

Effects of environmental and disturbance gradients on native bee diversity, abundance and composition in Alberta's prairies

by

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Abstract

Native bees provide pollination services to a range of crops, supporting food production and the global economy. They also support the fitness of native flowering plants and terrestrial plant diversity. These functions are delivered by a diverse community of bees with a broad spectrum of life history traits. Recent evidence indicates that many native bee species are in decline as a result of the cumulative effects of multiple human-induced stressors, such as habitat loss, pesticide exposure, disease, and climate change. These declines have raised interest in the status and trends of bee communities over time, and in tools that support management of bee communities and the services they deliver. Here, I use a two-year inventory of native bees from a large geographic area of the Canadian Prairies to evaluate patterns in bee communities along ecological and disturbance gradients. First, I evaluate the effects of two land use types—canola fields and rangelands—on native bee abundance, richness, diversity, and composition, across three ecological regions. Secondly, I evaluate response of bee abundance, diversity, richness, evenness, and composition to the proportion of undisturbed grassland habitat and surrounding landscape heterogeneity at three spatial scales. Composition of bee communities was different between canola fields and rangelands, with several species of cavity-nesting bees strongly associated with rangelands. I found evidence for clear differences in bee abundance and composition across ecoregions. Abundance was highest in the southern Grassland ecoregion when compared with the Parkland and Boreal regions. The Grassland region had a different community composition when compared than the Parklands and Boreal—a pattern that is likely driven by differences in climate. Both the proportion of undisturbed grassland habitat and the heterogeneity of the landscape surrounding a site had positive impacts on bee richness and community evenness. Not all bees, however, responded consistently to these variables. Bumble

bees, which are often resource generalists, were more abundant in more heterogeneous landscapes, and less abundant in landscapes with higher amounts of grassland cover, while megachilid bees, a group of typically cavity-nesting bees, showed the opposite response. These results present clear evidence of linkages between environmental, disturbance, and landscape gradients and bee communities. Of note is the tendency for different groups of bees to differ in their response patterns based on nesting strategy. This survey is one of the first to sample the complete bee community and its response to landscape disturbance across a broad spatial area of the prairies.

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Chapter One: Introduction to pollination services and native bees of the Canadian Prairies

Review of ecosystem services

There is growing interest from the public and land managers in the importance of ecological goods and services for human well-being (Tschamntke et al. 2005; Balvanera et al. 2006; Kremen et al. 2007; Malinga et al. 2015). Ecosystem services describe the value of direct and indirect benefits that humans receive from land and biodiversity (Chan et al. 2006). Categorization and definition of these services are variable, and techniques for determining their value are incredibly diverse (Hein 2009; Breeze et al. 2016).

Pollination is an example of an ecosystem service that describes the value humans receive when pollinating organisms support floral reproduction (Matias et al. 2017). This value is often realized in agricultural systems, where pollinators contribute to the reproduction of pollination-dependent crops (Garibaldi et al. 2016). Positive impacts of pollination can range from essential, where production declines by over 90% in the absence of pollination, to low, where production declines by less than 10% in the absence of pollination (Klein et al. 2007). Estimates of the value of pollination services at the global level are over €150 billion per year (Gallai et al. 2009). Pollinators also contribute to the fitness of many native flowering plants (Ollerton et al. 2011; Beiswmeijer et al. 2006). One of the largest contributors to pollination services in the Canadian Prairies are native bees (Morandin and Winston 2005; Winfree et al. 2008).

Bee biology and monitoring

Native bee communities are incredibly diverse, with estimates of over 20,000 bee species globally (Michener 2007) and over 380 species from six families in the Canadian Prairies (Sheffield et al. 2014). Our understanding of how bee assemblages are changing over time in response to factors such as land use and habitat loss is a burgeoning area of study with many questions still unanswered (Sheffield et al. 2014). Bees are in the order Hymenoptera, which also contains wasps, hornets, and sawflies. The superfamily Apoidea contains all bees, as well as apoid wasps (Discover Life). Within the prairies, native bees fall in the following six families: Apidae, Andrenidae, Halictidae, Colletidae, Megachilidae, and Melittidae.

There is growing interest globally in monitoring and management strategies for native bees due to evidence of declines (Goulson et al. 2015; Koh et al. 2016; Geijzendorffer et al. 2016). Bee declines are driven by the combined effects of habitat loss (Winfrey et al. 2009), pesticide use (Goulson 2013), disease (Furst et al. 2014), and climate change (Potts et al. 2010; Cameron et al. 2011; Kerr et al. 2015). The interest in bee monitoring and management is driven primarily because of their value as pollinators, but also due to increased public awareness and conservation concern (Melathopoulos et al. 2015; Kleijn et al. 2016). Policy options that encourage land-stewardship are being explored, such as agri-environmental schemes. These programs often offer financial compensation for management actions that mitigate the negative effects of agriculture on biodiversity, including bees (Kleijn and Sutherland 2003; Donald and Evans 2006).

Monitoring strategies that capture both the diversity and abundance of native bees across entire landscapes are necessary to determine the extent and amount of declines, and implications for pollination services. Globally, we are limited to distribution data on bumble bees from Europe and North America, with little data on other bee species and regions (Goulson et al.

2015). Researchers have suggested standardized approaches for conducting bee surveys (Westphal et al. 2008; Lebuhn et al. 2013), though there are drawbacks to these programs (Tepedino et al. 2015). Without long term data, we will be unable to identify at-risk species or take appropriate response measures (Goulson et al. 2015).

Bees in the prairie landscape

The prairies are part of the Great Plains, which range from the central United States to southern Canada and are dominated by agricultural land uses (Schrag and Olim 2012). The prairies contain a broad diversity of ecoregions that are defined by differences in climate, vegetation, soils, and surficial geology (Downing and Pettapiece 2006). Previous studies have found differences in the composition and richness of bee communities along climatic and latitudinal gradients (Abrahamczyk et al. 2011; Mouga and Neto 2012), but how bee communities vary among ecoregions of Alberta's prairies remains unstudied.

The prairies support a mix of agricultural, industrial, and urban developments, resulting in a highly fragmented and patchy landscape. Within this system, two dominant forms of land use are cultivation to support crop production, and grazing to support livestock. Cultivation is expected to have negative impacts on bee communities through frequent soil disturbance and pesticide applications, reducing the amount of nesting and floral resources available for bees (Kennedy et al. 2013). However, cultivation of mass-flowering crops, such as canola, may have positive impacts on bee abundance by providing a pulse of abundant food (Westphal et al. 2003). Grazing may have negative impacts on bee communities through trampling of plants (Black et al. 2011) or reductions in availability and diversity of flowers (Vuillamy et al. 2006). Understanding how land use affects pollination services is critical, as crop pollination contributes to the fruit-set

of canola, one of the most widespread and abundant crops in the prairies, with over 20 million acres grown annually in Canada (Canola Council of Canada 2016). Evidence from northern Alberta suggests that canola yield can be increased by up to 30% when full pollination services are provided (Morandin and Winston 2005).

A combination of landscape and local management tools have been proposed to support responsible, evidence-based bee management in agricultural systems (Garibaldi et al. 2014). Evidence suggests that ecological traits such as body size (Steffan-Dewenter et al. 2002; Le Feon et al 2013), above- or below-ground nesting (Williams et al. 2010), and cavity- or ground-nesting (Diekotter et al. 2014) can be used as predictors of response to landscape management. Both the amount of undisturbed habitat (Kremen et al. 2002) and the heterogeneity (Senapathi et al. 2015) of habitat types in the landscape are important factors in supporting bee diversity and abundance. Undisturbed habitats provide nesting and floral reservoirs for bees and may be particularly important for supporting disturbance-sensitive species (Potts et al. 2005; Mallinger et al. 2016). Heterogeneous landscapes, with a more evenly distributed proportion of habitat types, may support more diverse communities (Steffan-Dewenter et al. 2002).

Research objectives and questions

Long term, large scale compositional studies are critical to understanding regional variation and developing customized management practices that are responsive to changes in bee communities over time. In the following two chapters, I evaluate the response of native bee communities to land use (canola and rangeland) across three ecoregions of Alberta's prairies. In Chapter 2, I test for differences in native bee richness, abundance, diversity, and composition between two land use types — canola fields and rangelands — across the Grasslands, Parklands,

and Boreal ecoregions of Alberta. In Chapter 3, I test for relationships between native bee richness, abundance, diversity, evenness, and composition and proportion grassland cover and landscape heterogeneity at three spatial scales.

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Chapter Two: Native bee communities in rangelands and croplands in three ecological regions of Alberta's prairies

Introduction

Changes in species diversity as a result of human activity can cause disruptions of critical ecosystem services, such as pollination (Chapin et al. 2000). This is particularly true in areas of intensive agriculture, where large amounts of land have been converted from natural ecosystems to cropland (Tscharntke et al. 2005). In these areas, native bees provide a valuable ecosystem service by pollinating flowering crops and in many cases contributing to crop yields (Kremen et al. 2002; Garibaldi et al. 2013). In addition to supporting agricultural production, native bees pollinate native plants and support terrestrial plant diversity and productivity (Beismeyer et al. 2006; Fontaine et al. 2006). Recent evidence suggests native bees are in decline due to the cumulative effects of multiple stressors, including habitat loss (Winfree et al. 2009), pesticide use (Goulson 2013), disease (Furst et al. 2014), and climate change (Potts et al. 2010; Cameron et al. 2011; Goulson et al. 2015). These declines have raised interest in monitoring and management strategies for native bees (Koh et al. 2016; Gejzendorffer et al. 2016). The lack of foundational information on native bee communities, including the distribution of different species and their response to disturbance, is a barrier to characterizing impacts to bees. Despite evidence of declines, populations of some bee species remain stable and common (Dupont et al. 2011), or are increasing over time (Bommarco et al. 2012). Documenting and understanding the details and potential drivers of this variability is critical for identifying which species may require conservation attention and for understanding the potential consequences of species loss on pollination services and plant diversity.

Bees live in most terrestrial ecosystems, and bee communities are most diverse in semi-arid habitats (Michener 1979). The prairies of North America host a variety of land uses including urban and industrial, but they are dominated by cropland and rangeland. These areas were historically covered by native grassland ecosystems, but conversion of grasslands to support human food production has resulted in less than 30% of native grassland habitats remaining in Canada (Gauthier and Wiken 2003). Croplands are highly modified to support efficient and cost-effective cultivation, which can be detrimental to bees, resulting in reduced bee richness and abundance caused by habitat loss (Kennedy et al. 2013). In most North American croplands, fields receive frequent soil disturbance, including seeding, tillage, pesticide application, and harvest practices. This frequent soil disturbance can reduce the amount of nesting habitat available, thereby restricting nesting to adjacent undisturbed areas (Vanbergen et al. 2013). In addition, loss of habitat can reduce the amount of available floral resources for bees, an important factor in regulating bee populations (Roulston and Goodell 2011). Mass-flowering crops, however, such as canola, may also provide food resources to some bee species during flowering (Westphal et al. 2003; Diekötter et al. 2014).

In contrast, rangelands, lands dedicated to livestock production, receive less direct soil disturbance than croplands but instead are impacted by grazing management practices and natural disturbance that may also have consequences for bees (Kruess and Tschardt 2002). Rangeland systems often provide a more continuous and diverse source of food for bees throughout a growing season relative to croplands (Mallinger et al. 2016), as well as a larger, more continuous area of potential nesting sites (Black et al. 2011). Many rangelands in North America remain dominated by native vegetation and are considered relatively pristine and intact in comparison with croplands.

