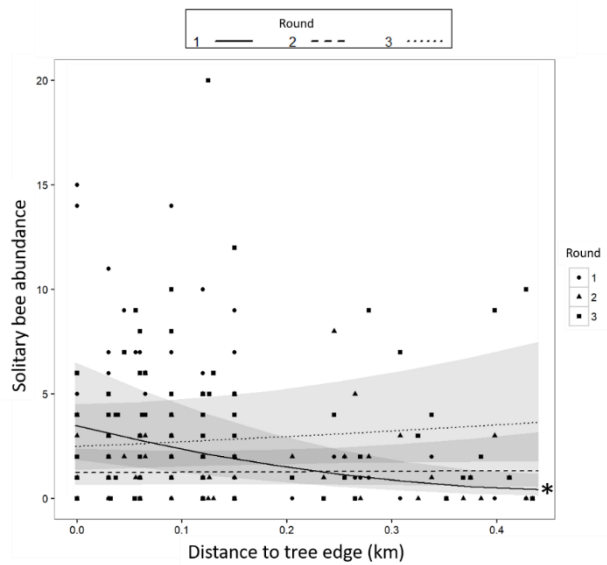
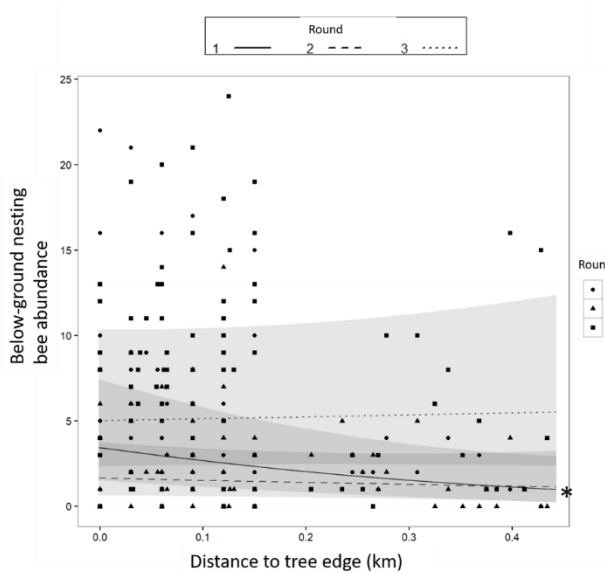


Figure 19: Predicted effects of increasing distance to tree edges on below-ground nesting bee abundance.



Figures 20-22: Predicted effects of increasing distance to road edges on bee abundance. Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.

Figure 20: Predicted effects of increasing distance to road edges on overall bee abundance

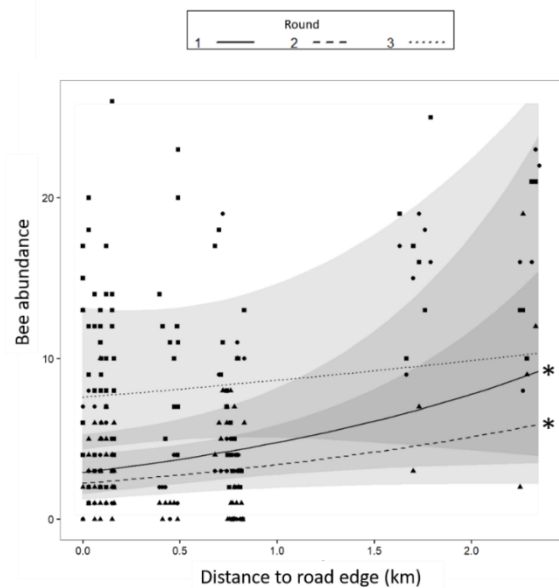


Figure 21: Predicted effects of increasing distance to road edges on social bee abundance

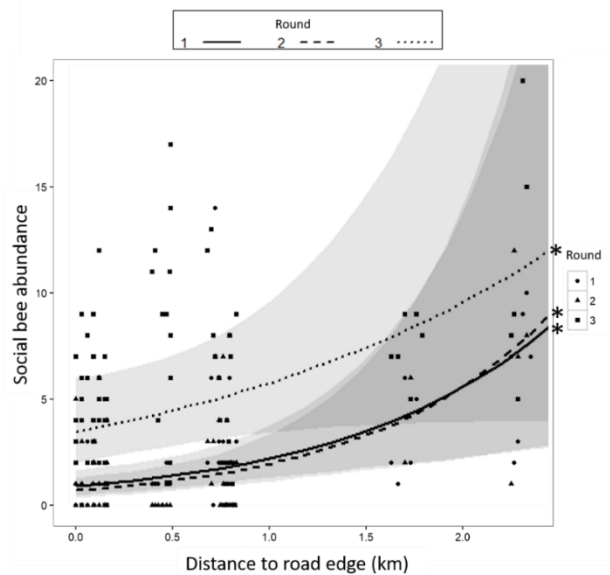
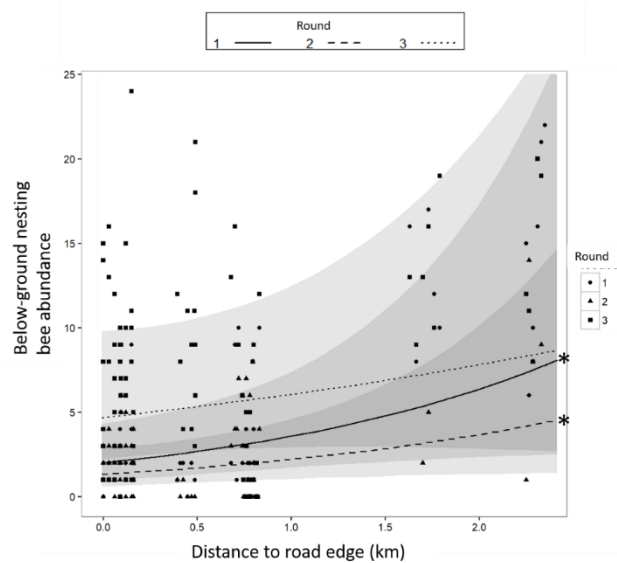


Figure 22: Predicted effects of increasing distance to road edges on below-ground nesting bee abundance.



Does bee abundance change with greater amounts of introduced vegetation?

Bee abundance responded strongly and consistently to amount of introduced forb cover and overall amounts of introduced vegetation per site (Table 7). The percentage of introduced forb cover showed a strong positive effect on overall bee abundance in Round 2 ($\beta=0.036$, $SE=0.014$, $p=0.009$) and Round 3 ($\beta=0.01$, $SE=0.006$, $p=0.089$) (Figure 23). This effect was most consistent for solitary bees, with positive effects of introduced forb cover found in Round 2 ($\beta=0.037$, $SE=0.017$, $p=0.028$) and Round 3 ($\beta=0.020$, $SE=0.006$, $p=0.001$) (Figure 25). This strong effect was also seen on social bees in Round 2 ($\beta=0.048$, $SE=0.024$, $p=.040$) (Figure 24) and on below-ground nesting bees in Round 3 ($\beta=0.014$, $SE=0.006$, $p=0.036$) (Figure 26). There was no significant effect on above-ground nesting bees ($p>0.10$).

Table 7: Summary of effects of introduced vegetation variables on response variables. “+” indicates significant positive effect, “-“ indicates significant negative effect, and “/” indicates no significant effect.

	% introduced forb cover			% introduced grass cover			% of flowering stems native species			% introduced vegetation per site		
<i>Round</i>	1	2	3	1	2	3	1	2	3	1	2	3
<i>All bees</i>	/	+	+	/	/	/	+	+	/	+	+	/
<i>Social Bees</i>	/	+	/	/	/	/	+	+	/	/	+	/
<i>Solitary bees</i>	/	+	+	/	/	/	/	+	/	+	+	+
<i>Below-ground nesting bees</i>	/	/	+	/	-	/	+	+	/	+	+	/
<i>Above-ground nesting bees</i>	/	/	/	/	/	/	/	+	/	/	/	/
<i>Seed set</i>	/		/	/		/	/		/	/		/

Figure 23-26: Predicted effects of increasing percentage of forb cover composed of introduced species on bee abundance. Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.

Figure 23: Predicted effects of increasing percentage of forb cover composed of introduced species on overall bee abundance

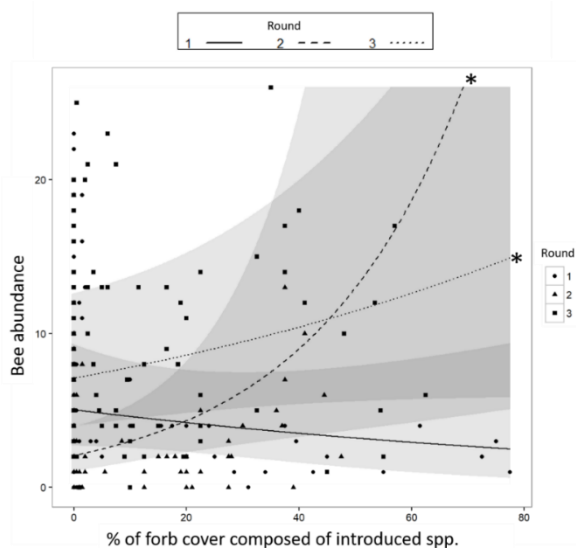


Figure 24: Predicted effects of increasing percentage of forb cover composed of introduced species on social bee abundance

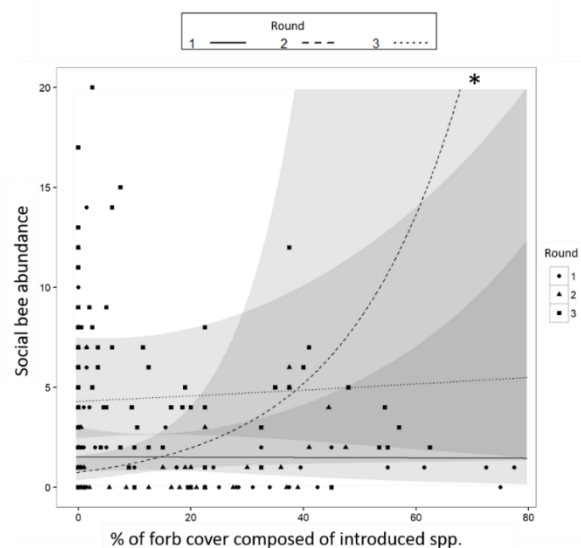


Figure 25: Predicted effects of increasing percentage of forb cover composed of introduced species on solitary bee abundance

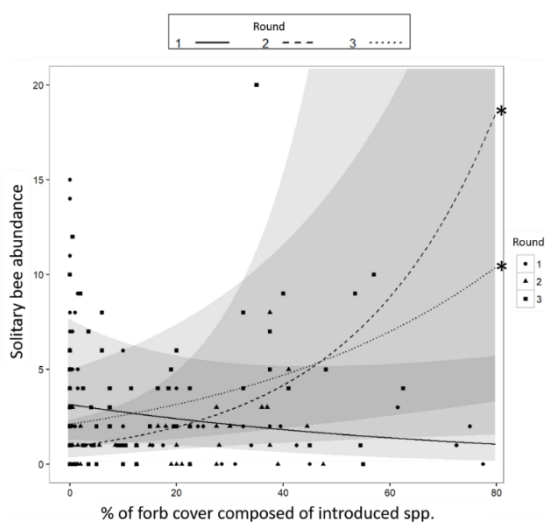
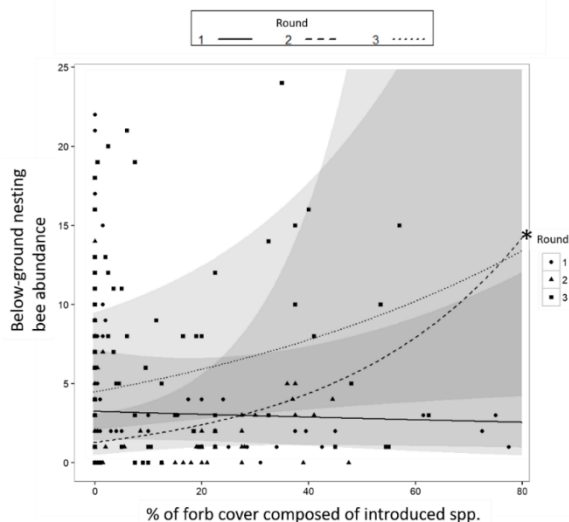


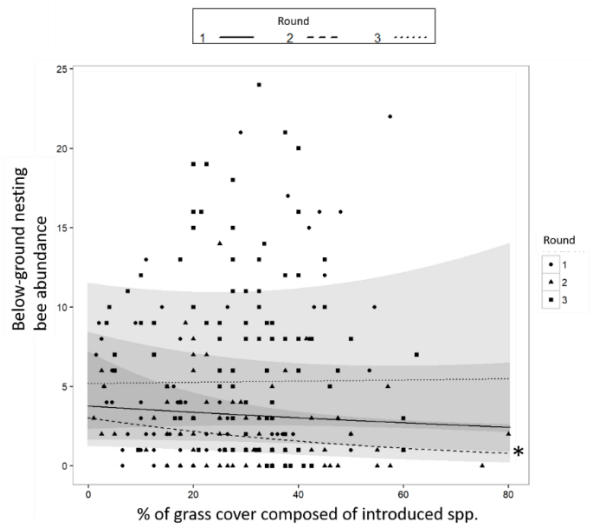
Figure 26: Predicted effects of increasing percentage of forb cover composed of introduced species on below-ground nesting bee abundance



The percentage of introduced grass cover at each plot had a significant but small negative effect on abundance of below-ground nesting bees in Round 2 ($\beta=-0.016$, $SE=0.009$, $p=0.057$) (Figure 27). Introduced grass cover did not have a significant effect in any other Round or on any other category of bees ($p>0.18$).

Figure 27: Predicted effects of increasing percentage of grass cover composed of introduced species on bee abundance.

Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.



An increasing percentage of native flowering stems at each sample plot had a positive effect on overall bee abundance in Round 1 ($\beta=0.009$, $SE=.005$, $p=.06$) and Round 2 ($\beta=0.025$, $SE=.005$, $p<0.0001$) (Figure 28). This effect was significant, but smaller, in Round 1 and Round 2 for social bees ($\beta=0.013$, $SE=.007$, $p=.054$; $\beta=0.042$, $SE=.009$, $p<0.001$, respectively) (Figure 29) and below-ground nesting bees ($\beta=0.011$, $SE=.0.005$, $p=.041$; $\beta=0.022$, $SE=0.006$, $p=.001$, respectively) (Figure 31). This positive effect was significant, but small in only Round 2 for solitary bees ($\beta=0.012$, $SE=0.007$, $p=.070$) (Figure 30). The probability of occurrence of above-ground nesting bees was positively affected by this variable as well ($\beta=0.029$, $SE=0.016$, $p=.078$) (Figure 32).

Figure 28-31: Predicted effects of increasing percentage of flowering stems that are native species on bee abundance. Significant slopes marked with '*'. Shading represents 95% confidence intervals for each round.

Figure 28: Predicted effects of increasing percentage of flowering stems that are native species on overall bee abundance.