The prairies of North America support a broad diversity of bee species, with current estimates of well over 380 species of bees living in the Canadian Prairies alone (Sheffield et al. 2014). There is also evidence that bees in this region have the potential to contribute to crop production and the agricultural economy (Kremen et al. 2002; Morandin and Winston 2005). Despite the importance of this region in supporting bee diversity, and the importance of bees in supporting crop production, our understanding of the current status of bee communities across this region is limited. In this study, I assessed: 1) differences in bee abundance, richness, diversity, and composition between cropland (canola fields) and rangelands (grazed by cattle), and 2) the extent to which these differences varied across three distinct ecological regions (Grasslands, Parklands, Boreal) found along a 650 km+ latitudinal gradient. The results set an important baseline in understanding patterns of response to spatial and disturbance gradients in native prairie bee communities.

Methods

Study area and site selection

Over the 2014 and 2015 growing seasons, I surveyed bee communities at 68 sites across an ecological gradient from dry grasslands to boreal forest in a temperate prairie region of North America, in Alberta, Canada. Sites were distributed across an area used for agricultural production, including cropland and rangeland systems (Figure 2.1). The maximum distance between sites was over 1000 km. As a result of this spatial range, sites fell in a variety of prairie ecotypes with differing climatic, vegetation, and soil characteristics (Downing and Pettapiece 2016). Southernmost sites occurred in a semi-arid Grassland region (hereafter Grasslands) with low precipitation and comparatively high annual temperatures, resulting in plant communities

that are dominated by grasses and forbs (Appendix I). Northernmost sites occurred in a Boreal region (hereafter Boreal) that receives less sunlight and has lower annual temperatures, but higher annual precipitation, which supports mature forests. A transitional aspen Parkland region (hereafter Parklands) connects these southern grasslands to northern forested areas. Mean temperatures in the summer months range annually from 17.5°C in the Grassland to 15.7°C in the Boreal, and mean annual precipitation ranges from 382 mm in the Grassland to 533 mm in the Boreal (Appendix I). The entire area is characterized by relatively fertile soils that resulted in extensive conversion of native ecosystems to cropland by European settlers in the early 19th century. Cropland, along with other forms of human land use, now dominate this landscape, with less than 30% of these prairie ecosystems free from disturbance (Gauthier and Wiken 2003).

Sites were distributed in 12 clusters across this range of prairie ecotypes and approximately half of the sites in each cluster were in cultivated canola fields ($n=29$ in 2014, $n=30$ in 2015) and half were in rangelands ($n=32$ in 2014, $n=30$ in 2015) which had never been previously cultivated. Cluster locations were chosen based on the presence of intact areas of rangeland; rangeland site locations in this study occurred primarily in protected areas, community pastures, or long-term research properties, all of which were grazed by cattle. Sites, within clusters, were placed a minimum of 3 km apart. Rangeland sites were re-sampled during the second year of field surveys, whereas new canola fields were surveyed in the second year, as canola is rarely grown in the same field for two consecutive years. These new canola fields were owned and managed by the same landowners and often adjacent to or in close proximity to canola fields sampled in 2014.

Bee sampling methods

Each year, I sampled the bee community twice at each site between mid-June to early August using two methods. First, I deployed yellow, blue, and white pan traps (3.25 oz, New Horizons Entomology Services) filled to $\frac{3}{4}$ full with soapy water every 3 m along three 36 m long transects. Bowls were originally white and were painted on the insides with either blue or yellow fluorescent Silica paint. White bowls were left unpainted. At rangeland sites, I established transects 100 m away from the road and spaced 150 m apart. All pan traps were placed directly on the ground in rangeland sites. In canola fields, I placed two transects in the field margins to survey bees living on crop edges—one along the road and one along an interior (i.e. between 2 crop edges, not along a road) crop edge. The two transects in the field margins were placed on the ground. I placed a third transect 10 m within the crop boundary using raised stakes so that pan traps were visible above the canola. Pan traps were deployed between 7:00-10:00 am at each site and were deployed for a minimum of 5 hrs, up to a maximum of 9 hrs. Specimens were collected at the end of each day and were pooled by bowl colour for each transects. Second, I conducted an hour of focal netting during each visit between 9:30AM-4:00PM. Netting was done by two people sampling for 30 min each at floral patches within a 50 m radius of the pan trap transects. Within canola fields, half the netting time was spent surveying bees on canola flowers, while the other half was spent surveying bees on non-crop flowers in the field margins. Honeybees (*Apis mellifera*) were identified and observationally counted in the field but were not systematically sampled while netting. Each day, three sites within a cluster were surveyed such that rangeland and canola were surveyed on the same day. Sampling was restricted to fair-weather days where the temperature was above 15 °C, wind was light, and vegetation was dry. In some cases, weather changed throughout the day, resulting in survey visits that did not meet

weather constraints. These sites were dropped from final analyses. Once captured, insect specimens were stored in 95% ethanol and placed in a refrigerator until processed.

I washed, dried, and pinned bees prior to identification. I identified bees to genus level using a combination of taxonomic keys (Mitchell 1962; Michener et al 1994; Packer et al. 2007; Sheffield et al. 2011; Dumesh and Sheffield 2012) and online taxonomic resources that are supported by identification experts (Discover Life (<http://www.discoverlife.org>), BugGuide (<http://bugguide.net/node/view/15740>)). When possible, I identified bees to either the species or morphospecies level, but some groups in the prairie region lack keys and were identified to genus level only (see Appendix II for full list, including level of taxonomic resolution). Voucher specimens are available in the Strickland Entomological Museum at the University of Alberta.

Statistical analyses

I conducted all statistical analyses in R (version x64 3.2.4) and evaluated each survey year separately due to different survey locations in the canola fields. I separated analyses based on survey method (netted vs. bowled), as different methods tend to target different types of bees (Popic et al. 2013). I estimated abundance, richness, and diversity (Simpson's diversity index) at each site. Richness was calculated using a combination of taxonomic resolutions—individuals identified at the genus, morphospecies, or species level were all included as independent taxonomic units within richness. The total number of taxonomic units at each site was summed to calculate richness. Simpson's diversity index was calculated using $1-D$, where $D = \sum p_i^2$ and p is the proportion that each species contributes to site abundance (Simpson 1949). Abundance variables were tested using generalized linear models (GLMs) with a negative binomial distribution and Wald's chi-square tests, whereas normally-distributed richness and diversity metrics were tested using GLMs with a normal distribution and Type III analysis of variance

(ANOVA) tests (Bolker et al. 2009). Differences across ecological region and land use type (canola vs. rangeland), including the interaction between these two variables, were included as explanatory variables. When explanatory variables were significant, I conducted post-hoc pairwise-comparisons using a Tukey test with a Bonferroni correction in the R package *multcomp* (Hothorn et al. 2016).

To examine differences in community composition across region and land use type, I used non-metric-multi-dimensional scaling (NMDS), a multivariate ordination method, using a Bray-Curtis distance estimation method with a 2 dimension solution specified in the *vegan* package (Oksanen et al. 2016). Bray-Curtis was selected as it is thought to provide the most meaningful and intuitive measure of community dissimilarity (McArdle and Anderson 2001). Forty singleton species (species with a single representative in the dataset) were removed from the ordination, as inclusion of rare species can impact ordination results (Cao et al. 2001). Separate permutational multivariate analyses of variance (perMANOVAs) were conducted for each year and survey method to test for differences in composition across regions and land uses. Because results were consistent across both survey methods, data for netted and bowled bees were pooled and evaluated together. Climate data for each site was extracted with the ClimateNA v5.10 software package, available at <http://tinyurl.com/ClimateNA>, based on methodology described by Wang et al. (2016). A suite of climate variables (eg. temperature, precipitation, and frost-free periods; Appendix VII) were overlaid on the ordination to identify important climatic factors driving differences in bee community composition across regions and land uses. Relationships between bee abundance, richness, and diversity with the four strongest environmental predictors of composition (i.e. the predictors with the strongest correlation (R^2) with the NMDS ordination) were tested using GLMs. These variables were latitude, mean annual

temperature, annual heat to moisture index, and degree days over 18°C. Finally, I used indicator species analysis to identify which species were associated with each region and land use type (De Caceres et al. 2009). Indicator species analysis identified individual taxa that are strongly associated with a particular grouping category based on both the fidelity (the proportion of a species overall abundance that is found in that category) and specificity (the proportion of study sites that contain that species) of the association between the species and the category.

Results

I collected a total of 19,142 native bee specimens that included 35 genera and six families over the two seasons of sample collection (Appendix II). I identified 170 unique taxa, of which the majority were identified to subgenus (three subgenera; 38% of individuals) or species (101 species; 35% of individuals), with the remaining individuals identified to genus. The most commonly identified taxon was *Lasioglossum (Dialictus)* spp. with 5,071 individuals over the two years (Appendix III). Singletons comprised less than 1% (40 individuals) of the total dataset. I observed two at-risk taxa: three individuals of *Bombus occidentalis occidentalis*, a threatened subspecies nationally (COSEWIC 2014), and 50 individuals of *Bombus terricola*, a species of special concern (COSEWIC 2015). *B. o. occidentalis* was observed only in rangeland sites in the Boreal in 2014, whereas *B. terricola* was found in similar abundances in both years and both land use types (5 in canola and 15 in range in 2014; 20 in canola and 20 in range in 2015). *Bombus terricola* was also identified as an indicator species for the combined grouping of rangelands in the Parkland and canola fields in the Boreal in 2014 ($R^2=0.763$, $p=0.002$), and for canola fields in the Boreal in 2015 ($R^2=0.915$, $p=0.001$). We observed 1833 honeybees (*Apis mellifera*) across the 2 seasons; honeybees were observed at every site (Appendix IV). In total,

10,772 bees were collected from canola sites, while 8,370 were collected from rangelands. More bees were collected during the second year of surveying, with 12,163 collected in 2015 compared to 6,979 collected in 2014. I also saw differences between the two survey methods. Across the study, 16,692 individuals encompassing 158 species were collected in pan traps, while 2,450 individuals encompassing 108 species were collected by netting. The composition of bees collected via these two survey methods also differed (Appendix V). Based on indicator species analysis, 26 different species were highly associated with pan traps, whereas only three species—*Bombus ternarius* ($R^2=0.605$, $p=0.001$), *Megachile inermis* ($R^2=0.527$, $p=0.003$), and *Megachile melanophaea* ($R^2=0.464$, $p=0.008$)—were strongly associated with netting (Appendix Vc).

There were patterns in both the abundance and richness of native bees across regions and land use types; however, there were no significant differences in diversity (Table 2.1). Patterns differed according to survey method and year. In both survey years, the number of bees caught in pan traps was highest in the Grasslands and lowest in the Boreal. Response of abundance to land use and ecoregion was inconsistent when results were separated by survey year and method (Figure 2.2). In 2014, more bees were caught in pan traps in rangelands than canola fields in the Grassland region (Figure 2.2A), whereas in 2015 abundance was higher in canola fields than in rangelands in the Parklands region (Figure 2.2C). In the Boreal, there was no difference in bee abundance between canola fields and rangelands. The abundance of bees caught in nets showed an opposite latitudinal trend to those in pan traps, with the highest abundance of netted bees in the northernmost region, the Boreal (Figures 2.2B & D). Across both years, netted bee abundance was higher in rangelands than in canola fields in the Parklands and Grasslands, but the trend was reversed in the Boreal, where canola fields had higher netted abundance. There

was a significant overall effect of region on both pan trap and netted abundance both years, but these patterns were also reversed for each sampling method (Table 2.1). In 2015, overall netted and pan trap abundance levels were higher in canola fields than in rangelands (193 ± 25 bees caught on average per site at canola fields compared to 126 ± 18 in rangelands using pan traps in 2015), whereas in 2014, pan trap abundance was marginally higher in rangelands (95 ± 19 bees caught on average in rangelands compared to 62 ± 12 in canola fields).

Overall patterns in species richness were similar to abundance but had fewer significant responses (Table 2.1; Figure 2.3). The average number of species caught at a site in the Grasslands was 16 ± 1 in 2014 and 22 ± 1 in 2015; in the Parklands, it was 16 ± 1 in 2014 and 21 ± 1 in 2015; and in the Boreal, it was 14 ± 1 in 2014 and 15 ± 2 in 2015. Across both years, the general trend was for richness to decrease from Grasslands to Parklands to Boreal. While these overall regional trends were not significant, there were significant differences among regions when both methods and land use types were considered (Table 2.1). In 2014, netted richness was highest in the Boreal region and lowest in the Grasslands (Figure 2.3B), with no overall difference in netted richness between land use types. However, in 2015, the effect of land use on netted richness differed across regions, with more bee species netted in canola fields in the Parklands and Boreal, whereas more species were netted in rangeland sites in the Grasslands (Figure 2.3D). This trend also existed in total bee richness (both methods combined) for 2015, and with marginal significance for 2014. Over both years, there were no differences in Simpson's diversity or the species richness of bees caught in pan traps across regions or land use types, with the exception of a marginally higher diversity in canola fields than rangelands in the 2015 pan trap surveys.

Across both years and methods, bee community composition was significantly different across regions and between land use types (Table 2.2). These results were visualized in NMDS ordinations with a 2-dimensional solution, which had a final stress value of 0.259 for the 2014 ordination, and 0.237 for the 2015 ordination (Figure 2.4). Pairwise comparisons of the different regions within years showed a different assemblage of bees within both rangeland and canola sites in the Grasslands region from all other combinations of region and land use across both years (Table 2.3). In addition, within the Grasslands region, composition was different between rangeland and canola sites for both years (Table 2.3). NMDS ordinations indicated that bee communities varied along both climatic and disturbance gradients (Figure 2.4). These climatic gradients were captured by a suite of environmental variables that were significantly correlated with the ordination (Appendix VII). Of these, the climatic predictors with the greatest R^2 value with bee community composition were latitude (2014: $R^2=0.684$, $p=0.001$; 2015: $R^2=0.787$, $p=0.001$) and degree days over 18°C (2014: $R^2=0.693$, $p=0.001$; 2015: $R^2=0.684$, $p=0.001$). These climate variables are correlated with ecoregion, such that latitude, temperature, and growing degree days decrease, whereas precipitation increases, from Grasslands to Parkland to Boreal (Downing and Pettapiece 2006). Climate was also correlated with overall abundance and richness (Appendix VIII). Bee abundance was higher in sites at lower latitudes (2014: $X^2_{1,59}=70.932$, $p<0.001$; 2015: $X^2_{1,58}=74.68$, $p<0.001$), with a higher heat-moisture index (2014: $X^2_{1,59}=76.75$, $p<0.001$; 2015: $X^2_{1,58}=75.992$, $p<0.001$), lower mean annual precipitation (2014: $X^2_{1,59}=72.293$, $p=0.022$; 2015: $X^2_{1,58}=72.679$, $p=0.022$), and more growing degree days in a year over 18°C (2014: $X^2_{1,59}=69.447$, $p<0.001$; 2015: $X^2_{1,58}=76.828$, $p<0.001$). In 11 of the climate models, bee response to climate factors interacted with land use. Across these 11 models, bee response to climate was stronger in rangelands while response in canola showed a weak or

neutral response (Appendix VIII). For example, bee richness in rangelands increased with annual heat-moisture index, whereas richness in canola showed no response (2014: $F_{1,57}=4.678$, $p=0.03$; 2015: $F_{1,56}=13.01$, $p<0.001$).

Indicator species analysis identified a number of species associated with either specific regions or land use types (Appendix VI). In 2014, I identified 22 indicator species for different combinations of region and land use; in 2015, this increased to 28 indicator species. Eleven species persisted as indicators across the two survey years. These 11 species were categorized as follows: *Agapostemon texanus* (2014: $R^2=0.907$, $p=0.001$, 2015: $R^2=0.944$, $p=0.001$) and *A. virescens* (2014: $R^2=0.789$, $p=0.002$, 2015: $R^2=0.866$, $p=0.001$) were consistently associated with the Grasslands region; *Andrena* spp. (2014: $R^2=0.912$, $p=0.016$, 2015: $R^2=0.975$, $p=0.001$) and *Lasioglossum (Sensu-stricto)* spp. (2014: $R^2=0.924$, $p=0.005$, 2015: $R^2=0.948$, $p=0.011$) were consistently associated with the combined grouping of the Grasslands and Parklands regions; *Bombus flavifrons* (2014: $R^2=0.634$, $p=0.021$, 2015: $R^2=0.96$, $p=0.001$), *B. vagans* (2014: $R^2=0.905$, $p=0.001$, 2015: $R^2=0.825$, $p=0.002$), *B. terricola* (2014: $R^2=0.763$, $p=0.002$, 2015: $R^2=0.915$, $p=0.001$) and *Megachile inermis* (2014: $R^2=0.644$, $p=0.019$, 2015: $R^2=0.762$, $p=0.005$) were consistently associated with the combination of the Parkland and Boreal regions; and *Bombus cryptarum* (2014: $R^2=0.886$, $p=0.001$, 2015: $R^2=0.932$, $p=0.001$) was consistently associated with the Boreal region. In addition, bees in the genera *Osmia* and *Hoplitis* were consistent indicators of rangeland habitat across regions and years (Appendix VI).

Discussion

Overall, I found differences in abundance, richness, and composition of native bee communities across three distinct ecological regions and between two land use types in Alberta.

Large-scale studies of bee communities across multiple disturbance regimes are important for documenting broad patterns and changes in bee abundance and diversity in response to land use. To my knowledge, this study is the first inventory of native bee communities across a broad geographic area of the western Canadian Prairies. These results are consistent with other studies showing differences in bee richness and community composition in response to geography and crop type (Carre et al. 2009), latitude (Mouga and Neto 2012), climate (Abrahamczyk et al. 2011), and cultivation (Le Feon et al. 2016). Patterns in bee abundance and richness also differed across survey methods and years, complicating the generalization of overall bee community response to environmental factors and disturbance.

Abundance differences between the two land uses varied across ecological regions. In 2014, I saw more bees in rangelands in the Grasslands and Boreal, and more bees in canola fields in the Parklands, whereas in 2015 I saw more bees in rangelands in the Boreal, and more bees in canola fields in the Grasslands and Parklands. These results suggest that response of bee abundance to cropland is variable across ecological regions. Variability in response across ecoregions may be driven by regional differences in bee community composition, by regional variation in cropping practices or disturbance history, by differences in the availability of non-canola flowers, or by a combination of these factors. Based on these findings, future assessments of impacts to native bees should incorporate potential variability in response across regions. The interaction of land use and region was different between years. In the Boreal, pan trap abundance was consistently (i.e. both survey years) higher in rangelands; in the Parklands, pan trap abundance was consistently higher in canola fields; but in the Grasslands, abundance was higher in rangelands in 2014, and in canola fields in 2015. Variability across the two survey years

suggests that climate may also play a role in patterns of response to land use—particularly in the Grasslands region.

Analysis of composition revealed not all bee species responded consistently to cropland habitat. Some studies have found that cultivation of canola on the landscape can result in an increase in abundance of generalist bee species (Westphal et al. 2003; Reidinger et al. 2015). However, other studies have shown that bee abundance declines with distance from natural habitat reservoirs (Bailey et al. 2014), suggesting that large, continuously cropped fields with no accessible natural habitat are likely detrimental to bee species. Response of bees to cropland can vary across species based on nesting preference (Kim et al. 2006). The strong effect of cropland on bee composition may be because above-ground nesters are more sensitive to overall loss of natural habitats than below-ground nesters (Williams et al. 2010; Forrest et al. 2015; Le Feon et al. 2016). Bee response to cropland may also depend on habitat heterogeneity before and after agricultural conversion; in some landscapes, disturbance can lead to a higher diversity of habitats and can provide more resources for bees and other pollinators (Rodriguez and Kouki 2017). In addition, common species and rare species likely do not respond in the same way to changes in habitat availability (Kleijn et al. 2006), and overall abundance and richness responses are likely dominated by response of common species. For *B. terricola*, a species of special concern, we found no strong association with one land use or the other; instead, this species was more common in the Parkland and Boreal than in the Grasslands. In general, areas of intense agriculture do not support rare bee species as readily as less intensively managed agricultural systems do (Basu et al. 2016). Given this potential, it is important to understand patterns not just in overall abundance and richness, but also in bee community composition and how different species are responding to these two land use types.

Variations in biological traits such as nesting have been linked to differing levels of bee sensitivity to agricultural intensification (Bartomeus et al. 2013; Rader et al. 2014). For example, solitary bees prefer natural habitats over mass-flowering crops (Rollin et al. 2013), and larger, more specialized solitary bees tend to be the first species lost from the bee community with increasing land use intensification (Rader et al. 2014). Differences in colony size, cycle length, and nesting location affect bumblebee response to habitat simplification (Persson et al. 2015). Of note in my results is the tendency for cavity-nesting bees, specifically *Osmia* and *Hoplitis*, to be highly associated with native rangelands. Cavity-nesting bees are above-ground nesters that not only require pre-existing cavities to build their nests in, but also often require soil and vegetative nesting materials to incorporate into their nests (Cane et al. 2007). Cavity-nesting bees have previously been identified as being potentially sensitive to habitat loss from agricultural conversion (Sheffield et al. 2013; Cusser et al. 2015) and can be important providers of ecosystem services (Sheffield et al. 2008). My results suggest that croplands are likely not providing sufficient nesting resources to support the same numbers of cavity-nesting bees as rangeland habitat and highlight that nesting biology is an important factor to consider when assessing bee response to cultivation (Williams et al. 2010).

In addition to differences in bee community composition between rangeland and canola, I also saw a different composition of bees in the southern ecoregion. In particular, two species of *Agapostemon* (Halictidae) were highly associated with the Grasslands region. These are fairly common and widespread ground-nesting sweat bees that exhibit a range of social nesting behaviours; the southern Grasslands in this study region represent the northern limit of their range (Abrams and Eickwort 1981). These two *Agapostemon* species represented 14% of total bee abundance in the Grasslands region in 2014, and 8% in 2015. The implications of regional

differences in abundance of individual species on pollination services remain unknown. I found that regional composition was highly correlated with temperature variables (number of degree days above 18°C, and the average temperature of the warmest and coldest months), suggesting that temperature plays a strong role in the distribution of different species across these regions. Overall bee abundance increased with higher annual heat-moisture index and degree days over 18°C, and decreased with latitude and mean annual precipitation, suggesting that climate factors are important in determining both the number and composition of bees present in a region. The amount of flight activity (and therefore foraging activity) that bees can undertake is limited by temperature, and different bee species have different lower thermal limits on their activity (Corbet et al. 1993). Temperature also plays an important role in the phenology of both bees and flowers, and the interplay of this relationship will be important to track as global climates warm (Bartomeus et al. 2011). Regional variation in both abundance and composition of bee communities should be considered in attempts to understand broad spatial patterns of bee communities and the pollination services they deliver.