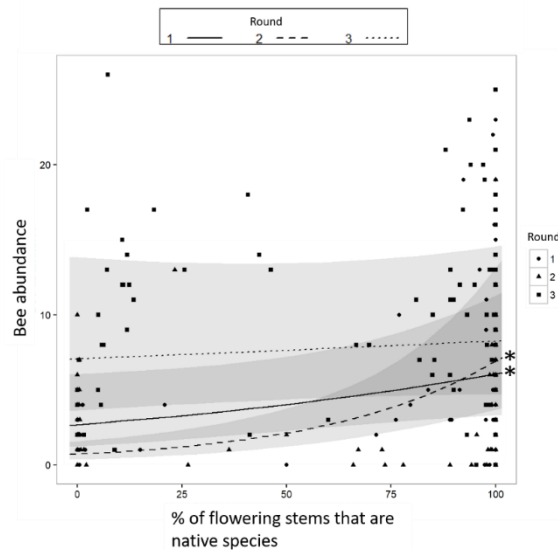


Figure 29: Predicted effects of increasing percentage of flowering stems that are native species on social bee abundance.

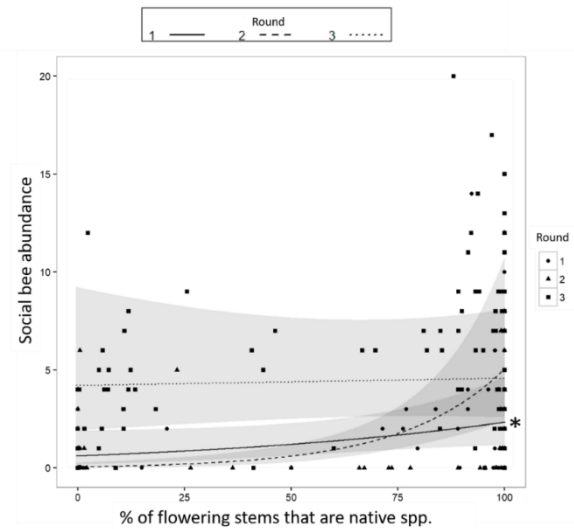


Figure 30: Predicted effects of increasing percentage of flowering stems that are native species on solitary bee abundance.

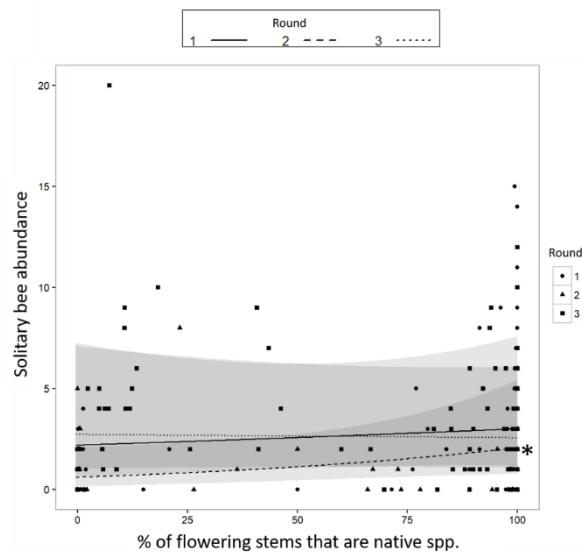


Figure 31: Predicted effects of increasing percentage of flowering stems that are native species on below-ground nesting bee abundance

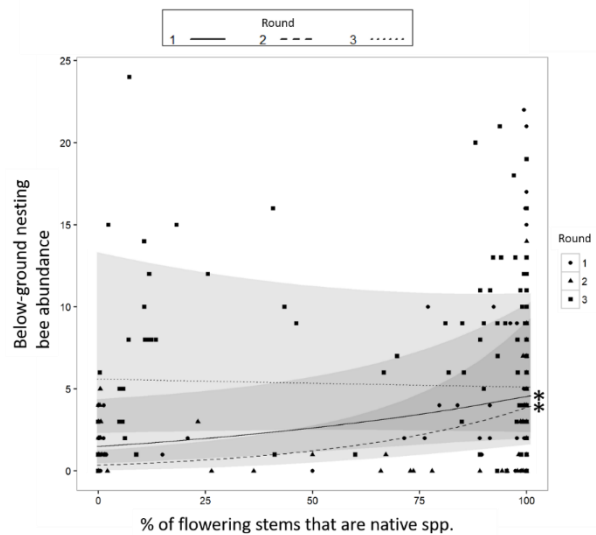
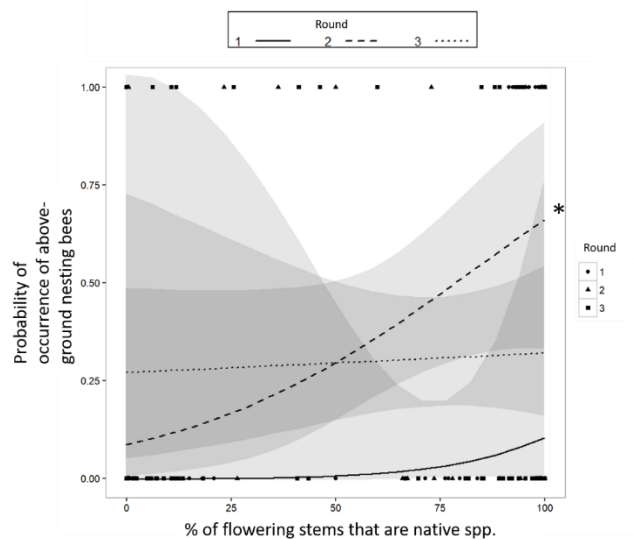


Figure 32: Predicted effects of increasing percentage of flowering stems that are native species on probability of occurrence of above-ground nesting bees. Significant slopes marked with '*'. Shading represents 95% confidence intervals for each round



The average amount of introduced vegetative cover per site had a significant positive effect on overall bee abundance in Round 1 ($\beta=0.024$, $SE=0.008$, $p=0.003$) and in Round 2 ($\beta=0.048$, $SE=0.013$, $p<0.001$) (Figure 33). There was a strong positive effect on solitary bees in all three sampling rounds ($\beta=0.048$, $SE=0.011$, $p<0.001$; $\beta=0.055$, $SE=0.017$, $p=0.001$; $\beta=0.038$, $SE=0.017$, $=0.028$, respectively) (Figure 35), but was only found for social bees in Round 2 ($\beta=0.052$, $SE=0.020$, $p=0.01$) (Figure 34). This effect was also found for below-ground nesting bees in Round 1 ($\beta=0.024$, $SE=0.009$, $p=0.01$) and Round 2 ($\beta=0.039$, $SE=0.016$, $p=0.014$) (Figure 36), but there was no significant effect on above-ground nesting bees ($p>0.26$).

Figures 33-36: Predicted effects of increasing percentage of vegetative cover per site composed of introduced species. Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.

Figure 33: Predicted effects of increasing percentage of vegetative cover per site composed of introduced species on overall bee abundance

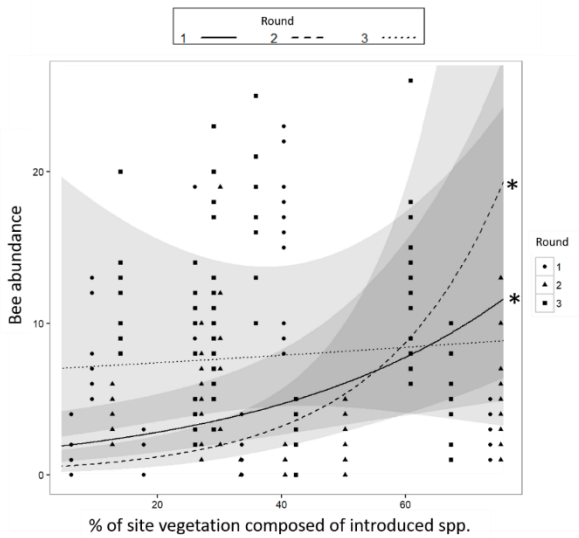


Figure 34: Predicted effects of increasing percentage of vegetative cover per site composed of introduced species on social bee abundance

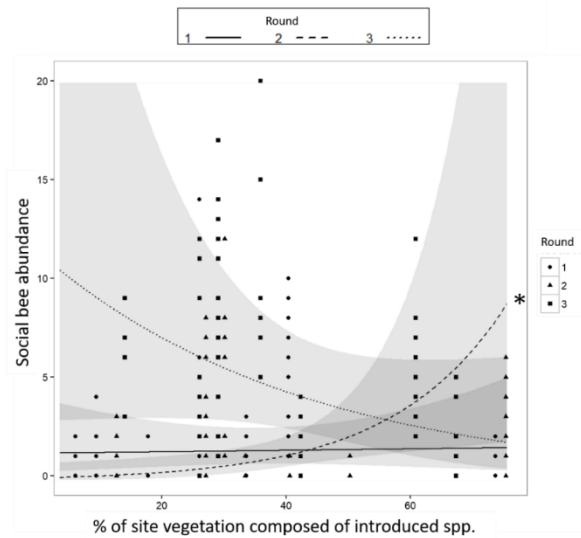


Figure 35: Predicted effects of increasing percentage of vegetative cover per site composed of introduced species on solitary bee abundance

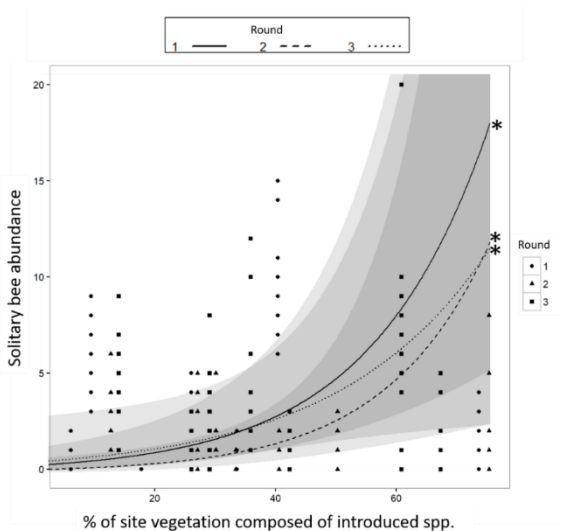
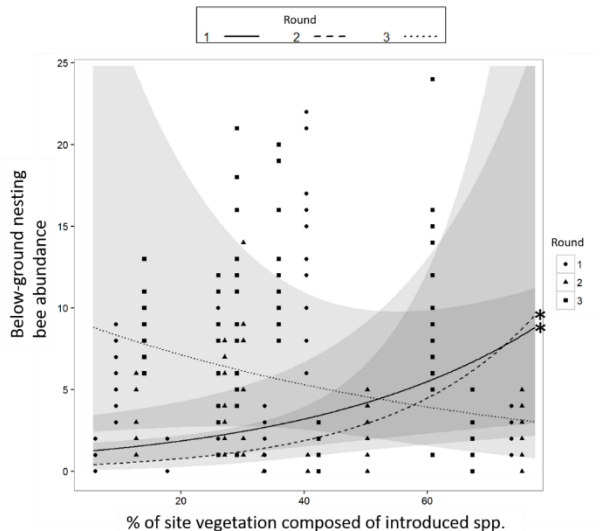


Figure 36: Predicted effects of increasing percentage of vegetative cover per site composed of introduced species on below-ground nesting bee abundance



Pollination services

In Round 1 seven individual phytometers were killed by frost or herbivory, for a total of 58 individual phytometers. In Round 3 three individuals were killed by herbivory, leaving a total of 57 individual phytometers. Pollination services to the phytometers ranged from 1.0 to 13.8 seeds per pod per phytometer in Round 1, and 1.9 to 20.3 seeds per pod per phytometer in Round 3.

Does seed set change with changes in pollinating bee abundance, species richness, or abundance of common genera?

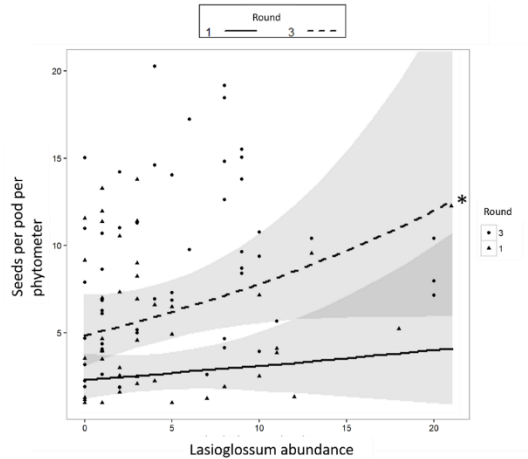
Seed set of the phytometers did not change with changes in bee abundance per plot ($p>0.18$), bee species richness per plot ($p>0.27$) or bee abundance per site ($p>0.11$) (Table 8). In Round 3, seed set per plot increased with increasing abundance of *Lasioglossum* genus bees ($\beta=0.21$, $SE=0.12$, $p=0.09$) (Figure 37). There were no significant effects of *Lasioglossum* abundance in Round 1 or of *Bombus* abundance in either Round ($p>0.34$).

Table 8: Summary of effects of bee abundance on seed set. “+” indicates significant positive effect, “-” indicates significant negative effect, and “/” indicates no significant effect.

	Bee abundance per plot			Bee richness per plot			Bee abundance per site			<i>Lasioglossum</i> abundance			<i>Bombus</i> abundance		
Round	1	2	3	1	2	3	1	2	3	1	2	3	1	2	3
Seed set	/		/	/		/	/		/	/		+	/		/

Figure 37: Predicted effects of increasing abundance of *Lasioglossum* bees on pollination services (seed set).

Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.



Does seed set change with changes in local or landscape bee habitat availability?

Litter depth showed different effects between Round 1 and Round 3, with increasing litter depth resulting in no effect in Round 1, and in decreased seed set in Round 3 ($\beta=-0.11$, $SE=0.03$, $p=0.001$) (Figure 38). In both sample Rounds, seed set of the phytometers was not significantly affected by woody cover ($p>0.21$), the indexed amount of flowering stems per plot ($p>0.28$), or by species richness of flowering stems ($p>0.32$). In Round 1 there was no effect of matrix habitat within 1km on seed set ($p=0.40$), but in Round 3 increased amounts of matrix habitat within 1km led to decreased seed set ($\beta=-0.017$, $SE=0.008$, $p=0.031$) (Figure 39).

Figure 38: Predicted effects of increasing litter depth on pollination services (seed set).

Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.

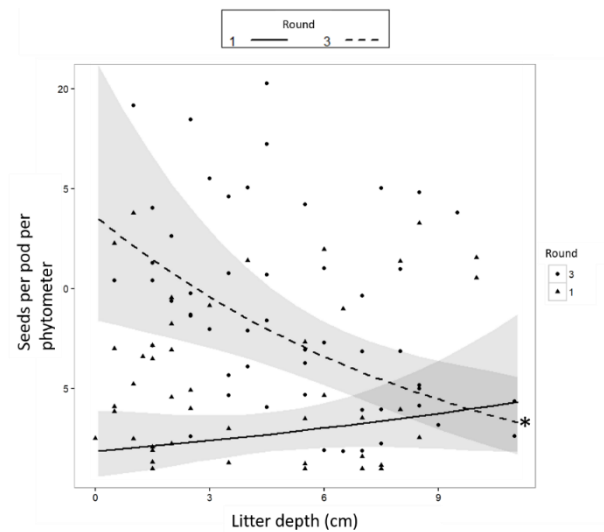
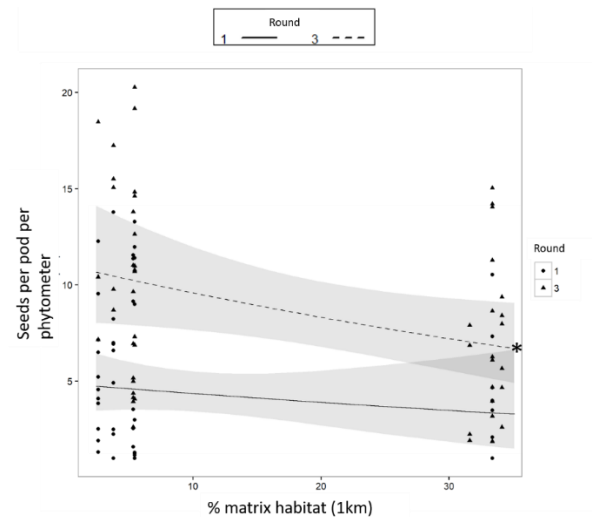


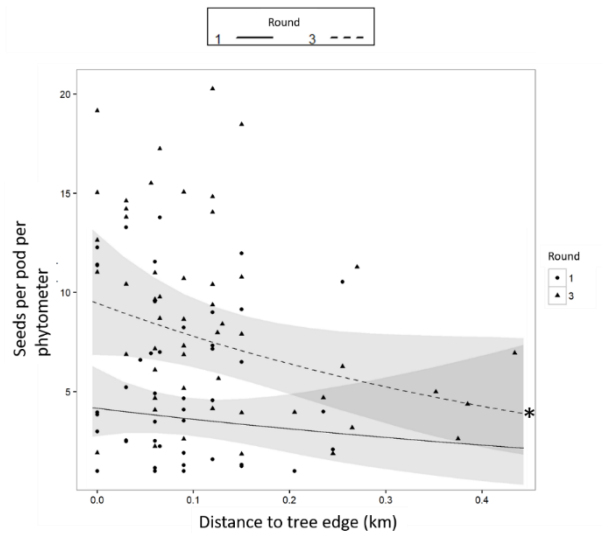
Figure 39: Predicted effects of increasing landscape matrix habitat on pollination services (seed set). Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.



Does seed set change with proximity to tree or road edges?

Seed set of the phytometers decreased with increasing distance to tree edge in Round 3 ($\beta=-16.15$, $SE=5.95$, $p=0.008$) (Figure 40) but there was no significant effect in Round 1 ($p=0.52$). This contrasts with the effects of distance to tree edge on bee abundance, which generally found effects in Round 1, but not Round 3. There was no significant effect of proximity to road edge in either Round 1 or Round 3 ($p>0.28$) (Table 5). (For complete results on pollination services, see Appendix 8).

Figure 40: Predicted effects of increasing distance to tree edge on pollination services (seed set). Significant slopes marked with ‘*’. Shading represents 95% confidence intervals for each round.



Does seed set change with greater amounts of introduced vegetation?

There were no significant effects on seed set with changes in introduced forb cover ($p>0.38$), introduced grass cover ($p>0.42$), native percentage of flowering stems ($p>0.52$), or introduced vegetation cover per site ($p>0.41$) for either Round (Table 6).

4.4 Discussion

My results varied among my three sample rounds, and both within and between years. This is not surprising as bee and pollinator communities are highly temporally variable. Phenological shifts occur over a single summer in northern prairies (Patenaude 2007), and variation in individual species and community composition varies from year to year in many ecosystems (Patenaude 2007, Roubik 2001, Williams et al. 2001). Four species made up 47.4% of my total PCF bee abundance and annual or seasonal changes in these and other common species may be driving some of the seasonal changes seen in my study. The varying effect sizes seen among sample rounds may also reflect seasonal shifts in weather, impacting floral and nesting resources, which could affect bee and pollinator behaviours such as foraging distances or floral constancy, and thus produce shifts in local bee abundance and pollination services (Grindeland et al. 2005, Richards 2004, Steffan-Dewenter and Schiele 2008). Many studies of landscape effects on bees and pollination services rely on limited temporal periods for data collection. My study demonstrates that ecological effects are not necessarily consistent among different temporal periods. As such, sampling and research design should attempt, as far as is reasonable, to capture these phenological shifts in order to provide a better understanding of effects on pollinators and pollination service in the prairies, and caution should be applied before drawing general conclusions from a limited temporal period. In my discussion, I will focus on effects that were found consistently through multiple sample rounds, as these are likelier to reflect general impacts in this ecosystem.

Bee populations in the northern prairies are influenced by habitat structure at both local and landscape scales. Surprisingly, my results did not show many positive effects of floral abundance or species richness, in contrast to the findings of many other studies that have

emphasized the importance of floral resources to bee populations at similar spatial scales (Winfree et al. 2011). In my study system, nesting resources or other changes may be greater limiters of bee abundance than floral resources. My results may also be because my generalized floral variables (abundance and richness) mask the larger role that certain flower taxa play relative to others as resources for bees in the region (Robson 2014, Semmler 2015).

My results show that ground-nesting bee abundance declined in response to increasing litter depth. Excessive plant litter can impede ground-nesting bees' access to preferred soil nest sites (USDA 2007) and it has been shown that community composition and abundance of ground-nesting bees are sensitive to changes to nest-site factors (Grundel et al. 2010, Potts et al. 2005, Sardinas and Kremen 2014). Since the majority of prairie bee species are below-ground nesting (Sheffield et al. 2014), my results underscore the importance of assessing and managing for adequate nesting sites in the northern prairies. I also found that decreasing amounts of local woody cover reduced social bee abundance in two of my sample Rounds, but did not affect above-ground nesting bee presence. This result may reflect the effects of structural elements on foraging behaviours of social bees, such as foraging around clusters or patches of trees and shrubs, which may result in lower social bee abundance in areas with more woody vegetation (Diekotter et al. 2006, Krewenka et al. 2011).

Increases in matrix land cover consistently resulted in decreases in social bees and below-ground nesting bees. I also found some evidence that matrix habitat influences seed set; however, surprisingly, this pattern was poorly explained by bee diversity or abundance. My results are similar to findings in crop systems, which show declines in pollinator abundance and diversity with decreasing natural habitat on the landscape, although these effects do not always lead to changes in crop fruit or seed set (Ricketts et al. 2008). Similarly, an investigation into

specialization in a pollination network has shown that bees and flowers may respond differently to habitat landscape loss, with bees showing faster and clearer shifts towards generalization (Taki and Kevan 2007). Since my study was only able to use one non-native phytometer species, it is possible that native flowering plants may respond to landscape changes in ways that more closely resemble bee responses (Biesmeijer et al. 2006).

Social bees and below-ground nesting bees were consistently more sensitive to landscape habitat changes than solitary or above-ground nesting bees. The sensitivity of below-ground nesting bees to landscape structure may be due to the presence of annual crops, which made up the majority of matrix habitat in my study region. Annual crops experience regular tilling, which negatively impacts most bees that nest in soils (Williams et al. 2010). Social bees often respond to habitat at a landscape scale more strongly than solitary bees, possibly due to their usually broader and more generalized foraging behaviours (Ricketts et al. 2008). Social bees may also decline in agricultural landscapes due to their greater sensitivity to pesticides (Williams et al. 2010, Winfree et al. 2009), which may be due to season-long foraging resulting in accumulation of pesticides in social colonies and reduced reproductive success (Gill et al. 2012). Some of the effects I found on social bees in my study may be partially due to effects of body size, but it is difficult to disentangle these traits in my system. In my study, sociality was moderately related to bee size, with social bees tending to be larger (body length >10mm) than solitary bees (Spearman's $\rho = 0.62$, $p < 0.001$). Bee responses to landscape effects sometimes vary with body size, with larger bees showing greater responses to landscape variables than smaller bees, likely due to the greater foraging range of larger bees (Gathmann and Tscharntke 2002, Steffan-Dewenter et al. 2002). However, social bees have been shown to respond to landscape changes

regardless of body size (Kennedy et al. 2013), and body size may not have as clear effects as sociality (Williams et al. 2010).

I found edge effects on bee abundance in fragmented northern prairies. I found inconsistent evidence of effects of tree edges, perhaps because bees in the aspen parkland ecoregion are adapted to a mosaic landscape featuring both open grassland and deciduous forests. In contrast, the clear and consistently negative effect of road edges on social bees and ground-nesting bees may be due to the evolutionary novelty of this edge type. At smaller scales of a few hundred metres, road edges can impact bee foraging behaviour or nest site selection. Road edges may affect bee foraging behaviour by acting as barriers to movement (Bhattacharya et al. 2003) and it has been hypothesized that pollinator behaviour could change at edges due to shifts in predation risk, or changes in the profitability of gap-crossing (Hadley and Betts 2012). Close proximity to road edges may change the suitability of nesting habitats for ground-nesting bees, which are sensitive to changes in soil conditions, such as compaction and slopes (Sardinas and Kremen 2014). My results showed impacts of road edges at distances of greater than 2km; this indicates that road effects are not limited to the immediate proximity of roads. Pollinator diet selection and community composition could be affected by changes in vegetation composition or floral abundance associated with road edges (Hadley and Betts 2012, Koper et al. 2010); such dietary and foraging changes have been shown to affect different bee functional group differently (Jha and Vandermeer 2009).

Road edges showed a consistently negative effect on abundance of social bees, which are already known to be more vulnerable to other anthropogenic impacts including agricultural intensification and habitat loss (Godfray et al. 2014, Klein et al. 2017). Jha and Kremen (2013) found that paved surfaces reduced nest densities of a ground-nesting bumblebee at local habitat

scales (<250m), so proximity to or density of roads could result in reduced bee nesting sites. Indeed, density of roads may be correlated with cropland and therefore with landscape habitat loss (Willms et al. 2011), which could potentially result in compounded effects of road edges and habitat loss. As such, preservation of remaining grasslands with fewer road edges may be of particular importance for social bees, especially since much of the northeastern prairies has a high density of roads. Further research into the mechanisms driving road edge effects is clearly needed to determine management and mitigation strategies in this region.

I found significant positive effects of introduced forb cover and introduced vegetation cover on bee abundance in multiple sample rounds. Introduced forbs that were common at the study sites included introduced legumes (*Melilotus alba*, *Melilotus officinalis*, *Medicago lupulina*, *Medicago sativa*, and *Trifolium hybridum*), as well as locally abundant introduced *Asteraceae* species (*Cirsium arvense*, *Sonchus arvensis*, and *Taraxacum officinale*) (See Appendix 2). The flowers of these introduced legumes are demonstrated foraging resources for native bees (Tepedino et al. 2008, Vaughan et al. 2015), and *T. officinale* (common dandelion) blooms abundantly early in the season, attracting bees when there are less species flowering. These data may reflect the positive effects that introduced forb cover may have in providing important food resources to visiting bees (Montero-Castano and Vila 2012). The positive effects of introduced vegetative cover may also reflect historic changes to bee populations in the region; Eurasian grasses and forage legumes have been widespread in the aspen parkland since the 1920s (Bird 1961), and it is possible that bee communities have shifted in the past to the advantage of bee species that benefited from these introductions. Since my variables measured percent cover, I cannot be certain that these results are the impact of specific species or groups of plant species. Despite the positive effects of introduced vegetative cover, I repeatedly found that a greater

percentage of native blooms resulted in higher bee abundances, although the strength of these effects was weaker than the effects of introduced forb cover (Figures 28-31). Previous studies have shown that native bees generally prefer native flowering species over introduced species if there is a choice (Chrobock et al. 2013), and that bee diversity is positively affected by local abundance of native flowers (Potts et al. 2003, Kremen et al. 2007). A higher percentage of native flowers may attract bees to a local area, but more detailed future studies may be able to tease out the impacts of specific species, whether native or introduced.

Although I found effects of introduced vegetation on bee abundance, I did not find effects on seed set of my phytometer species. This may reflect pollination services by taxa other than bees, which may not have the same responses as bees to introduced vegetation (Bjerknes et al. 2007). My phytometer species is not native to Manitoba grasslands, so I cannot generalize my results to effects on native flowering species. Indeed, repeated studies show that effects of introduced species on pollination services and reproduction success vary among plant species (Bjerknes et al. 2007, Morales and Traveset 2009).

It is clear that ecological effects on bees do not necessarily result in similar effects on pollination services. Effects on fruit and/or seed set can be related to changes in pollinator abundance and diversity (Albrecht et al. 2009, Garibaldi et al. 2011) but these variables may also exhibit their own responses to landscape effects depending on each plant species' needs. It is possible that plants that require a more specific functional group of pollinators may have fruit or seed set that more closely tracks habitat responses of their most effective pollinators (Biesmeijer et al. 2006). Although *Lasioglossum* abundance was a significant positive driver of phytometer seed set in one round of my study, my phytometer species is visited by a wide range of pollinators, including a variety of fly species (Rader et al. 2013). Flies differ from bees with

regards to how they can disperse in a fragmented landscape (Jauker et al. 2009), and how their abundance varies with agricultural intensification (Mogren et al. 2016) and habitat isolation (Grass et al. 2016). Understanding how plants with different pollinators respond to habitat changes is an avenue for future research in prairie systems.

3.5 Conclusion

My study is the first that I am aware of to demonstrate edge effects and impacts of landscape structure on bees in North America's northern prairies. Social bees and below-ground nesting bees showed the strongest and most consistent negative responses to both habitat loss and edge effects. Introduced plant species resulted in mixed effects but native flowers were important drivers of bee abundance. Effects on pollination services were less clear and show that these services must be considered separately from bee communities. My study also found temporal changes in effects, demonstrating the importance of longer-term, multi-season studies on pollination systems in this region.

Within a mosaic landscape impacted by agricultural land uses, such as my study system, ongoing preservation or restoration of habitat at scales that are relevant to bees and other mobile insect pollinators is an important element of pollinator and pollination conservation. As shown by my results, this means considering both local and landscape habitat resources. Actions aimed at conservation of birds or mammals will not necessarily ensure habitat conservation for grassland pollinators, since the scale of resource and habitat needs may be different (Arenz and Joern 1996). However, my results are consistent with findings from Europe that show that decreases in native bee abundance can be partially mitigated with the preservation of natural and semi-natural with increasing agricultural intensity (Le Feon et al. 2010). Negative impacts of

road edges also suggest that conserving less-fragmented, intact habitat is important, especially for social bees.

There is room for much more research on pollinators in prairie and grassland ecosystems. Habitat effects on individual species are generally poorly understood, especially over longer time-frames. I also have little information on impacts to pollination services of native plants in prairie ecosystems, and on how pollination services (or lack thereof) impact prairie plant diversity and persistence over time. Future research and management should also attempt to address the fact that multiple drivers are impacting pollinators and pollination services in prairie regions, including habitat loss, invasive species, agricultural intensification, and climate change. The interactions between these drivers are often poorly understood but must be considered for effective management and conservation of prairie pollination (Gonzalez-Varo et al. 2017).

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4. MANAGEMENT IMPLICATIONS

4.1 Management Goals

Managers may have several possible goals when managing wild bees and pollination services in grassland areas. The first may be to manage for as diverse bee populations as possible. Meeting this goal may require identifying and maintaining populations of rare or declining bee species. Management for this goal would require ensuring that a diverse array of floral and nesting resources are available in an area, particularly those needed by rare or declining species. Activities might include habitat restoration, such as plantings or seeding for floral hosts for specialist species.

A related management goal may be to conserve a functional diversity of bees and/or other insect pollinators. Rather than focus specifically on the number of species present, managers may try to ensure that groups of bees have healthy populations for long-term sustained presences (Jordan et al. 2014, Senapathi et al. 2015). These functional groupings can be based on ecological traits such as floral preference, seasonal emergence, nesting type, or sociality. Management activities for this goal would be similar to managing for species diversity, but would involve managing resources in a more general way, including ensuring that an area has a diversity of floral and nesting resources (Jordan et al. 2014). For example, habitat restoration might involve planting or seeding of floral species to ensure season-long floral resources are available for a functional diversity of bees.