Shifts in bee assemblages based on agricultural disturbance have not been consistent across studies. Nielsen et al. (2011) observed similar assemblages when comparing bee communities in cultivated areas with semi-natural systems in the Mediterranean. In contrast, there were marked differences in bee assemblages in disturbed areas compared to undisturbed, particularly concerning species dominance, in eastern Canada (Richards et al 2011). These inconsistencies are likely driven by a combination of differing agricultural practices, management history, and habitat availability in different study regions (Winfrey et al. 2009). Furthermore, bee abundance and bee diversity or richness do not always display the same response to variation in disturbance (Liow et al. 2001), with different factors driving patterns in

overall bee abundance compared to species diversity (Grundel et al. 2010). Bee communities may respond differently at the global or regional scale to land disturbance as a result of differences in bee community assemblages at these different scales. Addressing this variation is critical to understanding biological responses of bee communities, including how the status of bees and the services they deliver are changing over time. Inconsistent responses of bee abundance, richness, and community dynamics across studies and regions suggest that regional information is required and few generalizations can be applied at a broad global level.

While I found that total abundance of bees across both sampling methods was greater in the south and lower in the north, I found the opposite pattern when looking only at the netting data. I may have found a greater abundance of bees in the north using netting because netting is biased towards larger-bodied bees. Larger-bodied bees, especially several *Bombus* species, were associated with northern latitudes when pan trapping and netting were combined. Body size in bees can increase in northern, cooler latitudes for various taxa, including bumblebees (Scriven et al. 2016; Osorio-Canadas et al 2016). While some papers report that netting captures a greater abundance and richness of pollinator species (Popic et al. 2013), others have found that pan trapping captures a greater abundance of pollinators (Westphal et al. 2008). Despite abundance differences, I found no significant differences in diversity between methods. Differences in abundance, richness, and composition are common for these two methods (Popic et al. 2013). Previous studies have shown that certain groups, in particular halictid bees, are more susceptible to pan trapping (Wilson et al. 2008), whereas netting provides a more comprehensive assessment of overall species diversity (Roulston et al. 2007).

This study represents one of the first efforts to establish baseline information on all native bees in Alberta. There is growing interest in bee and pollinator monitoring programs (Goulson et

al. 2015; Koh et al. 2016; Geijzendorffer et al. 2016), including the need for standardized protocols (Lebuhn et al. 2013; Westphal et al. 2008). These results align with other studies demonstrating differences in the abundance, richness, and composition of bees captured depending on the type of survey method used. Given the differences in response across multiple studies, it is important to consider multiple methods of bee community sampling for future monitoring programs. Several studies recommend pan traps as the most effective method for pollinator surveys (Lebuhn et al. 2013; Westphal et al. 2008). While my results support this recommendation from the perspective of overall abundance and richness, they also indicate that different methods target different types of bees, and so the relative proportion of a community occupied by a given species will vary depending on the survey method employed. A combination of multiple methods may be most effective for capturing the full community of bee species. Historical or baseline data for this study region is lacking, and high inter-annual variability in bee communities is common (Russo et al. 2015), making it difficult to assess temporal trends without long term data sets. I recommend subsequent coordinated surveys across broad spatial scales using standardized protocols to begin to document how bees are changing over time.

My results show, for the first time in Alberta's prairies, effects of canola on species composition across regions, and regional differences in the abundance and composition of native bee communities. Climatic and geographic variables associated with these ecological regions are important factors affecting the distribution and abundance of bee species. Understanding the relative impacts of climatic factors and anthropogenic disturbances will be important in predicting future changes in bee communities as the climate warms and continued land use change occurs. Based on these findings, different species of bees can be expected to respond differently to change, and generalizations across taxa and regions should be made with caution.

Large-scale compositional studies of bee communities are essential for our understanding of the current status of native bees, and for long term monitoring of bee community trends over time.

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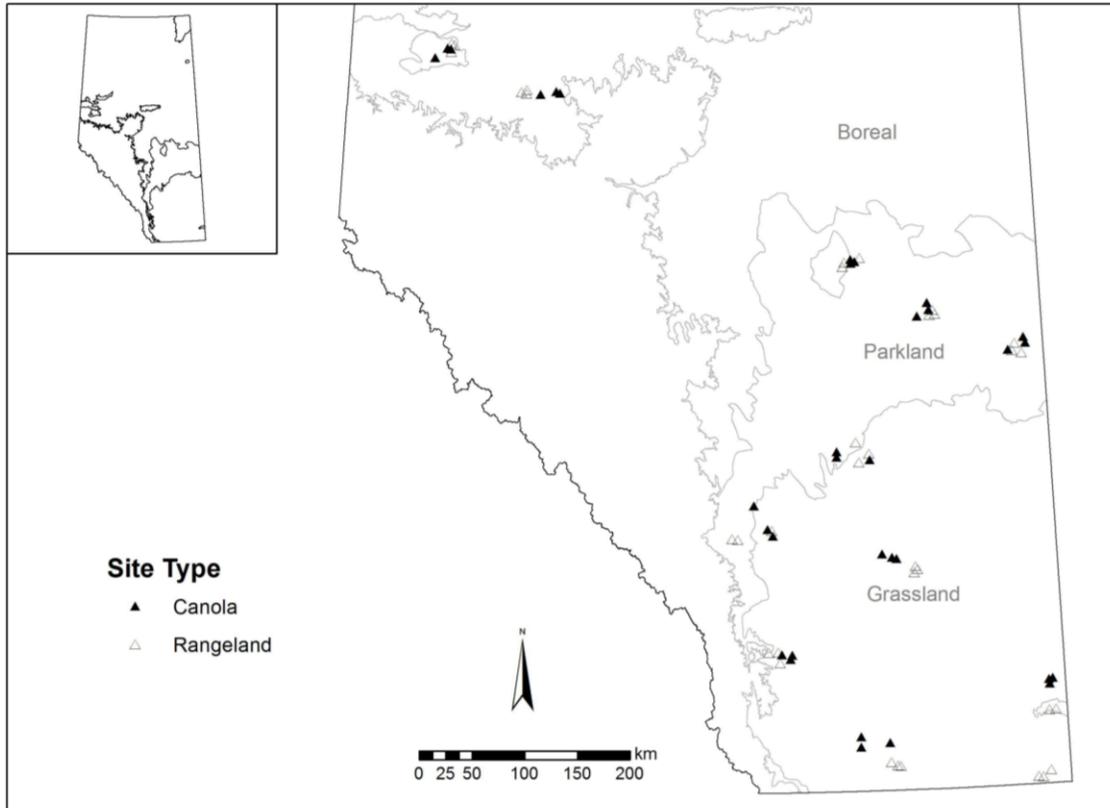


Figure 2. 1. Locations of study sites in the western prairies in Alberta, Canada. Sites occurred in either canola fields (filled in triangle) or native rangelands (open triangle). Sites were surveyed twice during the summers of 2014 and 2015 using pan traps and netting methods. Exact canola field locations varied slightly between the two seasons but were in the same general area and owned by the same landowners; only 2015 locations are shown here.

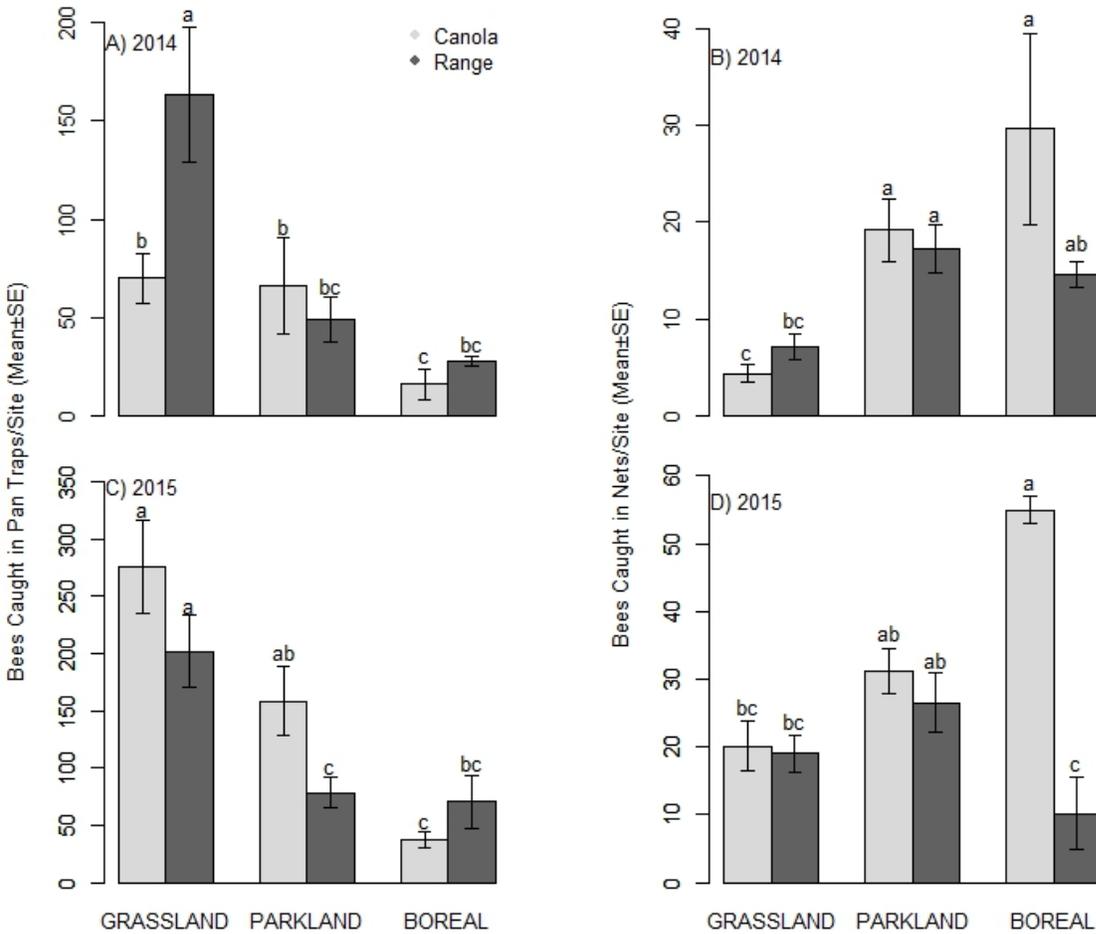


Figure 2. 2. Average bee abundance (\pm SE) per site over two years and two methods of data collection. Data are separated by year (figure rows) and trapping method (figure columns) as follows: A) 2014 abundance of bees caught in pan traps, B) 2014 abundance of bees caught by netting, C) 2015 abundance of bees caught in pan traps, and D) 2015 abundance of bees caught by netting. Abundance is compared across three ecological regions, arranged from the most southerly (Grasslands) to the most northerly (Boreal), and between two land use types—canola fields (light shading), and native rangelands (dark shading). Effects of region and land use were tested using generalized linear models; significant effects ($p < 0.05$) were followed up with pairwise Tukey comparisons which are represented by the lettering showing significant differences.