A management goal may be the conservation of pollination services for maximum diversity of grassland flowering plants. This goal would require similar activities as those described above for managing diverse and sustained bee populations to provide pollination services to these plants. As well, if a management area has rare flowering species, managers might work to ensure

these species receive pollination services by identifying the pollinators of these flowers. Management activities to promote pollination services to native flowering plants might include identifying, and then planting, species that facilitate pollination services to other species (Ghazoul 2006). Similarly, a management action may be the removal of introduced species that are shown to compete with native species for pollination services (Larson et al. 2006), but as my research shows, introduced species are not necessarily negatively impacting bee populations in the region, so careful consideration should be given to such an action since it can be expensive and difficult.

Another goal for managing pollination services is to conserve or promote wild pollination services to flowering crops that are on the same landscape as remaining prairie grasslands (Robson 2014). In the northern prairies, the main crop of concern for managers is canola (*Brassica napus* L.), which is pollinated by many species of wild bees and flies (Rader et al. 2013). Managing for crop pollination is different from managing for pollination services to diverse wild plants: most domestic crops, including canola, receive the majority of pollinator visits from a limited number of wild insect species and, theoretically, management for only few key wild bee species would be adequate to achieve the goal of sufficient crop pollination (Kleijn et al. 2015, Senapathi et al. 2015). Managing for this goal would require activities that ensure adequate pollinator habitat exists in close proximity to annual canola fields, including nesting resources as well as other floral species for forage when focal crops are not in bloom (Robson 2014).

4.2 Implications of Major Findings

My results have some implications for these different management goals. First, I found that proximity to roads consistently resulted in reduced abundance of social bees. This finding has

implications for managing to maximize bee diversity since Aspen Parkland grasslands are already heavily fragmented by existing roads. To manage for this goal, it becomes important to understand which species are particularly sensitive to proximity to road edges. This implies the need for further research and observations, particularly to identify if rare or declining species have reduced abundance near road edges. A species' sensitivity to road edges may be due to changes in nesting or floral resources, or in foraging behaviour (Hadley and Betts 2012). Identification of road-sensitive species will help identify which mechanisms could be driving this edge effect, and thus present potential management activities. If, for example, changes floral resources near roads are driving bee responses, management activities could include plantings or seedings to address declines of certain forage plants near roads. If sensitivity to road edges is driven by changes to below-ground nesting resources (for example, changes in soil compaction or composition), management options may be more limited as changes to transportation infrastructure, particularly for public roads, can be expensive and difficult to enact. Further research could also take into account soil factors, as these may have explanatory power for some of the effects I found, and may be a source of variation with different species.

Although my phytometers did not show a decline in pollination services received closer to road edges, I was only able to use one flowering species; it is a plausible hypothesis that a decrease in social bee abundance near road edges could result in a decrease in pollination services to some flowering plant species near roads. Again, identification of which bee species are most affected by road proximity is important in this context, since this could help identify which flower plant species might be more susceptible to a decline in pollination services. If generalist social bees, such as many bumblebees (genus *Bombus*), are affected by roads, pollination services near roads may be expected to decline near road edges. Management

recommendations in either case include surveying and monitoring flowering plant populations for changes in abundance relative to road edges. Monitoring could also include comparisons of fruit or seed set within a species at different distances to road edge. If some plant species are found to decline near roads, management options include planting or seeding these species at locations more conducive to receiving pollination services.

Managers seeking to conserve crop pollination services may have more options for dealing with potential road edge effects. Many social bees are bumblebees, which are known to be pollinators of canola (Zink 2013), so there is an incentive to ensure that road edges do not reduce pollination services to this economically valuable crop. Again, further research is needed to see if proximity to road edges affects canola seed set, but positive effects of forested edges have been demonstrated for this crop in Europe (Bailey et al. 2014). If road edges affect canola pollination, decisions by private landowners about where to conserve or restore natural grassland habitat should take proximity to road edges into account. As well, crop fields in areas with a greater density of roads might benefit from greater amounts of natural and semi-natural area adjacent to or near crops.

I found that reduced litter depth consistently resulted in greater abundance of below-ground nesting bees. This finding suggests that access to nesting resources is of particular importance to the bee populations in my study region. For managers, this means that they must consider more than just floral resources when managing bee habitat. The majority of prairie bee species nest below ground, so management activities that reduce litter build-up in grasslands, such as grazing or burning, can help ensure that these bees have access to nest sites. Indeed, these activities can also help promote nesting resource availability for above-ground nesting bees: if grazing or burning is conducted in a patchwork or rotational scheme, it can promote

diverse microhabitats with variation in vegetation and litter structure, providing a diverse range of nesting options for bee communities.

Crop fields often have little litter cover, but they may not necessarily provide good nesting habitat for ground-nesting bees. Agricultural practices such as tilling reduce abundances of ground-nesting bees (Williams et al. 2010). As my results showed, an increase in annual cropland on the landscape resulted in consistent decreases in abundance of ground-nesting bees, suggesting that even if this group of bees were accessing bare soils in croplands, other factors can outweigh this potential benefit.

I found that bee populations are affected by the surrounding landscape at a scale of 1km, as ground-nesting and social bees declined in abundance with increases in non-habitat matrix. In my study region, the majority of low-quality habitat on the landscape was annual cropland, a context that is similar across the northern and eastern Prairies ecozone. As noted in Chapter 2, bee populations in other ecosystems have been shown to respond to both local and landscape scale variables (Kennedy et al. 2013, Kremen et al. 2007, Schuepp et al. 2013). Similarly, my study shows that management decisions cannot simply focus on resource provision at a local site. If managers wish to conserve bee populations and their pollination services, maintaining sufficient natural habitat at a landscape scale is clearly important. At a broad scale, policies and activities that support conservation easements or other incentives for private landowners to retain and maintain natural areas on their properties may be particularly effective at conserving bee habitat. As agricultural intensification continues in the Aspen Parkland, conservation of remaining natural and semi-natural open upland areas, such as field margins and grazing pastures, may be important areas of focus for managers and policy-makers (Morandin et al. 2006, Senapathi et al. 2017). My results about landscape context also suggest that habitat

restoration may be an important tool for conservation of bees and pollination services. Research in other prairie locations has shown some long-term success in conserving bee populations in former croplands, and even along road edges (Hopwood 2008, Tonietto et al. 2017). Such restorations, if conducted within bee dispersal range of existing habitat, can help address the need for habitat on the landscape and provide connectivity among remaining high-quality habitats. Policies that educate, support, or incentivize these types of restorations on private lands should be part of a broader management approach.

My findings show that introduced species do not necessarily have a negative impact on bee abundance or on pollination services. While there may be some variation by species, introduced species can still provide habitat and resources to native bees. Given the difficulty of removing many naturalized introduced species (Ellis-Felege et al. 2013, Kettenring and Adams 2011), and my finding that bees often respond positively to the presence of native flower abundance, management resources might be best spent ensuring that native flowering species persist in invaded areas. Practices that promote heterogeneity and mimic historical prairie regimes, such as prescribed grazing and burning, can encourage the persistence of a diversity of native flowering species (Ellis-Felege et al. 2013, Fuhlendorf and Engle 2004, Grant et al. 2009).

There is clearly a need for more research on pollinators and pollination service in the northern prairies. The management implications of my study are necessarily broad, due to limited information on individual bee species or tested management approaches in this region. While management approaches can be borrowed from other regions and ecosystems, each regional landscape varies in how it affects bee populations and pollination services (Cariveau and Winfree 2015). However, as wild pollinators gain more attention, both with the public and with researchers and managers, more information is becoming available. Grassland managers in the

Canadian prairies are interested in managing for wild pollinators and this work is beginning to yield information and results. Going forward, my results suggest that there is a need for research and monitoring of bee populations and pollination services to identify impacts of specific changes and management decisions. Ongoing work must also consider the other drivers that can impact bees and pollination services and how these interact with the habitat effects I found. In the northern prairie, these include the effects of introduced species, climate change, and agricultural intensification (Gonzalez and Varo 2013).

4.3 Literature Cited

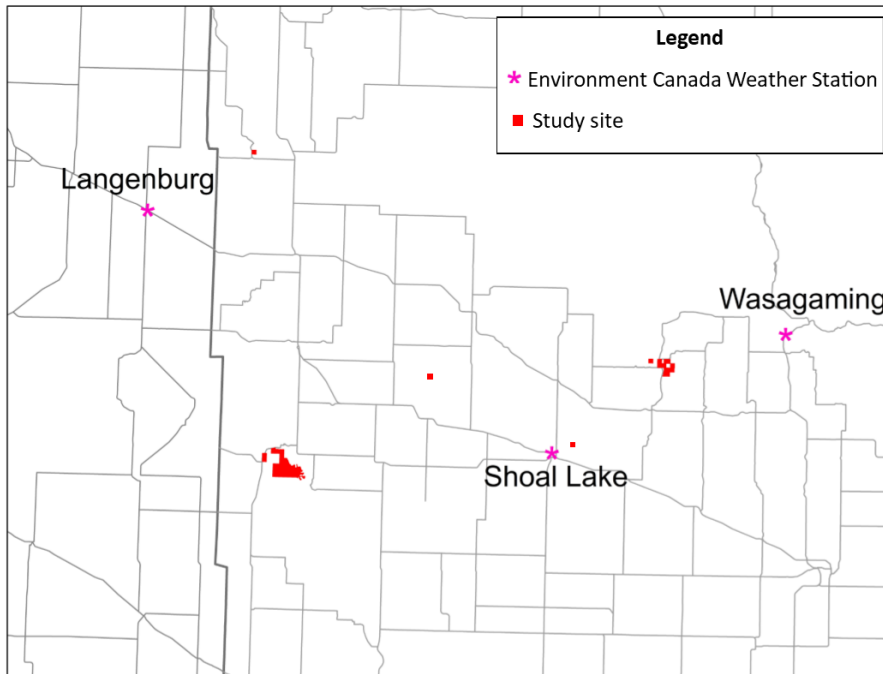
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APPENDIX 1: DETAILED WEATHER DATA

Map of weather stations used to derive study region weather data



Summary of weather data during each sampling round

	Mean Max. Temperature (°C)	Mean Min. Temperature (°C)	Mean Temperature (°C)	Total Rain (mm)	Mean Daily Rainfall (mm)
<i>Round 1 (June 5 - June 21 2014)</i>					
Average	19.1	7.3	13.2	59.6	3.8
Langenburg	20.4	8.0	14.3	86.2	5.1
Shoal Lake	19.0	8.2	13.5	54.0	3.9
Wasagaming	17.9	5.7	11.8	38.7	2.4
<i>Round 2 (August 7 - August 21 2014)</i>					
Average	25.3	12.7	19.0	39.3	2.7
Langenburg	26.4	13.6	20.0	21.4	1.5
Shoal Lake	24.9	12.9	18.9	47.0	3.4
Wasagaming	24.6	11.6	18.1	49.6	3.3
<i>Round 3 (June 10 - July 2 2015)</i>					
Average	23.7	9.0	16.4	37.6	1.7
Langenburg	24.7	9.8	17.3	14.6	0.6
Shoal Lake	23.1	10.1	16.6	38.2	1.7
Wasagaming	23.2	7.2	15.2	60.0	2.7

APPENDIX 2: SITE PHOTOS AND TRANSECT LOCATIONS

Site	Transect #	Transect Start	Transect End
<i>1- Pedrick</i>	Pedrick 1	50.57377 -100.9007	50.57366 -100.90279
	Pedrick 2	50.574899 -100.900703	50.574833 -100.902824
	Pedrick 3	50.57286 -100.9007	50.57287 -100.90279
<i>2- Pryzner</i>	Pryzner 1	50.461216 -100.519157	50.459885 -100.519628
	Pryzner 2	50.461228 -100.518569	50.459903 -100.519149
<i>3- Fairgrounds</i>	Fairgrounds 1	50.408947 -101.294518	50.408947 -101.294518
	Fairgrounds 2	50.407208 -101.294695	50.408551 -101.294403
	Fairgrounds 3	50.40804 -101.29082	50.40901 -101.29227
<i>4- Lefranc</i>	Lefranc 1	50.41747 -101.35963	50.41824 -101.35993
	Lefranc 2	50.41809 -101.36119	50.41834 -101.35912
<i>5- Marjerison</i>	Marjerison 1	50.602055 -100.278838	50.603415 -100.278845
	Marjerison 2	50.604606 -100.27671	50.60462 -100.278797
<i>6-Moster</i>	Moster 1	50.942048 -101.408894	50.943125 -101.41027
	Moster 2	50.942673 -101.415445	50.942674 -101.413297
<i>7- Pipit</i>	Pipit 1	50.403654 -101.305817	50.402415 -101.306831
	Pipit 2	50.403654 -101.305817	50.402304 -101.31206

Site 1: Pedrick



Site 2: Pryzner



Site 3: Fairgrounds



Site 4: Lefranc



Site 5: Marjerison



Site 6: Moster



Site 7 Pipit



APPENDIX 3: BEE AND FLOWER SPECIES ABUNDANCE DATA

Bee species abundance by site in each study round

<i>Species</i>	Round 1 (June 2014)							Round 2 (August 2014)							Round 3 (June 2015)						
	Site #							Site #							Site #						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7
<i>Agapostemon texanus</i>	0	0	0	0	0	8	0	0	0	0	0	0	3	0	0	1	0	0	0	10	0
<i>Andrena 12</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0
<i>Andrena 13</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
<i>Andrena 7</i>	2	0	0	0	0	1	0	0	0	0	0	0	0	0	5	3	0	1	0	4	0
<i>Andrena 9</i>	0	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	0	0	1	1	0
<i>Andrena barbilabrous</i>	1	2	3	0	1	28	0	0	0	0	0	0	0	0	1	0	1	0	1	3	0
<i>Andrena carlini</i>	16	16	2	0	0	1	0	0	0	0	0	0	0	0	5	9	2	0	2	0	0
<i>Andrena lupinorum</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	5	0	0
<i>Andrena miserabilis</i>	0	0	2	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Andrena nivalis</i>	0	0	1	0	0	1	0	0	0	0	0	0	0	0	3	0	0	0	1	0	0
<i>Andrena quintilis</i>	3	0	0	1	1	0	0	0	0	0	0	0	0	0	3	1	0	2	0	0	0
<i>Andrena regularis</i>	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
<i>Andrena salictaria</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	1	0	0	0
<i>Andrena wheeleri</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Anthidium clypeodentatum</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
<i>Anthophora terminalis</i>	0	0	0	0	0	0	0	0	0	2	0	0	3	1	0	1	3	1	2	1	1
<i>Apis mellifera</i>	0	0	0	0	0	0	0	0	0	3	1	0	0	0	0	0	0	0	0	0	0
<i>Augochlorella aurata</i>	3	0	0	0	3	0	0	0	0	0	0	1	0	0	1	1	0	0	21	0	0
<i>Bombus borealis</i>	1	2	0	0	0	3	0	3	0	9	0	0	1	0	2	1	1	0	5	9	2
<i>Bombus griseocollis</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0
<i>Bombus nevadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	0	0
<i>Bombus rufocinctus</i>	14	8	4	1	1	12	0	8	0	7	0	0	5	1	21	15	17	8	29	5	14
<i>Bombus sandersoni</i>	1	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	2	0	1	1	0
<i>Bombus terricola</i>	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
<i>Bombus ternarius</i>	7	2	0	2	1	2	1	4	3	3	0	0	0	0	3	0	1	1	20	5	2
<i>Bombus vagans</i>	1	0	0	1	0	0	0	1	2	1	0	0	0	0	0	0	1	1	1	0	0

Colletes brevicornis	0	0	0	0	0	0	0	0	2	0	0	0	1	0	0	0	0	0	0	0
Dufourea maura	0	0	0	0	0	0	0	0	2	0	0	2	0	0	0	0	0	0	0	0
Halictus confusus	5	0	0	0	1	1	1	9	0	0	0	1	0	0	16	1	0	0	1	1
Halictus rubicundus	0	0	2	0	1	2	0	4	0	8	0	1	3	0	4	0	1	0	2	3
Heriades carinata	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
Hoplitis pilosifrons	1	5	0	0	0	0	0	0	0	0	0	0	0	1	0	3	0	0	0	1
Hoplitis producta	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	0	0	0	2
Hoplitis spoliata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Hylaeus affinis	0	0	0	0	0	0	0	1	0	0	1	0	0	1	2	0	1	3	0	3
Hylaeus mesillae	1	8	0	0	0	0	0	3	8	0	0	0	1	1	0	3	0	0	0	1
Lasioglossum admirandum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0
Lasioglossum albipenne	9	1	3	2	1	8	0	0	0	0	0	2	4	0	76	28	0	49	21	7
Lasioglossum cinctipes	0	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0	0	1	0	0
Lasioglossum coriaceum	1	0	1	0	0	0	0	0	0	0	0	0	0	0	7	5	1	0	0	0
Lasioglossum 21	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0
Lasioglossum 22	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	2	1
Lasioglossum 24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Lasioglossum imitatum	1	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum laevissimum	1	1	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	4	0
Lasioglossum leucozonium	0	0	1	0	0	5	0	1	0	0	0	0	1	0	2	4	0	0	1	6
Lasioglossum lineatulum	1	0	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum novascotiae	0	0	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	3	0
Lasioglossum paraforbesii	1	1	3	2	0	28	0	0	0	1	0	0	3	0	3	0	0	3	4	14
Lasioglossum pectorale	1	21	0	0	0	18	0	0	0	0	0	0	0	0	0	3	0	0	0	5
Lasioglossum perpunctatum	0	1	0	0	0	17	0	0	0	0	0	0	0	0	1	1	0	0	1	2
Lasioglossum pilosum	0	0	0	0	0	0	0	0	0	0	0	0	6	0	0	0	0	0	0	4
Lasioglossum semicaeruleum	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum pruinatum	2	0	0	0	2	1	1	2	0	0	0	0	1	0	9	0	1	0	6	1
Lasioglossum sagax	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0	1	1
Lasioglossum subversans	0	2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	2
Lasioglossum succinipenne	0	3	0	0	0	15	0	2	1	0	0	0	44	0	2	11	0	0	0	82
Lasioglossum timothyi	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0

Lasioglossum versans	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	1	0	0	2	0	0	0
Lasioglossum zonulum	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	0	0	0
Lasioglossum zephyrum	1	4	6	1	2	32	0	0	1	0	2	0	10	5	1	8	13	16	3	84	25	4
Megachile campanulae	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Megachile centuncularis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Megachile inermis	0	0	0	0	0	0	0	0	1	0	18	0	0	0	0	0	0	1	1	1	0	0
Megachile latimanus	0	0	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0
Megachile melanophaea	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0
Megachile pugnata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Megachile relativa	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	1
Melissodes 1	0	0	0	0	0	0	0	0	4	14	0	2	0	6	0	0	0	0	0	0	0	0
Melissodes 2	0	0	0	0	0	0	0	0	3	1	0	0	0	2	0	0	0	0	0	0	0	0
Melissodes 3	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Melissodes 5	0	0	0	0	0	0	0	0	1	0	0	0	6	0	0	0	0	0	0	0	0	0
Melissodes agilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	4	0	0	0	0	0	0
Osmia 1	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmia 2	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmia 8	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Osmia distincta	3	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Osmia integra	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Osmia simillima	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0
Osmia tersula	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Perdita swenki	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0
Site Totals	79	81	31	11	15	189	5	70	36	56	7	22	94	7	197	109	51	79	232	198	34	

Bee species relative abundance by site and by round

<i>Species</i>	Round 1		Round 2		Round 3		TOTAL	
	Round Total	Round Relative Abundance (%)	Round Total	Round Relative Abundance (%)	Round Total	Round Relative Abundance (%)	Species Total	Species Relative Abundance (%)
<i>Agapostemon texanus</i>	8	1.95	3	1.03	11	1.22	22	1.37
<i>Andrena 12</i>	0	0.00	0	0.00	2	0.22	2	0.12
<i>Andrena 13</i>	0	0.00	0	0.00	1	0.11	1	0.06
<i>Andrena 7</i>	3	0.73	0	0.00	13	1.44	16	1.00
<i>Andrena 9</i>	1	0.24	1	0.34	2	0.22	4	0.25
<i>Andrena barbilabrous</i>	35	8.52	0	0.00	6	0.67	41	2.56
<i>Andrena carlini</i>	35	8.52	0	0.00	18	2.00	53	3.31
<i>Andrena lupinorum</i>	0	0.00	0	0.00	7	0.78	7	0.44
<i>Andrena miserabilis</i>	3	0.73	0	0.00	0	0.00	3	0.19
<i>Andrena nivalis</i>	2	0.49	0	0.00	4	0.44	6	0.37
<i>Andrena quintilis</i>	5	1.22	0	0.00	6	0.67	11	0.69
<i>Andrena regularis</i>	1	0.24	0	0.00	1	0.11	2	0.12
<i>Andrena salictaria</i>	1	0.24	0	0.00	10	1.11	11	0.69
<i>Andrena wheeleri</i>	1	0.24	0	0.00	0	0.00	1	0.06
<i>Anthidium clypeodentatum</i>	0	0.00	1	0.34	1	0.11	2	0.12
<i>Anthophora terminalis</i>	0	0.00	6	2.05	9	1.00	15	0.94
<i>Apis mellifera</i>	0	0.00	4	1.37	0	0.00	4	0.25
<i>Augochlorella aurata</i>	6	1.46	1	0.34	23	2.56	30	1.87
<i>Bombus borealis</i>	6	1.46	13	4.45	20	2.22	39	2.43
<i>Bombus griseocollis</i>	0	0.00	1	0.34	1	0.11	2	0.12
<i>Bombus nevadensis</i>	0	0.00	1	0.34	1	0.11	2	0.12
<i>Bombus rufocinctus</i>	40	9.73	21	7.19	109	12.11	170	10.61
<i>Bombus sandersoni</i>	1	0.24	0	0.00	5	0.56	6	0.37
<i>Bombus terricola</i>	0	0.00	1	0.34	0	0.00	1	0.06
<i>Bombus ternarius</i>	15	3.65	10	3.42	32	3.56	57	3.56
<i>Bombus vagans</i>	2	0.49	4	1.37	3	0.33	9	0.56
<i>Colletes brevicornis</i>	0	0.00	3	1.03	0	0.00	3	0.19
<i>Dufourea maura</i>	0	0.00	4	1.37	0	0.00	4	0.25

Halictus confusus	8	1.95	10	3.42	20	2.22	38	2.37
Halictus rubicundus	5	1.22	16	5.48	10	1.11	31	1.93
Heriades carinata	0	0.00	1	0.34	0	0.00	1	0.06
Hoplitis pilosifrons	6	1.46	1	0.34	4	0.44	11	0.69
Hoplitis producta	0	0.00	1	0.34	3	0.33	4	0.25
Hoplitis spoliata	0	0.00	0	0.00	1	0.11	1	0.06
Hylaeus affinis	0	0.00	3	1.03	9	1.00	12	0.75
Hylaeus mesillae	9	2.19	13	4.45	4	0.44	26	1.62
Lasioglossum admirandum	0	0.00	0	0.00	5	0.56	5	0.31
Lasioglossum albipenne	24	5.84	6	2.05	181	20.11	211	13.16
Lasioglossum cinctipes	1	0.24	2	0.68	1	0.11	4	0.25
Lasioglossum coriaceum	2	0.49	0	0.00	13	1.44	15	0.94
Lasioglossum 21	1	0.24	0	0.00	9	1.00	10	0.62
Lasioglossum 22	2	0.49	0	0.00	3	0.33	5	0.31
Lasioglossum 24	0	0.00	0	0.00	1	0.11	1	0.06
Lasioglossum imitatum	1	0.24	3	1.03	0	0.00	4	0.25
Lasioglossum laevisimum	2	0.49	5	1.71	4	0.44	11	0.69
Lasioglossum leucozonium	6	1.46	2	0.68	13	1.44	21	1.31
Lasioglossum lineatulum	1	0.24	2	0.68	0	0.00	3	0.19
Lasioglossum novascotiae	2	0.49	0	0.00	3	0.33	5	0.31
Lasioglossum paraforbesii	35	8.52	4	1.37	24	2.67	63	3.93
Lasioglossum pectorale	40	9.73	0	0.00	8	0.89	48	2.99
Lasioglossum perpunctatum	18	4.38	0	0.00	5	0.56	23	1.43
Lasioglossum pilosum	0	0.00	6	2.05	4	0.44	10	0.62
Lasioglossum semicaeruleum	0	0.00	0	0.00	5	0.56	5	0.31
Lasioglossum pruinosum	1	0.24	0	0.00	0	0.00	1	0.06
Lasioglossum sagax	6	1.46	3	1.03	17	1.89	26	1.62
Lasioglossum subversans	3	0.73	0	0.00	2	0.22	5	0.31
Lasioglossum succinipenne	18	4.38	47	16.10	95	10.56	160	9.98
Lasioglossum timothyi	0	0.00	1	0.34	0	0.00	1	0.06
Lasioglossum versans	0	0.00	1	0.34	3	0.33	4	0.25
Lasioglossum zonulum	46	11.19	19	6.51	153	17.00	218	13.60
Lasioglossum zephyrum	0	0.00	7	2.40	0	0.00	7	0.44
Megachile campanulae	0	0.00	1	0.34	0	0.00	1	0.06
Megachile centuncularis	0	0.00	0	0.00	1	0.11	1	0.06

Megachile inermis	0	0.00	19	6.51	3	0.33	22	1.37
Megachile latimanus	0	0.00	2	0.68	0	0.00	2	0.12
Megachile melanophaea	0	0.00	0	0.00	1	0.11	1	0.06
Megachile pugnata	0	0.00	0	0.00	1	0.11	1	0.06
Megachile relativa	0	0.00	1	0.34	1	0.11	2	0.12
Melissodes 1	0	0.00	26	8.90	0	0.00	26	1.62
Melissodes 2	0	0.00	6	2.05	0	0.00	6	0.37
Melissodes 3	0	0.00	1	0.34	0	0.00	1	0.06
Melissodes 5	0	0.00	7	2.40	0	0.00	7	0.44
Melissodes agilis	0	0.00	0	0.00	4	0.44	4	0.25
Osmia 1	1	0.24	0	0.00	0	0.00	1	0.06
Osmia 2	1	0.24	0	0.00	0	0.00	1	0.06
Osmia 8	3	0.73	0	0.00	0	0.00	3	0.19
Osmia distincta	4	0.97	0	0.00	1	0.11	5	0.31
Osmia integra	0	0.00	0	0.00	1	0.11	1	0.06
Osmia simillima	0	0.00	0	0.00	1	0.11	1	0.06
Osmia tersula	0	0.00	0	0.00	1	0.11	1	0.06
Perdita swenki	0	0.00	2	0.68	0	0.00	2	0.12

**Bee Species Total Abundance Sorted
by Abundance**

<i>Species</i>	<i>Total</i>
Lasioglossum zonulum	218
Lasioglossum albipenne	211
Bombus rufocinctus	170
Lasioglossum succinipenne	160
Lasioglossum paraforbesii	63
Bombus ternarius	57
Andrena carlini	53
Lasioglossum pectorale	48
Andrena barbilabrous	41
Bombus borealis	39
Halictus confusus	38
Halictus rubicundus	31
Augochlorella aurata	30
Hylaeus mesillae	26
Lasioglossum sagax	26
Melissodes 1	26
Lasioglossum perpunctatum	23
Agapostemon texanus	22
Megachile inermis	22
Lasioglossum leucozonium	21
Andrena 7	16
Anthophora terminalis	15
Lasioglossum coriaceum	15
Hylaeus affinis	12
Andrena quintilis	11

Andrena salictaria	11
Hoplitis pilosifrons	11
Lasioglossum laevisissimum	11
Lasioglossum 21	10
Lasioglossum pilosum	10
Bombus vagans	9
Andrena lupinorum	7
Lasioglossum zephyrum	7
Melissodes 5	7
Andrena nivalis	6
Bombus sandersoni	6
Melissodes 2	6
Lasioglossum admirandum	5
Lasioglossum 22	5
Lasioglossum novascotiae	5
Lasioglossum semicearuleum	5
Lasioglossum subversans	5
Osmia distincta	5
Andrena 9	4
Apis mellifera	4
Dufourea maura	4
Hoplitis producta	4
Lasioglossum cinctipes	4
Lasioglossum imitatum	4
Lasioglossum versans	4
Melissodes agilis	4
Andrena miserabilis	3
Colletes brevicornis	3
Lasioglossum lineatulum	3

Osmia 8	3
Andrena 12	2
Andrena regularis	2
Anthidium clypeodentatum	2
Bombus griseocollis	2
Bombus nevadensis	2
Megachile latimanus	2
Megachile relativa	2
Perdita swenki	2
Andrena 13	1
Andrena wheeleri	1
Bombus terricola	1
Heriades carinata	1
Hoplitis spoliata	1
Lasioglossum 24	1
Lasioglossum pruinosum	1
Lasioglossum timothyi	1
Megachile campanulae	1
Megachile centuncularis	1
Megachile melanophaea	1
Megachile pugnata	1
Melissodes 3	1
Osmia 1	1
Osmia 2	1
Osmia integra	1
Osmia simillima	1
Osmia tersula	1

Flowering stem abundances by site in each study round averaged by survey days

Species	Round 1 (June 2014)							Round 2 (August 2014)							Round 3 (June 2015)						
	Site #							Site #							Site #						
	1	2	3	4	5	6	7	1	2	3	4	5	6	7	1	2	3	4	5	6	7
<i>Achillea millefolium</i>	1.5	43.5	0	0	0	2	0	142.5	8	0	2.5	0	0	21	21	130.5	0	9	2.5	26.5	54.5
<i>Agoseris glauca</i>	0	0.5	0	0	0	0	0	1	0	0	0	0	0	0	5.5	0	0	0	0	0	0
<i>Allium stellatum</i>	0	0	0	0	0	0	0	32	256.5	0	17	0	0	44.5	0	0	0	0	0	0	0
<i>Allium textile</i>	30.5	39.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Amelanchier alnifolia</i>	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Androsace septentrionali</i>	134.5	12	0	0	0	462.5	0	0	0	0	0	0	0	0	1	0	0	0	0	77	0
<i>Anemone canadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0
<i>Anemone cylindrica</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.5	0	2	11.5	0	4
<i>Anemone multifida</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5	0	0	0	0	0	0
<i>Antennaria neglecta</i>	0	7.5	0	0	0	317.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Antennaria parvifolia</i>	0.5	118.5	0	0	0	476	0	0	0	0	0	0	0	0	13.5	536	0	18	381.5	1164	0
<i>Boechera stricta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0
<i>Arabis hirsuta</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	0
<i>Moehringia lateriflora</i>	0	1	0	6.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	7.5	0	0
<i>Astragalus agrestis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3.5	0.5	0	48	0	0	84
<i>Astragalus canadensis</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0
<i>Astragalus flexuosus</i>	0	0	0	0	0	0	0	0	0	0	0	0	0	0	39.5	0	0	0	0	0	0