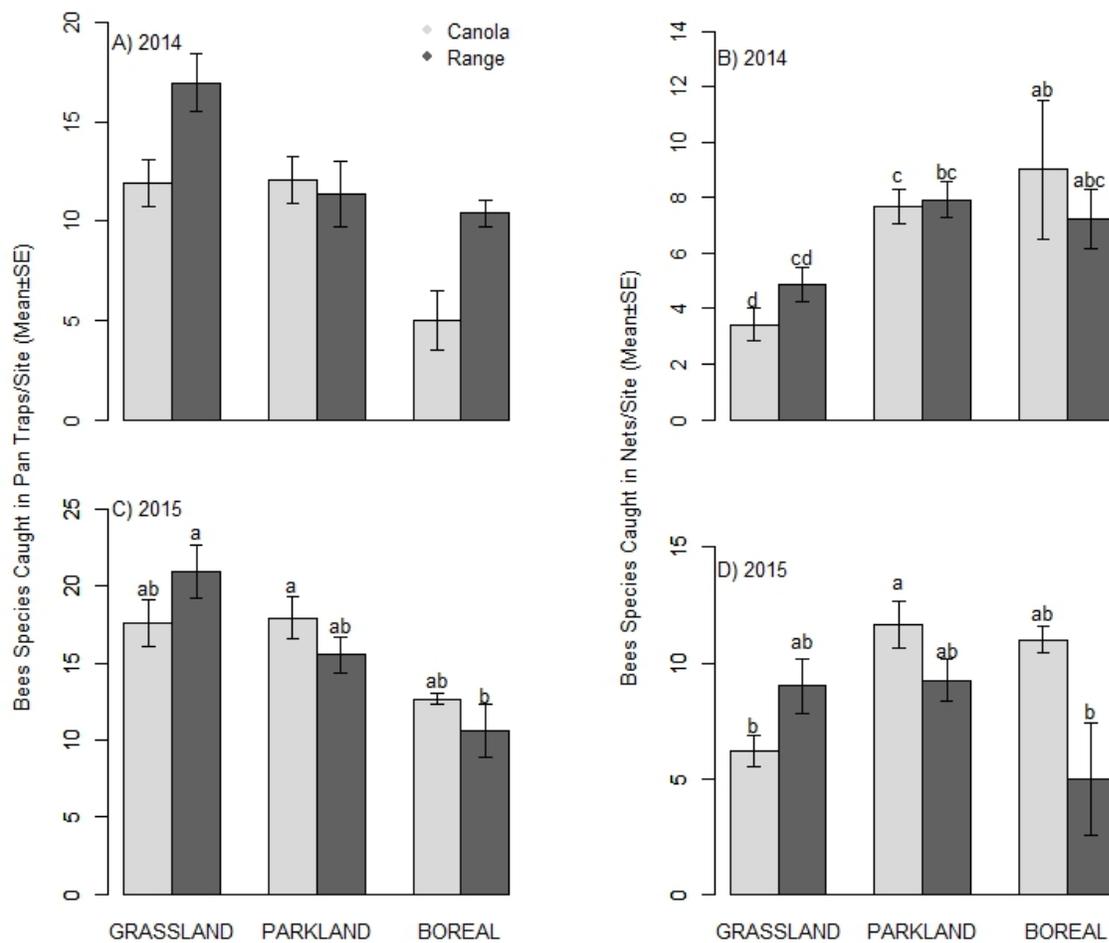


Figure 2. 3. Average bee richness (\pm SE) per site over two years and two methods of data collection. Data are separated by year (figure rows) and trapping method (figure columns) as follows: A) 2014 bee richness caught in pan traps, B) 2014 bee richness caught by netting, C) 2015 bee richness caught in pan traps, and D) 2015 bee richness caught by netting. Richness is compared across three ecological regions, arranged from the most southerly (Grasslands) to the most northerly (Boreal), and between two land use types—canola fields (light shading), and native rangelands (dark shading). Effects of region and land use were tested using generalized linear models; significant effects ($p < 0.05$) were followed up with pairwise Tukey comparisons which are represented by the lettering showing significant differences.

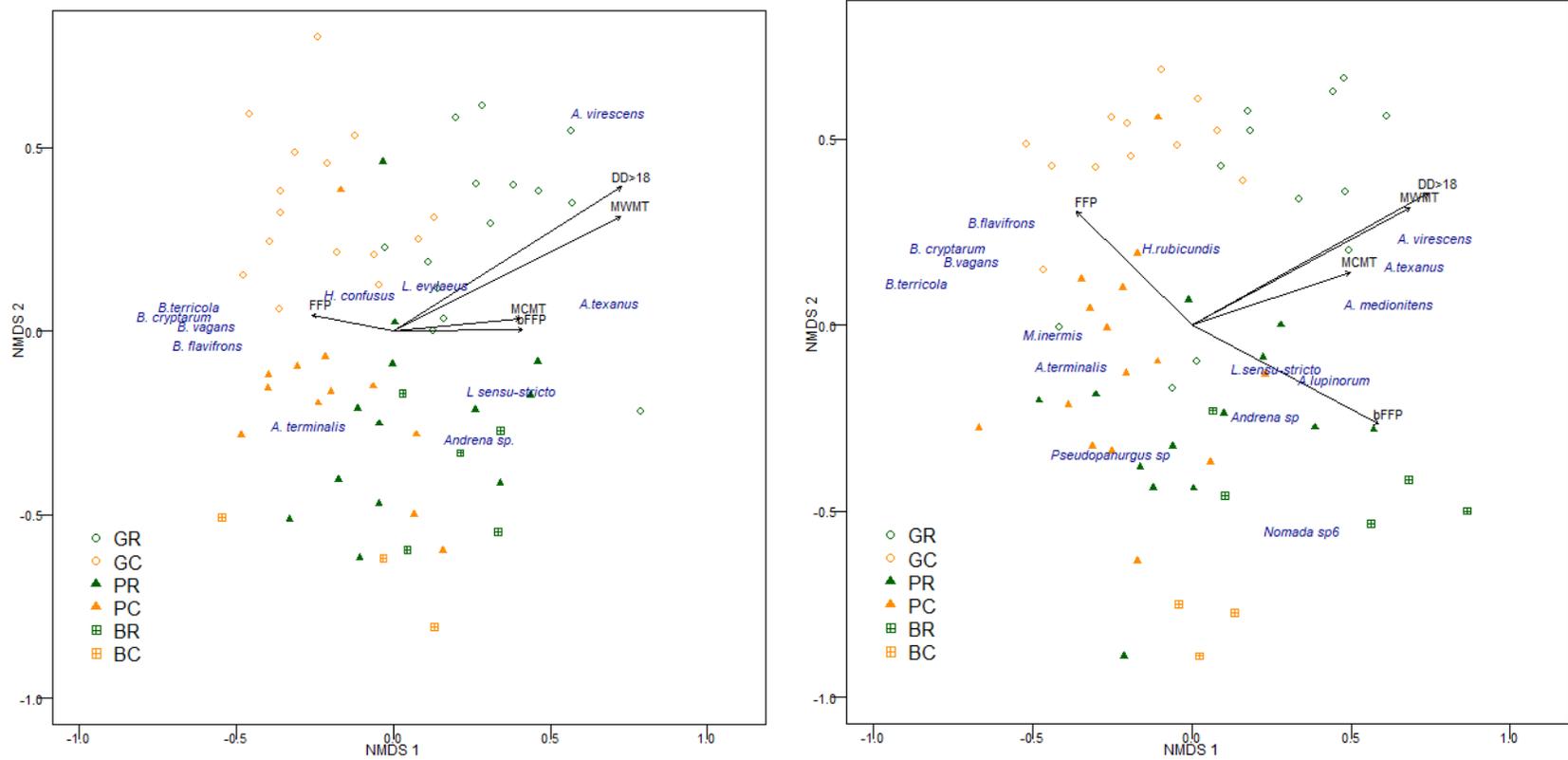


Figure 2. 4. Non-metric multidimensional scaling (NMDS) ordination of bee communities. Differences in community composition were assessed using Bray-Curtis distance estimation method across two survey years: A) 2014, and B) 2015. Differences were assessed across 3 ecoregions (Grassland, Parkland, Boreal) and two land uses (canola and rangelands), for a total of six region-land use combinations, as follows: GR=Grassland Rangeland, GC=Grassland Canola, PR=Parkland Rangeland, PC=Parkland Canola, BR=Boreal Range, BC=Boreal Canola. Plotted species are strongly associated ($p < 0.05$) with different regions based on species indicator analysis, and plotted environmental vectors are strongly correlated ($p < 0.05$) with the ordination based on regression with the NMDS ordination. These are: DD>18=degree days over 18°C, FFP=frost free period, MWMT=mean warmest month temperature, MCMT=mean coldest month temperature. These results represent a 2-dimensional solution, with final stress values of 0.259 for the 2014 ordination, and 0.237 for the 2015 ordination.

Table 2. 1. Results from generalized linear models testing effects of natural region, land use type, and their interaction on abundance, richness, and diversity of native bees. Abundance variables were tested using a negative binomial distribution and Wald’s chi-square tests, whereas richness and diversity followed a normal distribution and were tested with Type III analysis of variance (ANOVA). Total richness refers to the total number of taxonomic units caught via both trapping methods. Bolded *p*-values indicate significant ($p<0.05$) relationships, and italicized represent marginally significant ($p<0.10$) relationships.

Year	Variable	Natural Region			Land Use Type			Region x Use		
		<i>df</i>	X^2/F	<i>p</i>	<i>df</i>	X^2/F	<i>p</i>	<i>df</i>	X^2/F	<i>p</i>
2014	Pan Trap Abundance	2,58	28.25	<0.001	1,57	2.98	<i>0.08</i>	2,55	8.08	0.02
	Netting Abundance	2,58	63.52	<0.001	1,57	0.02	0.89	2,55	8.34	0.02
	Pan Trap Richness	2,55	2.84	<i>0.07</i>	1,55	2.35	0.13	2,55	2.69	<i>0.08</i>
	Netting Richness	2,55	13.61	<0.001	1,55	1.09	0.30	2,55	1.47	0.24
	Total Richness	2,55	1.44	0.25	1,55	0.53	0.47	2,55	1.94	0.15
	Pan Trap Diversity	2,55	1.41	0.25	1,55	1.25	0.27	2,55	0.92	0.41
	Netting Diversity	2,58	0.74	0.69	1,57	0.13	0.71	2,55	0.13	0.94
2015	Pan Trap Abundance	2,57	32.64	<0.001	1,56	5.73	0.02	2,54	6.32	0.04
	Netting Abundance	2,57	6.34	0.04	1,56	4.62	0.03	2,54	13.12	0.00
	Pan Trap Richness	2,54	1.43	0.25	1,54	0.32	0.57	2,54	2.30	0.11
	Netting Richness	2,54	8.02	0.00	1,54	5.15	0.03	2,54	5.67	0.01
	Total Richness	2,54	1.91	0.16	1,54	1.63	0.21	2,54	4.67	0.01
	Pan Trap Diversity	2,54	0.14	0.87	1,54	2.68	0.11	2,54	0.84	0.44
	Netting Diversity	2,57	0.52	0.77	1,56	0.01	0.92	2,54	0.81	0.67

Table 2. 2. Results of permutation multivariate analysis of variance (perMANOVA) comparing bee community composition between three natural regions and two land use types separated by year and method. Significant results ($p < 0.05$) are in bold; marginally significant results ($p > 0.10$) are italicized.

Year	Variable	Natural Region				Land Use Type				Region x Use			
		<i>df</i>	<i>F</i>	<i>R</i> ²	<i>p</i>	<i>df</i>	<i>F</i>	<i>R</i> ²	<i>p</i>	<i>df</i>	<i>F</i>	<i>R</i> ²	<i>p</i>
2014	2014 Pan Traps	2,61	4.327	0.122	0.001	1,56	3.502	0.049	0.002	2,61	1.401	0.039	<i>0.094</i>
	2014 Nets	2,56	2.273	0.035	0.001	1,56	1.211	0.038	0.009	2,56	1.211	0.038	0.208
	2014 Total	2,61	6.111	0.162	0.001	1,56	3.805	0.050	0.001	2,61	1.728	0.046	0.032
2015	2015 Pan Traps	2,59	6.478	0.177	0.001	1,59	3.453	0.047	0.004	1,59	1.396	0.038	0.120
	2015 Nets	2,57	4.974	0.141	0.001	1,57	4.346	0.062	0.001	2,57	2.164	0.061	0.003
	2015 Total	2,59	7.020	0.184	0.001	1,59	4.153	0.054	0.001	2,59	2.098	0.055	0.005

Table 2. 3. Post-hoc pairwise comparisons of total bee community composition (perMANOVA) differences in composition across three ecological regions and two land uses. The three regions tested were Grassland, Parkland, and Boreal, while the two land uses were canola fields and rangelands, resulting in six combinations of these two categories. Tests were conducted separately by survey year, with 2015 shown above the diagonal line (shaded), and 2014 shown below the diagonal line. Significant results ($p < 0.05$) are in bold.

	Grassland Range	Grassland Canola	Parkland Canola	Parkland Range	Boreal Canola	Boreal Range
2015						
Grassland Range	--	0.015	0.015	0.015	0.045	0.09
Grassland Canola	0.03	--	0.015	0.015	0.06	0.03
Parkland Canola	0.015	0.015	--	0.165	0.03	0.015
Parkland Range	0.03	0.015	0.735	--	0.09	0.885
Boreal Canola	0.06	0.045	0.12	0.48	--	0.345
Boreal Range	0.015	0.015	0.57	1	1	--
2014						

Chapter Three: Relationships between native bee communities and grassland cover and landscape heterogeneity in Alberta's prairies

Introduction

Native bees are important pollinators of crops worldwide (Klein et al. 2007; Gallai et al. 2009) and are beneficial, and often essential, to the fitness of most flowering plants in natural ecosystems (Fontaine et al. 2006; Ollerton et al. 2011). There is growing evidence for declines in native bee species, driven by a combination of factors including loss of habitat (Winfree et al. 2009), disease (Furst et al. 2014), pesticide use (Goulson 2013), and climate change (Potts et al. 2010; Cameron et al. 2011; Kerr et al. 2015). These declines can disrupt pollination services, particularly in areas that support intensive agricultural production where vast areas of habitat have been lost and/or fragmented (Klein et al. 2007). Understanding the linkages between bee assemblages and landscape elements such as the amount of undisturbed habitat and landscape heterogeneity is critical to ensuring long-term viability of bee populations.

Bees respond to habitat features across a range of spatial scales (Kennedy et al. 2013), with patterns of response differing with biological traits of bees, such as nesting strategy (Hopfenmuller et al. 2014), or dispersal ability (Kormann et al. 2015). For example: abundance and richness of smaller, solitary bees responded positively to the amount of undisturbed habitat at smaller spatial scales than larger, social bees, likely as a result of differences in their foraging ranges (Steffan-Dewenter et al. 2002); abundance of above-ground nesters was more sensitive to habitat isolation than below-ground nesters (Williams et al. 2010); and diversity of cavity-nesting bees at the landscape scale was driven primarily by the amount of undisturbed habitat such as field margins, tree and shrub patches, and forest edges (Diekotter et al. 2014). Response of bee assemblages to landscape change is regionally variable, based on local differences in the

degree of sensitivity of different species and the nature of landscape change (De Palma et al. 2016). Prairie bee communities are diverse, containing hundreds of species that encompass a spectrum of life history traits (Sheffield et al. 2014). These diverse communities inhabit highly modified landscapes that support agricultural, urban, and industrial developments. As different types of bees have unique responses to different elements of landscape structure, such as landscape heterogeneity or amount of a particular habitat (Williams et al. 2010; Hopfenmuller et al. 2014), the responses of individual bee species to habitat change is predicted to vary according to their life history traits.

The availability of undisturbed habitat (i.e. areas that have not been paved and do not receive regular tillage or soil disturbance) is often a critical landscape factor for maintaining bee abundance and richness in agriculturally productive areas (Kremen et al. 2002; Klein et al. 2012). These areas of undisturbed habitats are predicted to become increasingly important as reservoirs for off-setting the negative impacts of climate change on native bees (Papanikolaou et al. 2017). Undisturbed habitats can exist in multiple configurations or amounts, for example as large, contiguous reserves, or as small patches or edges surrounding cropped lands. These areas may have diverse vegetation types, including native grasses, forbs, shrubs, and trees, many of which play a role for supporting diverse bee communities (Soderstrom et al. 2001). Grasslands are important undisturbed habitats for native bees in the prairies, but are also increasingly rare (Hammermeister et al. 2001; Gauthier and Wiken 2003). Grasslands support bee communities through the provision of nesting habitat (Black et al. 2011), and floral resources throughout the growing season (Mallinger et al. 2016; Grover et al. 2017). The availability of floral resources from grasslands changes phenologically, and so too does their value for bees and other pollinators (Cole et al. 2017). There is evidence that large grasslands are important reservoirs for

bee communities, acting as population sources that sustain the abundance and richness of bee communities in nearby disturbed landscapes (Ockinger and Smith 2007). Within highly disturbed landscapes, smaller habitat pockets are also important, as provision of pollination services declines with distance from patches of undisturbed habitat (Bailey et al. 2014).

The proportions of different habitat types in a given area, or landscape heterogeneity, is an important factor for understanding how bee communities are structured and how they respond to landscape change (Rundlof et al. 2008; Senapathi et al. 2015). Heterogeneity can be generated by having a mix of several different undisturbed habitat types (eg. grassland types, forests, shrublands), a mix of several disturbance types (eg. industrial, cropped, and residential), or a combination of both disturbed and undisturbed areas. In some situations, disturbance may increase habitat heterogeneity up to a certain point, but as disturbance becomes dominant in a given area, it will cause landscape heterogeneity to decline (Plotnick and Gardner 2002; Vanbergen et al. 2005). In this way, increased heterogeneity could be predicted to have either positive impacts (eg. diverse types of native vegetation at small scales), or negative impacts (eg. multiple widespread disturbance types at larger scales) on bee communities depending on the landscape context.

Landscape heterogeneity varies with spatial scale (Frazier 2015), with a trend towards increased heterogeneity, and therefore increased diversity of landscape features at larger scales. Increasing habitat diversity at both local and landscape scales, primarily of undisturbed habitats, has been found to increase bee diversity (Senapathi et al. 2015), likely through the provision of a greater diversity of nesting and floral resources, creating more available niche space (Holzshuh et al 2007; Mallinger et al. 2016). In highly homogeneous but undisturbed landscapes, disturbance may increase landscape heterogeneity, resulting in positive impacts to some aspects

of the bee community. For example, Roberts et al. (2017) found positive effects of harvesting in forested areas on bee abundance and diversity as a result of greater diversity of forest age classes and flowering plants. Many studies have found an interaction in the response of bees to local and landscape factors where the negative effects of habitat loss become stronger in landscapes dominated by disturbance (Weibull and Ostman 2003; Winfree et al. 2009; Senapathi et al. 2017). In addition, recent evidence suggests that positive effects of increasing landscape complexity interact with broader farming management practices such as insecticide and fertilizer use (Carrie et al. 2017). Overall, relationships between bees and landscape structure varies across regions based on local bee community assemblages (De Palma et al. 2016). Few studies have explored relationships between landscape structure and native bee communities across broad spectrums of both ecological and disturbance gradients in the Canadian prairies.

Historically, native grasslands dominated the prairies; however, only 30% of these habitats remain (Gauthier and Wiken 2003). Human impacts from agricultural, industrial, and residential development have resulted in a highly modified landscape with a mix of intensely modified areas such as monocultural croplands and managed grasslands. Using data on bee communities collected from three different prairie ecoregions, I sought to address the following questions: 1) How does overall bee diversity, richness, evenness, and abundance respond to varying proportions of grassland habitat and landscape heterogeneity across three spatial scales? And 2) how do three selected bee groups with different nesting strategies (*Bombus*, *Lasioglossum*, and Megachilidae) respond to these variables across different spatial scales? I hypothesized that bee richness, abundance, and diversity would increase with higher amounts of grassland cover as a result of greater availability of nesting and floral resources. Landscape heterogeneity could be expected to have either positive or negative impacts on bee abundance,

richness, and diversity depending on the relative contributions of disturbed vs. undisturbed habitats to higher heterogeneity.

Methods

Study region

The study region encompassed an ecological gradient from dry grasslands to boreal forest in a temperate prairie region of North America, in Alberta, Canada. This region supports an active agricultural industry, including both cultivated and rangeland systems and accounts for a large and diverse area of land in the Great Plains ecoregion (Figure 3.1). Study sites fell in three different ecotypes, with different climatic characteristics: a warm, dry Grassland region, a transitional aspen Parkland region, and a forested Boreal region with higher precipitation and comparatively lower temperatures (Downing and Pettapiece 2006; Appendix I). Mean annual precipitation for all regions ranges from 382 mm in the Grasslands to 533 mm in the Boreal, summer month temperatures range annually from an average 17.5°C in the Grassland to 15.7°C in the Boreal. The Boreal is generally colder and wetter, supporting mature forests; whereas the hotter, drier Grasslands are dominated by grasses and forbs. The Parkland is a transitional zone containing a mix of aspen forests, shrublands, and grasses. Extensive settlement and conversion of native ecosystems to cultivation by European settlers has occurred in the region since the early 19th century. The landscape forms a patchwork of various human land uses and habitat types, including cropland, grassland, forest patches, and areas of residential or industrial development. Cultivation, along with other forms of human land use, often dominate this landscape.

Study sites

I visited 68 sites over the 2014 and 2015 growing seasons to inventory the native bee community. I surveyed cultivated canola fields (2014, $n = 29$; 2015, $n = 30$) and rangelands used for cattle grazing (2014, $n = 32$; 2015, $n = 30$) across the prairie region in Alberta, Canada. Sites were placed a minimum of 3 km apart in a series of 12 clusters, which were selected based largely on the presence of intact grassland areas. I re-sampled rangeland sites during the second survey year, but visited new canola fields in 2015 as canola is rarely grown in the same field for two consecutive years. These new canola fields were owned and managed by the same landowners and were often adjacent to or nearby the first-year canola fields.