Astragalus laxmannii	65.5	32	0	18.5	0	0	11.5	3.5	0.5	0	0	0	0	0	0	0	10.5	0	2	0.5	1	0.5	
Astragalus spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	54.5	0	0	12	0	0	0
Brassica rapa	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Brassica spp.	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0
Campanula rotundifolia	0	0	0	0	0	0	0	145.5	27	0	52	0	0.5	13	0	0	10	2	0	3	0	2.5	2
Cerastium arvense	67.5	310.5	0	19	0	1013	100	0	0	0	0	0	0	0	0	0	9	11	0	11	0	7.5	69
Cirsium arvense	0	0	0	0	0	0	0	0.5	0	20	0	1	0	101	0	0	0	0	0	0	0	0	0
Cirsium flodmanii	0	0	0	0	0	0	0	5	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0
Comandra umbellata	1.5	103	0	37.5	0	0	0	0	0	0	0	0	0	0	0	0	1.5	78.5	0	15	0	0	6.5
Cypripedium parviflorum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.5	
Dalea purpurea	0	0	0	0	0	0	0	20	751.5	0	195.5	0	0	0	0	0	0	0	0	0	0	0	0
Draba nemorosa	0	0	0	0	0	728	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Elaeagnus commutata	12.5	0	0	0	0	0	57.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	230	
Erigeron annuus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	1.5	0	3
Erigeron glabellus	48	29.5	0	4	0	7	0	0	0	0	0	0	0	0	0	0	0	74.5	0	8	24.5	18.5	160.5
Conyza canadensis	0	0	0	0	0	0	0	0	3.5	0	0	0	3.5	0	0	0	0	0	0	0	0	0	0
Erigeron glabellus	0	0	0	0	0	0	0	0.5	42.5	0	8	1.5	0	20	0	0	0	0	0	9	0	0	0
Erigeron philadelphicu	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	10	0	0	0	0
Erigeron spp.	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	6.5	0	0	0	0.5	0	0
Erysimum inconspicuum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.5	0	1.5	0	0	0	0

Fragaria virginiana	0	10	0	70	115	0	146	0	0	0	0	0	0	0	0	0	5	0	9.5	5.5	0	45	
Gaillardia aristata	0	0	0	0	0	0	0	3.5	0.5	0	9	0	0	0	0	0	1.5	5	0	66.5	0	0	0
Galium boreale	0	32	0	0	0	0	0	2	0	0	5	0	0	0	1	0	21	20	0.5	14.5	0	0	15.5
Oenothera suffrutescens	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Geum triflorum	351.5	488.5	0	6.5	0	5.5	6	0	0	0	0.5	0	0	0	0	0	78.5	164	0	11.5	0	0	1
Glycyrrhiza lepidota	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	
Helianthus pauciflorus	0	0	0	0	0	0	0	0	1031	0	2	0	0	0	0	0	0	0	0	0	0	0	
Heterotheca villosa	0	0	0	0	0	0	0	36.5	386.5	0	12	0	6.5	0	0	0	0	0	0	0	0	0	
Heucherea richardsonii	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	
Houstonia longifolia	0	14	0	1	0	1	2.5	0	0	0	1.5	0	0	0	0	0	18	96.5	0	1.5	7	61	6
Lathyrus venosus	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	2
Liatris ligulistylis	0	0	0	0	0	0	0	0	14	0	0	0	0	0	3	0	0	0	0	0	0	0	
Liatris punctata	0	0	0	0	0	0	0	56	50.5	0	32	0	0	0	0	0	0	0	0	0	0	0	
Linum lewisii	0	0.5	0	0.5	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	7	0	0	0
Lithospermum canescens	14	45.5	0	71.5	0	2.5	0	0	0	0	0	0	0	0	0	0	2.5	6.5	0	23	0	0	0
Lithospermum incisum	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	
Maianthemum canadense	0	0	0	0	0	0	29.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1.5	
Medicago lupulina	0	0	0	0	0	0	0	0.5	0	47.5	0	3545	0	2	0	0	34	19.5	17	0	5634	0	0
Medicago sativa	0	0	0	0	0	0	0	0	0	529	0	2.5	0	0.5	0	0	0	0	80.5	0	50.5	6.5	0
Melilotus alba	0	0	0	0	0	0	0	1	0	0.5	56	149	0	1.5	0	0	0	0	0	1	55.5	0	0

Melilotus officinalis	0	0	0	0	0	0	0	0.5	0	3	4	183.5	0	1	0	3	3.5	0	337.5	0	0
Monarda fistulosa	0	0	0	0	0	0	0	0	3	0	4	0	0	0	0	0	0	0	0	0	0
Orthocarpus luteus	0	0	0	0	0	0	0	0	246.5	0	0.5	0	0	0	0	0	0	0	0	0	0
Oxytropis campestris	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	22	2.5	0	3.5	0	0
Oxytropis spp.	0	0	0	5.5	0	0	0	0	0.5	0	0	0	0	0	0	0	0	0	0	0	0
Pedimelum esculentum	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0
Penstemon gracilis	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9	0	0	12.5	0
Polygala senega	0	0	0	6.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	60.5	96.5	0
Persicaria amphibia	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0	0	0	0
Potentilla anserina	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	19.5
Potentilla arguta	0	0	0	0	0	0	0	0	0	0	3.5	0	0	0	0	0.5	2	0	4.5	0	0
Potentilla bipinnatifida	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8.5	0.5	0	0	0	18
Potentilla gracilis	0	0	0	0	0	0	0	0	0	0	5.5	0	0	0	0	0	0	0	0	0	0
Potentilla hippiana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	0	0	0
Potentilla norvegica	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	0	0	1
Prunus spp.	0	38.5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.5	0	0	0	0
Ranunculus spp.	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Ribes spp.	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
Rosa spp.	0	0	0	0	0	0	0	0.5	0.5	0	0	0	0	0	0	0.5	0.5	0	0	0	2
Rudbeckia hirta	0	0	0	0	0	0	0	0	0	0	0	0	0	7.5	0	0	0	0	0.5	0	0

Packera cana	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	9.5	0	11.5	0	0	0
Sisyrinchium montanum	1	0	7.5	0	0	0	2	0	0	0	0	1	0	0	4	10.5	0	10	15	0.5	29
Smilacina stellata	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	
Solidago canadensis	0	0	0	0	0	0	0	0	0	2.5	0	0	0	0	0	0	0	0	0	0	
Solidago gigantea	0	0	0	0	0	0	0	0	0	5	0	0	0	0	0	0	0	0	0	0	
Solidago missouriensis	0	0	0	0	0	0	0	9	214.5	0	2	0	0	0	0	0	0	0	0	0	
Solidago rigida	0	0	0	0	0	0	0	0	0	0	0	0	0	115.5	0	0	0	0	0	0	
Solidago spp.	0	0	0	0	0	0	0	2.5	26	0	0	0	1.5	18.5	0	0	0	0	0	0	
Sonchus arvensis	0	0	0	0	0	0	0	0	0	0.5	0	0	0	89	0	0	0	0	0	0	
Stellaria longipes	0	0	0	1.5	0	0	0	0	0	0	0	0	0	0	0	0	0	2.5	0	41	
Symphyotrichum ericoides	0	0	0	0	0	0	0	239	507	0.5	17	7	4	293.5	0	0	0	0	0	0	
Symphyotrichum falcatum	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	
Symphyotrichum laeve	0	0	0	0	0	0	0	1	0.5	0.5	0	4.5	0	52.5	0	0	0	0	0	0	
Symphyotrichum	0	0	0	0	0	0	0	0	0	0	2.5	0	0	10	0	0	0	0	0	0	
Symphyotrichum spp.	0	0	0	0	0	0	0	0	0	1	0	0.5	0	4.5	41	0	0	0	5	3	
Symphoricarpos	0	0	0	0	0	0	0	161	0	0	64	0	0	200.5	0	0	0	0	0	0	
Taraxacum officinale	106.5	8.5	4464	0	2751	1.5	19.5	0	0	4.5	0	1.5	0	0.5	1	0	380	0	14.5	0	
Tragopogon spp.	0	0	0	0	0	0	0	0	0	0	0.5	0	0	2	0	0	0	0	0	0	
Trifolium hybridum	0	0	0	0	0	0	0	0	0	14	0	13.5	0	0	79	0	256.5	0	197.5	0	
Trifolium pratense	0	0	0	0	0	0	0	0	0	7	0	0	0	0	0	0	0	0	0	0	

Vicia americana	0.5	0	7.5	1	1	0	0	0	0	0	0	1	0	0.5	0.5	0	76.5	0.5	376.5	0	14
Viola spp.	1	10	0	4.5	0	0	32.5	0	0	0	0	0	0	0	0	0	0	3.5	0	0	0
Zizia aptera	0	0	0	0	0	0	16	0	0	0	0	0	0	0	0	0	0	0	0	0	120
Site Totals	836.5	1346	4479	254	2867	3017	432	864.5	3570	635.5	500.5	3912	16	1007	485	1205	829.5	371	7222	1402	915

Flowering species relative abundance by site and by round

<i>Species</i>	Round 1		Round 2		Round 3		Total	
	Round Total	Relative Abundance (%)	Round Total	Relative Abundance (%)	Round Total	Relative Abundance (%)	Total Abundance	Relative Abundance (%)
<i>Achillea millefolium</i>	47	0.36	174	1.66	244	1.96	465	1.29
<i>Agoseris glauca</i>	0.5	0.00	1	0.01	5.5	0.04	7	0.02
<i>Allium stellatum</i>	0	0.00	350	3.33	0	0.00	350	0.97
<i>Allium textile</i>	70	0.53	0	0.00	0	0.00	70	0.19
<i>Amelanchier alnifolia</i>	5	0.04	0	0.00	0	0.00	5	0.01
<i>Androsace septentrionalis</i>	609	4.60	0	0.00	78	0.63	687	1.90
<i>Anemone canadensis</i>	0	0.00	0	0.00	0.5	0.00	0.5	0.00
<i>Anemone cylindrica</i>	0	0.00	0	0.00	21	0.17	21	0.06
<i>Anemone multifida</i>	0	0.00	0	0.00	2.5	0.02	2.5	0.01
<i>Antennaria neglecta</i>	325	2.46	0	0.00	0	0.00	325	0.90
<i>Antennaria parvifolia</i>	595	4.50	0	0.00	2113	17.00	2708	7.49
<i>Boechera stricta</i>	0	0.00	0	0.00	0.5	0.00	0.5	0.00
<i>Arabis hirsuta</i>	0	0.00	0	0.00	3	0.02	3	0.01
<i>Moehringia lateriflora</i>	7.5	0.06	0	0.00	7.5	0.06	15	0.04
<i>Astragalus agrestis</i>	0	0.00	0	0.00	136	1.09	136	0.38
<i>Astragalus canadensis</i>	0	0.00	0	0.00	0.5	0.00	0.5	0.00
<i>Astragalus flexuosus</i>	0	0.00	0	0.00	39.5	0.32	39.5	0.11
<i>Astragalus laxmannii</i>	127.5	0.96	4	0.04	14.5	0.12	146	0.40
<i>Astragalus spp.</i>	0	0.00	0	0.00	66.5	0.54	66.5	0.18
<i>Brassica rapa</i>	0.5	0.00	0	0.00	0	0.00	0.5	0.00
<i>Brassica spp.</i>	0	0.00	0.5	0.00	0.5	0.00	1	0.00
<i>Campanula rotundifolia</i>	0	0.00	238	2.27	19.5	0.16	257.5	0.71
<i>Cerastium arvense</i>	1510	11.41	0	0.00	107.5	0.86	1617.5	4.47
<i>Cirsium arvense</i>	0	0.00	122.5	1.17	0	0.00	122.5	0.34
<i>Cirsium flodmanii</i>	0	0.00	5.5	0.05	0	0.00	5.5	0.02
<i>Comandra umbellata</i>	142	1.07	0	0.00	101.5	0.82	243.5	0.67
<i>Cypripedium parviflorum</i>	0	0.00	0	0.00	1.5	0.01	1.5	0.00
<i>Dalea purpurea</i>	0	0.00	967	9.21	0	0.00	967	2.67
<i>Draba nemorosa</i>	728	5.50	0	0.00	0	0.00	728	2.01

Elaeagnus commutata	70	0.53	0	0.00	230	1.85	300	0.83
Erigeron annuus	0	0.00	0	0.00	5	0.04	5	0.01
Erigeron glabellus	88.5	0.67	0	0.00	286	2.30	374.5	1.04
Conyza canadensis	0	0.00	7	0.07	0	0.00	7	0.02
Erigeron glabellus	0	0.00	72.5	0.69	9	0.07	81.5	0.23
Erigeron philadelphicus	0	0.00	0.5	0.00	10	0.08	10.5	0.03
Erigeron spp.	0	0.00	0.5	0.00	7	0.06	7.5	0.02
Erysimum inconspicuum	0	0.00	0	0.00	3	0.02	3	0.01
Fragaria virginiana	341	2.58	0	0.00	65	0.52	406	1.12
Gaillardia aristata	0	0.00	13	0.12	73	0.59	86	0.24
Galium boreale	32	0.24	8	0.08	71.5	0.58	111.5	0.31
Oenothera suffrutescens	0	0.00	0.5	0.00	0	0.00	0.5	0.00
Geum triflorum	858	6.48	0.5	0.00	255	2.05	1113.5	3.08
Glycyrrhiza lepidota	0	0.00	1	0.01	0	0.00	1	0.00
Helianthus pauciflorus	0	0.00	1032.5	9.83	0	0.00	1032.5	2.86
Heterotheca villosa	0	0.00	441.5	4.20	0	0.00	441.5	1.22
Heucherea richardsonii	0	0.00	0.5	0.00	0	0.00	0.5	0.00
Houstonia longifolia	18.5	0.14	1.5	0.01	190	1.53	210	0.58
Lathyrus venosus	0	0.00	0	0.00	2.5	0.02	2.5	0.01
Liatris ligulistylis	0	0.00	17	0.16	0	0.00	17	0.05
Liatris punctata	0	0.00	138.5	1.32	0	0.00	138.5	0.38
Linum lewisii	1	0.01	3	0.03	7	0.06	11	0.03
Lithospermum canescens	133.5	1.01	0	0.00	32	0.26	165.5	0.46
Lithospermum incisum	1	0.01	0	0.00	2	0.02	3	0.01
Maianthemum canadense	29.5	0.22	0	0.00	1.5	0.01	31	0.09
Medicago lupulina	0	0.00	3595	34.22	5704.5	45.90	9299.5	25.71
Medicago sativa	0	0.00	532	5.06	137.5	1.11	669.5	1.85
Melilotus alba	0	0.00	208	1.98	56.5	0.45	264.5	0.73
Melilotus officinalis	0	0.00	192	1.83	344	2.77	536	1.48
Monarda fistulosa	0	0.00	7	0.07	0	0.00	7	0.02
Orthocarpus luteus	0	0.00	247	2.35	0	0.00	247	0.68
Oxytropis campestris	0	0.00	0.5	0.00	28	0.23	28.5	0.08
Oxytropis spp.	5.5	0.04	0.5	0.00	0	0.00	6	0.02
Pediomelum esculentum	0	0.00	0	0.00	1	0.01	1	0.00
Penstemon gracilis	0	0.00	0	0.00	21.5	0.17	21.5	0.06