Bee sampling methods

I sampled the bee communities using both pan traps and focal netting. Pan traps were painted with fluorescent Silica paint to be either blue or yellow, or were left unpainted to be white. At each site, I deployed yellow, blue, and white pan traps (3.25 oz, © New Horizons Entomology Services) which were $\frac{3}{4}$ filled with soapy water every 3 m along three 36 m long transects. The placement of these three transects was slightly varied between canola vs rangeland sites. At canola sites, I placed two transects in the field edges—one along the road and one along an interior (i.e. non road) crop edge. These field edge transects were both placed on the ground. To ensure traps were visible above the crop, I then placed a third transect on raised stakes 10 m inside the growing canola. At rangeland sites, I located pan trap transects 100 m away from the road and spaced 150 m apart on the ground. Each day, pan traps were placed at a site between 7:00-10:00 am and were left out for a minimum of 5 hrs. Secondly, two people each completed 30 min of focal netting each visit between 9:30AM-4:00PM. Netting took place by meandering through nearby floral patches, with half the effort in canola fields placed on netting within the

crop, and half placed on non-crop flowers in the field margins. When honeybees (*Apis mellifera*) were present in the field, they were identified and observationally tracked during survey but were not targeted during netting. These methods were repeated twice at each site between mid-June to early August each survey year. Three sites within a cluster, often a mix of range and canola, were surveyed each day. I restricted sampling to days that were above 15°C, wind was light, and vegetation was dry. On certain days, weather changed partway through sampling such that these weather restrictions were not met. In these cases, sites that did not meet weather constraints were removed from the analyses. Once captured, insect specimens were stored in 95% ethanol and placed in a refrigerator until processing.

I identified all bees to genera using taxonomic keys (Mitchell 1962; Michener et al 1994; Packer et al. 2007; Sheffield et al. 2011; Dumesh and Sheffield 2012) and online, expert-based taxonomic resources (Discover Life (<http://www.discoverlife.org/>), BugGuide (<http://bugguide.net/node/view/15740>)). When possible, I identified bees to either the species or morphospecies level, but some groups were identified only to the genus level. Voucher specimens can be found at the Strickland Entomological Museum at the University of Alberta.

I selected three ecologically different bee taxa in order to evaluate differences in response, two at genus level and one at family level: *Bombus*, *Lasioglossum*, and Megachilidae. *Bombus* represents a commonly studied and well-understood genus of large bodied, primarily social ground-nesters. *Lasioglossum* species are solitary to eusocial, small to medium-bodied ground-nesters. Megachilidae is a family composed mainly of medium to large-bodied cavity-nesters. Sheffield et al. (2014) estimated that the prairies contain approximately 60 species of *Lasioglossum*, 80 of Megachilidae, and 30 of *Bombus*. Members of all three of these groups were

abundant and widespread across the study region, making it possible to draw inferences on variation in bee abundance for these groups across a broad spatial scale.

Land cover data

I extracted spatial information on the surrounding land cover characteristics for each site from the provincial land cover inventory produced by the Alberta Biodiversity Monitoring Institute (ABMI; www.abmi.ca). In this inventory, the ABMI assigns polygons to 9 different land cover categories based on 30 m resolution Landsat satellite images (ABMI 2010). Land cover types were categorized by ABMI based on specific criteria (ABMI 2010). Grassland habitat included areas dominated primarily by native grasses and other herbaceous plants with greater than 20% vegetation cover and less than 10% tree cover; cropped land included annually cultivated crops, tame pasture and forage crops. The forest category included coniferous, broadleaf and mixed forest types with at least 10% crown closure; the shrub category contained at least 30% shrubs; and developed land included urban, residential, industrial, and transportation features (Appendix IX). I defined a “site centre” point location at the start of the middle pan trap transect. In the canola fields, the transect that was within the crop boundary was the middle transect. Around each site centre, I created circular buffers at the 2 km, 1 km, and 500 m radius scale. Within these buffers, I calculated the percentage of area occupied by each land cover category. To pool land cover types that occurred in small proportions, specifically different forest types that occurred at less than 5% in each region, I merged the 9 original categories into 7 land cover categories within each buffer. Final land cover categories included: forest, shrubland, cropped land, grassland, developed land, bare ground, and open water (Appendix IX).

Sites covered a wide range of land cover types. Land cover variables ranged from dominant or common habitats, such as cover of cropland or grassland habitat, to less common cover types such as shrubland or open water (Appendix X). Grassland cover ranged from 0-95% cover at the 2 km scale, 0-96% at the 1 km scale, and 0-99% at the 500 m scale.

Landscape heterogeneity was calculated by applying Pielou's equation for evenness (described in statistical analyses) to the matrix of land cover variables at each spatial scale. With this approach, I characterized landscape heterogeneity as ranging from low (sites dominated by a single cover type) to high (sites with a more evenly balanced proportion of multiple cover types). To conduct indicator species analyses, I converted both grassland cover and landscape heterogeneity into categorical variables by assigning sites to categories based on arbitrary breaks in these variables. These arbitrary breaks for categorical grassland cover were as follows: None (0% grassland cover; n=5), Low, (0-30% cover; n=32), Medium (30-60% cover; n=17), and High (60-100% cover; n=7). For categorical landscape heterogeneity, sites were ranked based by landscape heterogeneity (calculated by applying evenness equation to the matrix of land cover variables) and divided in half as low (n=30) vs high (n=31) heterogeneity.

Statistical analyses

I conducted all statistical analyses in R (version x64 3.2.4). I analyzed years separately due to differing site locations in the canola fields, and differing climate and vegetation traits across the two years. At each site, I calculated Simpson's diversity, and Pielou's species evenness of the bee community. I also calculated species richness for each site. Richness included a combination of taxonomic resolutions—individuals identified to species, morphospecies, or genus were all included as independent taxonomic units. Richness was calculated by summing all the independent taxonomic units for each site. Simpson's diversity

was calculated as $1-D$, where $D = \sum p_i^2$, where p is the proportion of each species abundance for each site (Simpson 1949). Evenness was calculated as $J = H/\ln(S)$, where H is Shannon Weiner diversity index, and S is the total number of species at a site (McCune and Grace 2002). As an exploratory step to evaluate the impact of different land cover variables, I conducted model selection using the *stepAIC* function in the R package MASS to determine how different land cover variables influence bee abundance, richness, and diversity (Venables and Ripley 2002). I conducted this model selection at each of the three spatial scales (2 km buffer, 1 km buffer, and 500 m buffer), separated by year and land use type around each site. Bare ground was excluded from the model selection process as it covered less than 1% of the area around any given site. I constructed final models using the parameters from *stepAIC* and analyzed selected parameters using Type III Analysis of Variance (ANOVA) Wald's F tests.

To determine the effects of grassland cover on bees at different spatial scales, I ran linear mixed effect models on total bee abundance, richness, evenness and diversity at each spatial scale (500 m, 1 km, 2 km). I conducted linear mixed effects modelling using the *lmer* function in the R package *nlme* (Pinheiro et al. 2017). Separate models were built for different years and spatial scales due to collinearity among scales. I included land use type (canola or rangeland) as a fixed factor and ecoregion as a random factor. Model significance was tested using Type III ANOVA Wald's F-tests. To investigate differing responses across taxa, I performed the same set of tests for abundance of the selected groups of interest (*Bombus*, *Lasioglossum*, and Megachilidae). Within-taxon richness and diversity were not tested for these specific groups as a result of differing levels of taxonomic resolution in bee identification. All abundance data was log transformed prior to performing analyses. The same set of analyses were then completed on

the entire bee community as well as the targeted bee groups using landscape heterogeneity as the explanatory variable.

To test for differences in bee community composition across grassland cover and landscape heterogeneity categories, I used permutational multivariate analysis of variance (perMANOVA), with a Bray Curtis distance estimation method (Oksanen et al. 2016). Bray-Curtis was selected as it is generally recognized as providing the most meaningful and intuitive estimate of dissimilarity in community structure (McArdle and Anderson 2001). Land use type was included as a fixed factor in the perMANOVAs and permutations were constrained by ecoregion. Differences in grassland cover were followed up with pairwise comparisons using Bonferroni correction. I conducted indicator species analyses (De Caceres et al. 2009) for each year to identify particular species highly associated with these grassland cover categories.

Results

I collected a total of 19,142 native bee specimens that included 35 genera and 6 families over the two seasons of sample collection (Appendix II). Of these, 7,402 were within the genus *Lasioglossum* (across nine unique taxonomic units), 1,762 within the genus *Bombus* (across 24 taxonomic units), and 800 within the family Megachilidae (across 45 taxonomic units). The minimum value for all land cover variables was near 0%, with maximums ranging from dominant covers of grassland and crop cover (upper ranges in the 90-100%), to less common covers like water and developed cover which were never found above 30% cover (Appendix X). Average percentage grassland cover at the 2 km scale was 41 ± 6 in the Grassland, 25 ± 6 in the Parkland, and 14 ± 7 in the Boreal, while landscape heterogeneity at the same scale was 0.41 ± 0.04 in the Grassland, 0.46 ± 0.03 in the Parkland, and 0.57 ± 0.03 in the Boreal.

Based on exploratory model selection, parameters included in the final models examining effects of land cover on bees varied across response variables, land use types, years, and spatial scales. Water cover was the least commonly selected parameter, appearing in 9 of the 36 models, and crop cover was the most common, appearing in 22 of the 36 models. There were no consistent patterns in terms of either the final variables selected across years, land use type, and scale, or in the significant variables (Appendix XI). While no consistent pattern was identified via model selection, visual inspection of significant variables revealed clear signals in bee response to grassland cover.

The proportion of grassland cover was associated with a greater abundance, richness, and diversity of bee species in different combinations of year and spatial scale (Table 3.1). Patterns of grassland cover on richness differed between years: in 2015, bee richness had a positive relationship with grassland cover at all three spatial scales (Figure 3.2), while in 2014 it had a marginally significant positive effect only at the 1 km scale (Table 3.1). Bee diversity was slightly higher with higher amounts of grassland cover in 2015 at the 500 m scale, and bee abundance increased marginally with grassland cover at the 2 km scale in 2014. While there were no significant effects of land use type on any of these variables in 2014, there were differences across all spatial scales and bee variables in 2015 (Table 3.1). Bee richness and abundance were all higher in canola fields than in rangelands that year (Table 3.1); The average abundance of bees caught in canola fields was 210 ± 26 , whereas in rangelands it was 143 ± 18 ; the average bee richness in canola fields was 21 ± 1 , while in rangelands it was 20 ± 1 . Species evenness did not vary with grassland cover or land use type at any scale (Table 3.1).

Greater landscape heterogeneity was associated with higher bee diversity, evenness, and richness at both the 2 km and 1 km scales. In 2014, at the 2 km scale, higher landscape

heterogeneity was correlated with both higher diversity and species evenness (Table 3.2, Figure 3.3). Bee richness was also associated with increasing landscape heterogeneity at the 1 km scale in both survey years, and with marginal significance at the 500 m scale in 2014 (Figure 3.3).

There were no significant relationships between landscape heterogeneity on overall bee abundance at any scale in either year (Table 3.2). Landscape heterogeneity was not exclusively associated with one land use type (canola vs range): rangeland heterogeneity ranged from 0.094 to 0.78, and canola heterogeneity ranged from 0.18 to 0.71.