Polygala senega	6.5	0.05	0	0.00	157	1.26	163.5	0.45
Persicaria amphibia	0	0.00	0.5	0.00	0	0.00	0.5	0.00
Potentilla anserina	0	0.00	0	0.00	19.5	0.16	19.5	0.05
Potentilla arguta	0	0.00	3.5	0.03	7	0.06	10.5	0.03
Potentilla bipinnatifida	0	0.00	0	0.00	27	0.22	27	0.07
Potentilla gracilis	0	0.00	5.5	0.05	0	0.00	5.5	0.02
Potentilla hippiana	0	0.00	0	0.00	2	0.02	2	0.01
Potentilla norvegica	0	0.00	0	0.00	4	0.03	4	0.01
Prunus spp.	38.5	0.29	0	0.00	0.5	0.00	39	0.11
Ranunculus spp.	3	0.02	0	0.00	0	0.00	3	0.01
Ribes spp.	1	0.01	0	0.00	0	0.00	1	0.00
Rosa spp.	0	0.00	1	0.01	3	0.02	4	0.01
Rudbeckia hirta	0	0.00	7.5	0.07	0.5	0.00	8	0.02
Packera cana	0	0.00	0	0.00	21	0.17	21	0.06
Sisyrinchium montanum	10.5	0.08	1	0.01	69	0.56	80.5	0.22
Smilacina stellata	0	0.00	0	0.00	0	0.00	0	0.00
Solidago canadensis	0	0.00	2.5	0.02	0	0.00	2.5	0.01
Solidago gigantea	0	0.00	5	0.05	0	0.00	5	0.01
Solidago missouriensis	0	0.00	225.5	2.15	0	0.00	225.5	0.62
Solidago rigida	0	0.00	115.5	1.10	0	0.00	115.5	0.32
Solidago spp.	0	0.00	48.5	0.46	0	0.00	48.5	0.13
Sonchus arvensis uliginosis	0	0.00	89.5	0.85	0	0.00	89.5	0.25
Stellaria longipes	1.5	0.01	0	0.00	43.5	0.35	45	0.12
Symphyotrichum ericoides	0	0.00	1068	10.17	0	0.00	1068	2.95
Symphyotrichum falcatum	0	0.00	1	0.01	0	0.00	1	0.00
Symphyotrichum laeve	0	0.00	59	0.56	0	0.00	59	0.16
Symphyotrichum lanceolatum	0	0.00	12.5	0.12	0	0.00	12.5	0.03
Symphyotrichum spp.	0	0.00	6	0.06	49	0.39	55	0.15
Symphoricarpos occidentalis	0	0.00	425.5	4.05	0	0.00	425.5	1.18
Taraxacum officinale	7350.5	55.56	6.5	0.06	395.5	3.18	7752.5	21.44
Tragopogon spp.	0	0.00	2.5	0.02	0	0.00	2.5	0.01
Trifolium hybridum	0	0.00	27.5	0.26	533	4.29	560.5	1.55
Trifolium pratense	0	0.00	7	0.07	0	0.00	7	0.02

Vicia americana	10	0.08	1.5	0.01	468	3.77	479.5	1.33
Viola spp.	48	0.36	0	0.00	3.5	0.03	51.5	0.14
Zizia aptera	16	0.12	0	0.00	120	0.97	136	0.38

APPENDICES 4-9: FULL RESULTS TABLES

Appendix 4: Total bee abundance generalized linear mixed effects models results

Test	Round 1			Round 2			Round 3		
	Beta	SE	p	Beta	SE	p	Beta	SE	p
<i>Bee Habitat Model</i>									
litdepth	-0.074	0.040	0.061	-0.115	0.043	0.008	-0.039	0.027	0.144
woodycov	0.008	0.007	0.291	0.012	0.008	0.119	0.012	0.010	0.234
totalbloomindex	0.224	0.409	0.584	-1.107	0.484	0.022	0.412	0.371	0.267
spprich	-0.015	0.036	0.678	0.013	0.033	0.684	0.036	0.022	0.101
matrix1k	-0.041	0.016	0.012	-0.018	0.014	0.200	-0.019	0.014	0.174
round 1				0.486	0.364	0.182	0.127	0.333	0.703
round2	-0.486	0.364	0.182				-0.358	0.290	0.216
round3	-0.127	0.333	0.703	0.358	0.290	0.216			
litdepth:round1									
litdepth:round2	-0.041	0.055	0.451	0.041	0.055	0.451	-0.076	0.047	0.104
litdepth:round3	0.035	0.043	0.411	0.076	0.047	0.104	-0.035	0.043	0.411
woodycov:round1				-0.005	0.010	0.662	-0.004	0.012	0.736
woodycov:round2	0.005	0.010	0.662				0.001	0.012	0.962
woodycov:round3	0.004	0.012	0.736	-0.001	0.012	0.962			
totalbloomindex:round1				1.331	0.648	0.040	-0.188	0.553	0.734
totalbloomindex:round2	-1.331	0.648	0.040				-1.519	0.574	0.008
totalbloomindex:round3	0.188	0.553	0.734	1.519	0.574	0.008			
spprich:round1				-0.028	0.044	0.520	-0.051	0.037	0.168
spprich:round2	0.028	0.044	0.520				-0.023	0.037	0.538
spprich:round3	0.051	0.037	0.168	0.023	0.037	0.538			
matrix1k:round1				-0.023	0.012	0.052	-0.023	0.011	0.037
matrix1k:round2	0.023	0.012	0.052				0.000	0.008	0.973
matrix1k:round3	0.023	0.011	0.037	0.000	0.008	0.973			
<i>Introduced Vegetation Model</i>									
introforbcov	-0.009	0.009	0.326	0.036	0.014	0.009	0.010	0.006	0.089
intrograsscov	-0.003	0.006	0.602	-0.009	0.007	0.199	0.001	0.005	0.905
percnativeblooms	0.009	0.005	0.060	0.025	0.005	<0.001	0.002	0.003	0.555
introvegsite	0.024	0.008	0.003	0.048	0.013	<0.001	0.003	0.012	0.791
round1				2.736	0.733	<0.001	-1.531	0.635	0.016
round2	-2.736	0.733	<0.001				-4.267	0.727	<0.001
round3	1.531	0.635	0.016	4.267	0.727	<0.001			
introforbcov:round1				-0.045	0.016	0.006	-0.018	0.010	0.078
introforbcov:round2	0.045	0.016	0.006				0.027	0.015	0.073
introforbcov:round3	0.018	0.010	0.078	-0.027	0.015	0.073			
intrograsscov:round1				0.006	0.009	0.481	-0.003	0.007	0.640
intrograsscov:round2	-0.006	0.009	0.481				-0.010	0.009	0.265
intrograsscov:round3	0.003	0.007	0.640	0.010	0.009	0.265			
percnativeblooms:round1				-0.017	0.006	0.006	0.007	0.005	0.148
percnativeblooms:round2	0.017	0.006	0.006				0.024	0.005	<0.001
percnativeblooms:round3	-0.007	0.005	0.148	-0.024	0.005	<0.001			
introvegsite:round1				-0.024	0.013	0.068	0.021	0.011	0.050
introvegsite:round2	0.024	0.013	0.068				0.045	0.014	0.001
introvegsite:round3	-0.021	0.011	0.050	-0.045	0.014	0.001			

Edge Model

treedistkm	-2.084	0.925	0.024	0.214	0.832	0.797	0.315	0.556	0.571
roaddistkm	0.478	0.237	0.044	0.398	0.236	0.092	0.130	0.231	0.575
round1				0.535	0.224	0.017	-0.630	0.193	0.001
round2	-0.535	0.224	0.017				-1.165	0.197	<0.001
round3	0.630	0.193	0.001	1.165	0.197	<0.001			
treedistkm:round1				-2.297	1.181	0.052	-2.399	1.034	0.020
treedistkm:round2	2.298	1.181	0.052				-0.102	0.946	0.914
treedistkm:round3	2.399	1.034	0.020	0.102	0.946	0.914			
roaddistkm:round1				0.080	0.155	0.607	0.348	0.131	0.008
roaddistkm:round2	-0.080	0.155	0.607				0.268	0.150	0.075
roaddistkm:round3	-0.348	0.131	0.008	-0.268	0.150	0.075			

Appendix 5: Social bee abundance generalized linear mixed effects models results

Test	Round 1			Round 2			Round 3		
	Beta	SE	p	Beta	SE	p	Beta	SE	p
<i>Bee Habitat Model</i>									
litdepth	-0.006	0.058	0.912	-0.207	0.068	0.002	-0.035	0.037	0.344
woodycov	0.010	0.010	0.332	0.020	0.011	0.066	0.003	0.013	0.789
totalbloomindex	0.347	0.650	0.593	-2.202	0.842	0.009	-0.203	0.581	0.727
spprich	-0.048	0.055	0.390	-0.028	0.051	0.584	0.031	0.030	0.306
matrix1k	-0.055	0.019	0.003	-0.031	0.014	0.028	-0.027	0.012	0.022
round1				-0.559	0.542	0.303	-0.485	0.503	0.335
round2	0.559	0.542	0.303				0.073	0.402	0.855
round3	0.485	0.503	0.335	-0.073	0.402	0.855			
litdepth:round1				0.172	0.072	0.017	0.028	0.061	0.645
litdepth:round2	-0.201	0.084	0.018	0.201	0.084	0.018	-0.172	0.072	0.017
litdepth:round3	-0.028	0.061	0.645						
woodycov:round1				-0.010	0.015	0.514	0.007	0.016	0.682
woodycov:round2	0.010	0.015	0.514				0.016	0.016	0.316
woodycov:round3	-0.007	0.016	0.682	-0.016	0.016	0.316			
totalbloomindex:round1				2.550	1.076	0.018	0.550	0.866	0.525
totalbloomindex:round2	-2.550	1.076	0.018				-2.000	0.971	0.039
totalbloomindex:round3	-0.550	0.866	0.525	2.000	0.971	0.039			
spprich:round1				-0.020	0.069	0.776	-0.079	0.057	0.165
spprich:round2	0.020	0.069	0.776				-0.059	0.056	0.288
spprich:round3	0.079	0.057	0.165	0.059	0.056	0.288			
matrix1k:round1				-0.024	0.018	0.179	-0.028	0.016	0.090
matrix1k:round2	0.024	0.018	0.179				-0.003	0.011	0.763
matrix1k:round3	0.028	0.016	0.090	0.003	0.011	0.763			
<i>Introduced Vegetation Model</i>									
introforbcov	-0.001	0.015	0.969	0.048	0.024	0.040	0.003	0.009	0.721
intrograsscov	-0.002	0.009	0.787	-0.010	0.011	0.346	0.002	0.007	0.809
percnativeblooms	0.013	0.007	0.054	0.042	0.009	<0.001	0.001	0.004	0.835
introvegsite	0.002	0.012	0.853	0.052	0.020	0.010	-0.022	0.014	0.123
round1				4.349	1.258	0.001	-2.688	0.909	0.003
round2	-4.349	1.258	0.001				-7.037	1.216	<0.001
round3	2.688	0.909	0.003	7.037	1.216	<0.001			
introforbcov:round1				-0.049	0.028	0.081	-0.004	0.017	0.833
introforbcov:round2	0.049	0.028	0.081				0.045	0.025	0.070
introforbcov:round3	0.004	0.017	0.833	-0.045	0.025	0.070			
intrograsscov:round1				0.008	0.014	0.575	-0.004	0.012	0.714
intrograsscov:round2	-0.008	0.014	0.575				-0.012	0.013	0.358
intrograsscov:round3	0.004	0.012	0.714	0.012	0.013	0.358			
percnativeblooms:round1				-0.029	0.010	0.005	0.012	0.007	0.097
percnativeblooms:round2	0.029	0.010	0.005				0.041	0.009	<0.001
percnativeblooms:round3	-0.012	0.007	0.097	-0.041	0.009	<0.001			
introvegsite:round1				-0.049	0.022	0.022	0.025	0.016	0.125
introvegsite:round2	0.049	0.022	0.022				0.074	0.021	0.001
introvegsite:round3	-0.025	0.016	0.125	-0.074	0.021	0.001			

<i>Edge Model</i>									
treedistkm	0.488	1.349	0.718	-0.050	1.273	0.969	0.070	0.755	0.926
roaddistkm	0.921	0.290	0.002	1.047	0.292	<0.001	0.507	0.273	0.064
round1				0.179	0.343	0.601	-1.425	0.286	<0.001
round2	-0.179	0.343	0.601				-1.604	0.283	<0.001
round3	1.425	0.286	<0.001	1.604	0.283	<0.001			
treedistkm:round1				0.538	1.781	0.763	0.417	1.489	0.779
treedistkm:round2	-0.538	1.781	0.763				-0.120	1.412	0.932
treedistkm:round3	-0.417	1.489	0.779	0.120	1.413	0.932			
roaddistkm:round1				-0.126	0.218	0.564	0.414	0.183	0.024
roaddistkm:round2	0.126	0.218	0.564				0.540	0.200	0.007
roaddistkm:round3	-0.414	0.183	0.024	-0.540	0.200	0.007			

Appendix 6: Solitary bee abundance generalized linear mixed effects models results

Test	Round 1			Round 2			Round 3		
	Beta	SE	p	Beta	SE	p	Beta	SE	p
<i>Bee Habitat Model</i>									
litdepth	-0.115	0.053	0.031	-0.028	0.056	0.613	-0.080	0.038	0.035
woodycov	0.000	0.010	0.982	0.004	0.012	0.758	0.018	0.014	0.205
totalbloomindex	0.029	0.478	0.952	-0.372	0.581	0.522	0.835	0.422	0.048
spprich	-0.038	0.042	0.365	0.084	0.043	0.053	0.021	0.029	0.465
matrix1k	-0.048	0.019	0.012	-0.004	0.016	0.826	-0.005	0.015	0.731
round1				2.231	0.489	<0.001	1.017	0.398	0.011
round2	-2.231	0.489	<0.001				-1.214	0.431	0.005
round3	-1.017	0.398	0.011	1.214	0.431	0.005			
litdepth:round1				-0.087	0.070	0.219	-0.035	0.058	0.544
litdepth:round2	0.087	0.070	0.219				0.051	0.062	0.408
litdepth:round3	0.035	0.058	0.544	-0.051	0.062	0.408			
woodycov:round1				-0.003	0.015	0.818	-0.017	0.016	0.291
woodycov:round2	0.003	0.015	0.818				-0.014	0.017	0.423
woodycov:round3	0.017	0.016	0.291	0.014	0.017	0.423			
totalbloomindex:round1				0.401	0.769	0.602	-0.806	0.636	0.205
totalbloomindex:round2	-0.401	0.769	0.602				-1.207	0.678	0.075
totalbloomindex:round3	0.806	0.636	0.205	1.207	0.678	0.075			
spprich:round1				-0.122	0.054	0.026	-0.059	0.043	0.171
spprich:round2	0.122	0.054	0.026				0.062	0.049	0.206
spprich:round3	0.059	0.043	0.171	-0.062	0.049	0.206			
matrix1k:round1				-0.045	0.015	0.004	-0.043	0.014	0.002
matrix1k:round2	0.045	0.015	0.004				0.002	0.010	0.870
matrix1k:round3	0.043	0.014	0.002	-0.002	0.010	0.870			
<i>Introduced Vegetation Model</i>									
introforbcov	-0.014	0.011	0.209	0.037	0.017	0.028	0.020	0.006	0.001
intrograsscov	0.000	0.005	0.968	-0.012	0.009	0.184	-0.004	0.006	0.545
percnativeblooms	0.003	0.006	0.607	0.012	0.007	0.070	-0.001	0.003	0.844
introvegsite	0.048	0.011	<0.001	0.055	0.017	0.001	0.038	0.017	0.028
round1				1.747	0.880	0.047	-0.345	0.788	0.661
round2	-1.747	0.880	0.047				-2.093	0.874	0.017
round3	0.345	0.788	0.661	2.092	0.874	0.017			
introforbcov:round1				-0.051	0.020	0.011	-0.033	0.012	0.005
introforbcov:round2	0.051	0.020	0.011				0.017	0.018	0.327
introforbcov:round3	0.033	0.012	0.005	-0.018	0.018	0.327			
intrograsscov:round1				0.012	0.010	0.254	0.003	0.008	0.655
intrograsscov:round2	-0.012	0.010	0.254				-0.008	0.011	0.445
intrograsscov:round3	-0.003	0.008	0.655	0.008	0.011	0.445			
percnativeblooms:round1				-0.009	0.008	0.234	0.004	0.006	0.543
percnativeblooms:round2	0.009	0.008	0.234				0.013	0.007	0.057
percnativeblooms:round3	-0.004	0.006	0.543	-0.013	0.007	0.057			
introvegsite:round1				-0.006	0.015	0.669	0.010	0.012	0.401
introvegsite:round2	0.006	0.015	0.669				0.017	0.016	0.303
introvegsite:round3	-0.010	0.012	0.401	-0.017	0.016	0.303			

<i>Edge Model</i>									
treedistkm	-4.342	1.177	<0.001	0.153	1.044	0.883	0.860	0.704	0.221
roaddistkm	0.152	0.284	0.593	-0.323	0.305	0.291	-0.313	0.291	0.282
round1				0.757	0.265	0.004	0.074	0.224	0.739
round2	-0.757	0.265	0.004				-0.683	0.245	0.005
round3	-0.074	0.224	0.739	0.683	0.245	0.005			
treedistkm:round1				-4.495	1.501	0.003	-5.202	1.316	<0.001
treedistkm:round2	4.495	1.501	0.003				-0.707	1.180	0.549
treedistkm:round3	5.202	1.316	<0.001	0.707	1.180	0.549			
roaddistkm:round1				0.474	0.202	0.019	0.464	0.153	0.002
roaddistkm:round2	-0.474	0.202	0.019				-0.010	0.205	0.962
roaddistkm:round3	-0.464	0.153	0.002	0.010	0.205	0.962			

Appendix 7: Below-ground nesting bee abundance generalized linear mixed effects models results

Test	Round 1			Round 2			Round 3		
	Beta	SE	p	Beta	SE	p	Beta	SE	p
<i>Bee Habitat Model</i>									
litdepth	-0.090	0.044	0.039	-0.131	0.054	0.014	-0.061	0.029	0.039
woodycov	0.001	0.008	0.875	0.016	0.009	0.072	0.008	0.011	0.471
totalbloomindex	0.385	0.437	0.379	-0.460	0.582	0.430	0.441	0.391	0.260
spprich	-0.003	0.039	0.931	-0.008	0.040	0.833	0.044	0.024	0.064
matrix1k	-0.041	0.021	0.046	-0.036	0.019	0.064	-0.033	0.018	0.075
round1				0.388	0.399	0.330	-0.011	0.356	0.975
round2	-0.388	0.399	0.330				-0.399	0.324	0.217
round3	0.011	0.356	0.975	0.399	0.324	0.217			
litdepth:round1				0.041	0.065	0.526	-0.029	0.047	0.530
litdepth:round2	-0.041	0.065	0.526				-0.071	0.057	0.216
litdepth:round3	0.029	0.047	0.530	0.071	0.057	0.216			
woodycov:round1				-0.014	0.012	0.215	-0.007	0.013	0.616
woodycov:round2	0.014	0.012	0.215				0.008	0.013	0.560
woodycov:round3	0.007	0.013	0.616	-0.008	0.013	0.560			
totalbloomindex:round1				0.845	0.743	0.255	-0.056	0.587	0.924
totalbloomindex:round2	-0.845	0.743	0.255				-0.901	0.670	0.178
totalbloomindex:round3	0.056	0.587	0.924	0.901	0.670	0.178			
spprich:round1				0.005	0.051	0.920	-0.048	0.040	0.228
spprich:round2	-0.005	0.051	0.920				-0.053	0.044	0.227
spprich:round3	0.048	0.040	0.228	0.053	0.044	0.227			
matrix1k:round1				-0.006	0.014	0.667	-0.009	0.012	0.450
matrix1k:round2	0.006	0.014	0.667				-0.003	0.009	0.744
matrix1k:round3	0.009	0.012	0.450	0.003	0.009	0.744			
<i>Introduced Vegetation Model</i>									
introforbcov	-0.003	0.010	0.773	0.029	0.018	0.106	0.014	0.006	0.036
intrograsscov	-0.005	0.006	0.376	-0.016	0.009	0.057	0.001	0.006	0.906
percnativeblooms	0.011	0.005	0.041	0.022	0.006	0.001	-0.001	0.003	0.778
introvegsite	0.024	0.009	0.010	0.039	0.016	0.014	-0.013	0.014	0.328
round1				1.887	0.859	0.028	-2.367	0.726	0.001
round2	-1.886	0.860	0.028				-4.253	0.879	<0.001
round3	2.367	0.726	0.001	4.253	0.878	<0.001			
introforbcov:round1				-0.032	0.020	0.118	-0.016	0.012	0.159
introforbcov:round2	0.032	0.020	0.118				0.016	0.019	0.414
introforbcov:round3	0.016	0.012	0.159	-0.016	0.019	0.414			
intrograsscov:round1				0.011	0.011	0.294	-0.006	0.008	0.464
intrograsscov:round2	-0.011	0.011	0.294				-0.017	0.010	0.099
intrograsscov:round3	0.006	0.008	0.464	0.017	0.010	0.099			
percnativeblooms:round1				-0.011	0.007	0.115	0.012	0.006	0.036
percnativeblooms:round2	0.011	0.007	0.115				0.023	0.007	<0.001
percnativeblooms:round3	-0.012	0.006	0.036	-0.023	0.007	<0.001			
introvegsite:round1				-0.015	0.016	0.348	0.037	0.012	0.003
introvegsite:round2	0.015	0.016	0.348				0.052	0.016	0.002
introvegsite:round3	-0.037	0.012	0.003	-0.052	0.016	0.002			

<i>Edge Model</i>									
treedistkm	-2.363	0.962	0.014	-0.698	0.944	0.460	0.200	0.575	0.728
roaddistkm	0.557	0.253	0.028	0.491	0.255	0.054	0.246	0.248	0.321
round1									
round2	-0.620	0.241	0.010	0.620	0.241	0.010	-1.147	0.212	<0.001
round3	0.527	0.200	0.008	1.147	0.212	<0.001	-0.527	0.200	0.008
treedistkm:round1				-1.665	1.282	0.194	-2.563	1.071	0.017
treedistkm:round2	1.665	1.282	0.194				-0.898	1.048	0.392
treedistkm:round3	2.563	1.071	0.017	0.898	1.048	0.392			
roaddistkm:round1				0.066	0.160	0.679	0.311	0.131	0.017
roaddistkm:round2	-0.066	0.160	0.679				0.245	0.154	0.112
roaddistkm:round3	-0.311	0.131	0.017	-0.245	0.154	0.112			

Appendix 8: Above-ground nesting bee presence generalized linear mixed effects models results

Test	Round 1			Round 2			Round 3		
	Beta	SE	p	Beta	SE	p	Beta	SE	p
<i>Bee Habitat Model</i>									
litdepth	-0.191	0.313	0.542	-0.078	0.118	0.510	0.149	0.113	0.188
woodycov	0.038	0.036	0.290	0.042	0.028	0.133	0.016	0.039	0.685
totalbloomindex	-7.557	7.200	0.294	-2.634	1.791	0.141	-0.181	2.095	0.931
spprich	0.241	0.216	0.264	-0.144	0.108	0.184	0.095	0.096	0.322
matrix1k	-0.092	0.178	0.604	-0.009	0.027	0.740	0.010	0.027	0.705
round1				-3.160	2.330	0.175	0.514	2.367	0.828
round2	3.160	2.330	0.175				3.667	1.303	0.005
round3	-0.514	2.367	0.828	-3.667	1.303	0.005			
litdepth:round1				-0.114	0.326	0.728	-0.340	0.321	0.289
litdepth:round2	0.114	0.326	0.728				-0.227	0.152	0.135
litdepth:round3	0.340	0.321	0.289	0.227	0.152	0.135			
woodycov:round1				-0.003	0.044	0.938	0.022	0.052	0.666
woodycov:round2	0.003	0.044	0.938				0.026	0.046	0.571
woodycov:round3	-0.022	0.052	0.666	-0.026	0.046	0.571			
totalbloomindex:round1				-4.925	7.436	0.508	-7.380	7.486	0.324
totalbloomindex:round2	4.925	7.436	0.508				-2.463	2.628	0.349
totalbloomindex:round3	7.380	7.486	0.324	2.463	2.628	0.349			
spprich:round1				0.385	0.234	0.100	0.145	0.227	0.524
spprich:round2	-0.385	0.234	0.100				-0.239	0.138	0.084
spprich:round3	-0.145	0.227	0.524	0.239	0.138	0.084			
matrix1k:round1				-0.083	0.178	0.639	-0.103	0.178	0.563
matrix1k:round2	0.083	0.178	0.639				-0.019	0.028	0.502
matrix1k:round3	0.103	0.178	0.563	0.019	0.028	0.502			
<i>Introduced Vegetation Model</i>									
introforbcov	0.088	0.103	0.393	0.065	0.045	0.147	-0.019	0.029	0.509
intrograsscov	0.024	0.045	0.591	0.023	0.023	0.315	0.012	0.024	0.636
percnativeblooms	0.049	0.066	0.452	0.029	0.016	0.078	0.002	0.012	0.842
introvegsite	-0.069	0.063	0.270	0.031	0.036	0.389	0.006	0.036	0.866
round1				-1.163	7.019	0.868	-4.734	6.911	0.493
round2	1.163	7.019	0.868				-3.549	2.678	0.185
round3	4.734	6.911	0.493	3.549	2.678	0.185			
introforbcov:round1				0.023	0.113	0.841	0.107	0.106	0.313
introforbcov:round2	-0.023	0.113	0.841				0.084	0.054	0.117
introforbcov:round3	-0.107	0.106	0.313	-0.084	0.054	0.117			
intrograsscov:round1				0.001	0.050	0.988	0.012	0.051	0.805
intrograsscov:round2	-0.001	0.050	0.988				0.012	0.033	0.727
intrograsscov:round3	-0.012	0.051	0.805	-0.012	0.033	0.727			
percnativeblooms:round1				0.021	0.068	0.762	0.047	0.067	0.482
percnativeblooms:round2	-0.021	0.068	0.762				0.026	0.019	0.166
percnativeblooms:round3	-0.047	0.067	0.482	-0.026	0.019	0.166			
introvegsite:round1				-0.100	0.072	0.162	-0.075	0.071	0.289
introvegsite:round2	0.100	0.072	0.162				0.025	0.048	0.598
introvegsite:round3	0.075	0.071	0.289	-0.025	0.048	0.598			

<i>Edge Model</i>									
treedistkm	-8.913	6.879	0.195	-0.946	2.437	0.698	-3.405	2.507	0.174
roaddistkm	-1.483	1.211	0.221	0.350	0.535	0.513	-0.589	0.538	0.274
round1				-0.420	0.977	0.668			
round2	0.420	0.977	0.668				-0.379	0.687	0.581
round3	0.799	0.982	0.416	0.379	0.687	0.581	-0.799	0.982	0.416
treedistkm:round1				-7.965	7.230	0.271			
treedistkm:round2	7.967	7.230	0.270				2.459	3.380	0.467
treedistkm:round3	5.508	7.272	0.449	-2.459	3.381	0.467	-5.507	7.269	0.449
roaddistkm:round1				-1.833	1.246	0.141			
roaddistkm:round2	1.833	1.246	0.141				0.938	0.639	0.142
roaddistkm:round3	0.895	1.255	0.476	-0.938	0.639	0.142	-0.895	1.255	0.476

Appendix 9: Pollination services (seed set per flower per phytometer) linear mixed effects models results

Test	Round 1			Round 3		
	Beta	SE	p	Beta	SE	p
<i>Bees Model</i>						
totalpcfabund	0.055	0.039	0.186	-0.001	0.026	0.969
beespprich	0.027	0.074	0.720	0.068	0.060	0.271
sitebeeadj	-0.007	0.004	0.114	0.004	0.004	0.297
round	0.050	0.323	0.880	-0.050	0.323	0.880
totalpcfabund:round	-0.056	0.047	0.256	0.056	0.047	0.256
beespprich:round	0.041	0.095	0.671	-0.041	0.095	0.671
sitebeeadj:round	0.011	0.006	0.073	-0.011	0.006	0.073
<i>Bee Genera Model</i>						
bomabund	0.348	0.361	0.343	0.225	0.402	0.578
lasabund	0.075	0.151	0.622	0.217	0.126	0.090
round	2.844	1.427	0.055	-2.844	1.427	0.050
bomabund:round	-0.123	0.546	0.823	0.123	0.546	0.822
lasabund:round	0.141	0.182	0.444	-0.141	0.182	0.441
<i>Habitat Model</i>						
litter depth	0.054	0.046	0.241	-0.113	0.035	0.001
woody cover	-0.015	0.012	0.214	0.016	0.016	0.316
fivemflowerindex	0.849	0.786	0.28	-0.029	0.473	0.950
fivemrich	0.060	0.061	0.320	-0.013	0.057	0.817
matrix1km	-0.013	0.015	0.404	-0.017	0.008	0.031
round	1.944	0.568	0.000	-1.944	0.568	0.000
litdepth:round	-0.167	0.058	0.004	0.167	0.058	0.004
woodycov:round	0.031	0.020	0.123	-0.031	0.020	0.123
fivemflowerindex:round	-0.879	0.918	0.338	0.879	0.918	0.338
fivemrich:round	-0.074	0.084	0.379	0.074	0.084	0.379
matrix1km:round	-0.005	0.017	0.794	0.005	0.017	0.794
<i>Edge Model</i>						
treedistkm	-6.330	9.710	0.516	-16.155	5.953	0.008
roaddistkm	-0.078	0.814	0.924	1.098	1.025	0.287
round	4.144	1.721	0.018	-4.144	1.721	0.018
treedistkm:round	-9.824	11.389	0.390	9.824	11.389	0.390
roaddistkm:round	1.176	1.309	0.371	-1.176	1.309	0.371
<i>Introduced Vegetation Model</i>						
introforb	0.067	0.074	0.386	-0.034	0.070	0.631
intrograss	0.043	0.051	0.422	-0.004	0.061	0.950
perbloomnative	0.026	0.039	0.520	-0.011	0.019	0.544
introvegsite	-0.047	0.067	0.500	-0.056	0.069	0.420
round	9.179	5.192	0.109	-9.179	5.192	0.080
introforb:round	-0.101	0.102	0.345	0.101	0.102	0.322
intrograss:round	-0.047	0.079	0.571	0.047	0.079	0.558
perbloomnative:round	-0.038	0.044	0.407	0.038	0.044	0.388
introvegsite:round	-0.009	0.096	0.927	0.009	0.096	0.925