Bombus abundance had no significant relationships with grassland cover across years or spatial scales, with the exception of a marginally significant negative relationship with grassland cover at the 500 m scale in 2014 (Table 3.3). However, in 2015, *Bombus* abundance increased with higher levels of landscape heterogeneity (Table 3.3; Figure 3.4). Megachilidae had positive relationships with grassland cover at the 500 and 1 km scales in 2015, but a negative relationship with landscape heterogeneity in 2014 at the 2 km scale (Figure 3.4). Similarly, higher *Lasioglossum* abundance was associated with greater grassland cover at the 2 km and 1 km scales in 2014, and with marginal significance at these scales in 2015. *Lasioglossum* also responded negatively to increasing landscape heterogeneity at the 2 km scale in 2014. There was no effect of land use type on *Bombus* within any of the models. Higher abundances of Megachilidae were found in rangelands both years and across all three scales—an average of 8 ± 1 megachilid bees were caught in rangelands in 2015 compared to 5 ± 1 in canola; and in 2014, an average of 9 ± 1 were caught in rangelands and 2 ± 1 in canola (Table 3.3). In 2014, this was also true for *Lasioglossum*, with an average 47 ± 11 caught in rangelands and 24 ± 5 in canola; however, in 2015 there was no effect of land use on *Lasioglossum* abundance.

No interactions were found between the percentage of grassland cover and land use for any of the total bee or individual bee taxa variables at any scale or year (Appendix XII). In addition, no interactions between landscape heterogeneity and land use were found for any total bee variables across scales and years (Appendix XII). Interaction terms were dropped from subsequent analyses based on lack of significance. For individual taxa, three interaction terms between landscape heterogeneity and land use were significant (out of a total of 84 assessed interaction terms). These were: *Lasioglossum* abundance decreased in rangelands with higher heterogeneity whereas it showed a neutral response to increasing heterogeneity in canola fields at the 2 km scale in 2014 ($F_{1,54}=4.72$, $p=0.03$) and the 1 km scale in 2015 ($F_{1,55}=10.42$, $p<0.001$); and Megachilidae abundance increased in response to heterogeneity in canola fields and showed a neutral response in rangelands at the 1 km scale in 2015 ($F_{1,55}=4.27$, $p=0.04$; Appendix XIIb).

Sites with high landscape heterogeneity had a different composition of bees than those with low landscape heterogeneity in 2014 ($F_{1,60}= 1.97$, $p= 0.045$) and 2015 ($F_{1,59}=4.84$, $p=0.012$; Appendix XIII). In addition, bee community composition differed both years across categories of grassland cover (2014: $F_{3,60}= 3.37$, $p= 0.001$; 2015: $F_{3,59}= 1.78$, $p= 0.021$; Appendix XIII). In 2014, sites with high grassland cover had a different assemblage of bees than all other categories of cover, and medium grassland cover sites had a different composition from sites with no grassland cover (Table 3.4; Appendix XIII). In 2015, the high grassland cover sites had a different composition than low grassland sites. Indicator species analysis identified six species in 2014 and 14 species in 2015 that were strongly associated with high grassland cover (Table 3.5). When considering the three taxa of interest, three species of megachilid bee were associated with high grassland cover in 2014, and nine in 2015. No *Bombus* or *Lasioglossum* species were identified as indicators in 2014. In 2015, two *Bombus* species were indicators of the combined

grouping of none, medium, and high grassland cover, *B. rufocinctus* was associated with the combination of none, low, and medium cover categories, and *B. fervidus* was associated with the combination of low and none (Table 3.5). The same year, two *Lasioglossum* taxa were also associated with the combined grouping of none, medium, and high.

Discussion

Understanding relationships between bee communities and their surrounding landscape is important for predicting impacts of land use changes on pollinator communities and developing management options for land-use decision makers. Overall, I found a positive relationship between both the proportion of grassland cover and landscape heterogeneity on bees across different spatial scales. These impacts, however, were not consistent for three specific bee taxa with differing life history traits. My findings align with previous studies showing positive impacts of semi-natural habitats (Kremen et al. 2002; Klein et al. 2012) and landscape diversity (Senapathi et al. 2015) on whole bee communities, and variability in taxa-specific responses to landscape features (Aguirre-Guiterrez et al. 2015).

The proportion of grassland cover in each site had positive impacts on bee communities across spatial scales. In particular, species richness increased both years with higher amounts of grassland cover. These richer bee communities can result in a greater provisioning of pollination services in areas closer to natural habitats (Ricketts et al. 2008; Carvelheiro et al. 2010). Native grassland habitat provides a wider variety of both nesting (Potts et al. 2005; Black et al. 2011) and floral (Mallinger et al. 2016) resources compared to cropped fields. The configuration of undisturbed habitat is also an important factor for management to support bee communities (Hopfenmuller et al. 2014). Large, continuous areas of grassland habitat can act as a population

source (Ockinger and Smith 2007), with lower bee abundance and richness of bees further from areas of undisturbed habitat (Bailey et al. 2014). While, smaller, more dispersed patches of grassland habitat in areas of intensive agriculture result in more abundant and diverse bee communities (Kim et al. 2006). For example, undisturbed areas in field edges or margins of crops can provide important nesting habitat for bees (Stanley and Stout 2014). This suggests that both large intact areas of grassland, as well as small dispersed patches are important for maintaining bee communities (Brosi et al. 2008; Hopfenmuller et al. 2014). Chan et al. (2006) suggest that smaller, dispersed patches are important for maintaining an even distribution of pollination services across the landscape. However, bees living in isolated habitat patches are likely at a higher risk of extirpation (Rouget et al. 2003), and larger reserves may be important for conservation of bee diversity and rare bee species (Zou et al. 2017). Surprisingly, I found few overall impacts of proportion grassland cover on bee abundance, suggesting that other factors, such as climate, may be more important for supporting high numbers of bees (Abrahamczyk et al. 2011). This result aligns with current work showing that highly modified landscapes can continue to support a high abundance of bees, but not necessarily a high diversity (Zou et al. 2017).

Higher landscape heterogeneity was associated with higher species richness, diversity, and evenness in native bee communities. Landscape heterogeneity is a complex term and has been defined in many different ways (Cadenasso et al. 2006). It generally refers to the number of different habitat types within a given area (Hendrickx et al. 2007), and/or the proportion of a given area occupied by different habitat types. For example, in this approach, a homogeneous site would be dominated by a single cover type, whereas a more heterogeneous landscape would contain a more balanced proportion of multiple cover types. Many studies have found interacting

effects on bees between landscape heterogeneity and management of specific land cover types. A common finding is that landscapes that are highly disturbed and homogeneous (e.g. a monocultural crop) experience the greatest increases in bee abundance and richness when factors such as grassland cover are increased through management (Weibull and Ostman 2003; Winfree et al. 2009; Senapati et al. 2017). However, I found that even in relatively undisturbed landscapes (i.e. rangeland sites), greater landscape heterogeneity is correlated with higher bee diversity and evenness. Brandt et al. (2017) suggest that diverse landscapes and crop rotations are required in agricultural areas in order to support both a range of habitat requirements, and to provide floral resources throughout the growing season. This response is likely caused by a greater diversity in nesting and floral resources provided by multiple land cover types within rangeland sites (Rundlof et al. 2008; Mallinger et al. 2016), suggesting that landscape heterogeneity may be an important consideration when making land management decisions that support rare or less common bee species (Carre et al. 2009).

Despite positive relationships between both grassland cover and landscape heterogeneity on the overall bee community, I found variability in response when evaluating specific taxa of interest. I found opposite responses between bumble bees (*Bombus* sp) and cavity-nesting bees (megachilid bees). Bumble bees had a marginally negative response to the proportion of grassland cover but responded positively to greater landscape heterogeneity, while cavity-nesting bees responded positively to grassland cover and negatively to landscape heterogeneity. Variability in taxa-specific response to landscape variables is poorly understood, likely because the biological and taxonomic traits of all taxa are not well-described. For example, the natural history of bumble bees, including their foraging preferences and nesting habits, has been studied extensively, while relatively little is known about the natural history of many other native bees.

My results for megachilid bees, which are cavity-nesters, support previous studies showing that bees with this nesting habit are highly associated with undisturbed landscapes (Cusser et al. 2015). Other studies have suggested that a taxon's dispersal ability (Kormann et al 2015), or degree of specialization (Steffan-Dewenter 2003) likely impact variability in response across species or taxonomic groups. Bumble bee abundance has previously been found to increase with greater amounts of landscape edge (Aguirre-Guiterrez et al. 2015) and landscape heterogeneity (Rundlof et al. 2008). In comparison with other bee groups, bumble bees are often characterized as generalist species—able to use floral and nesting resources from a range of habitat types (Rollin et al. 2013). Steffan-Dewenter (2003) suggests that generalist species likely benefit from a more heterogeneous landscape as they are able to use the more diverse resources available; alternatively, specialist bees will respond more specifically to amount and connectivity of their preferred habitat type. Under this paradigm, my results suggest that cavity-nesters are more specialized to undisturbed grassland habitat, while in comparison bumble bees behave more as resource generalists in the landscape. This explanation has some drawbacks, as there is within-group variation in terms of resource specializations in both bumble bees (eg. floral specialization based on tongue length) and megachilid bees. Subsequent studies that test this hypothesis at the individual species level, as opposed to the genus/family approach used here, would greatly improve our understanding of how ecological traits influence habitat use. Bumble bees are also the only bee group I evaluated which forms a social colony. Species within Megachilidae and/or *Lasgioglossum* exhibit a range of solitary to eusocial behavior. The social nature of bumble bees may contribute to their ability to identify and capitalize on resources from a diversity of cover types, as a result of communal foraging and sharing of information. The importance of social

learning in the success of insect communities is largely understudied (Dukas 2008), and linkages between sociality and resource generalization in bees remain unexplored.

When evaluating all bees together, there was no single spatial scale at which the landscape variables were significant predictors of richness, abundance, diversity, or evenness. Instead, across two years, different bee variables were significant at different combinations of scales. Similarly, when investigating specific taxa, the scale at which significant patterns existed was not consistent across taxa and between years. Weather patterns were markedly different between the 2 years of survey, with much lower precipitation across most of the study region in 2015 as compared to 2014; this likely contributed to differences in the bee community assemblage and response to landscape structure. In particular, I observed lower availability of flowers in native systems in the drier survey year (2015), which may have resulted in bees being more drawn to flowering crops such as canola. Much of the literature on spatial scale has found differing responses in bee taxa based on a division of the bee community between bumblebees and ‘solitary bees’ (i.e. all non-*Bombus* species). These studies have often found that bumble bees respond at larger spatial scales, while solitary bees respond at smaller spatial scales, likely as a result in differing body sizes and therefore flight distances (Steffan-Dewenter et al. 2002). In contrast, significant bumble bee responses in this study were only found at the smallest spatial scale (500 m), whereas cavity-nesting and *Lasioglossum* bees responded to landscape variables across all three spatial scales. The mechanisms behind these responses are not known and is an area requiring further investigation.

These results display clear evidence of the importance of grassland habitat in maintaining bee richness, and diversity, and the importance of landscape heterogeneity in supporting bee community evenness and generalist bees. Furthermore, these findings suggest that in this system,

cavity-nesting bees are more commonly found in grassland habitat, whereas bumble bees behave more as resource generalists and therefore may not be as limited by the availability of grasslands. Overall, conservation of large and intact areas of grassland habitat is important for total bee species richness, and for supporting species of bees with grassland habitat needs. Maintaining a heterogeneous landscape is important for supporting generalist bee species and less common or rare bee species. These findings are important for understanding how different landscape management options may impact different taxa within pollinator communities.

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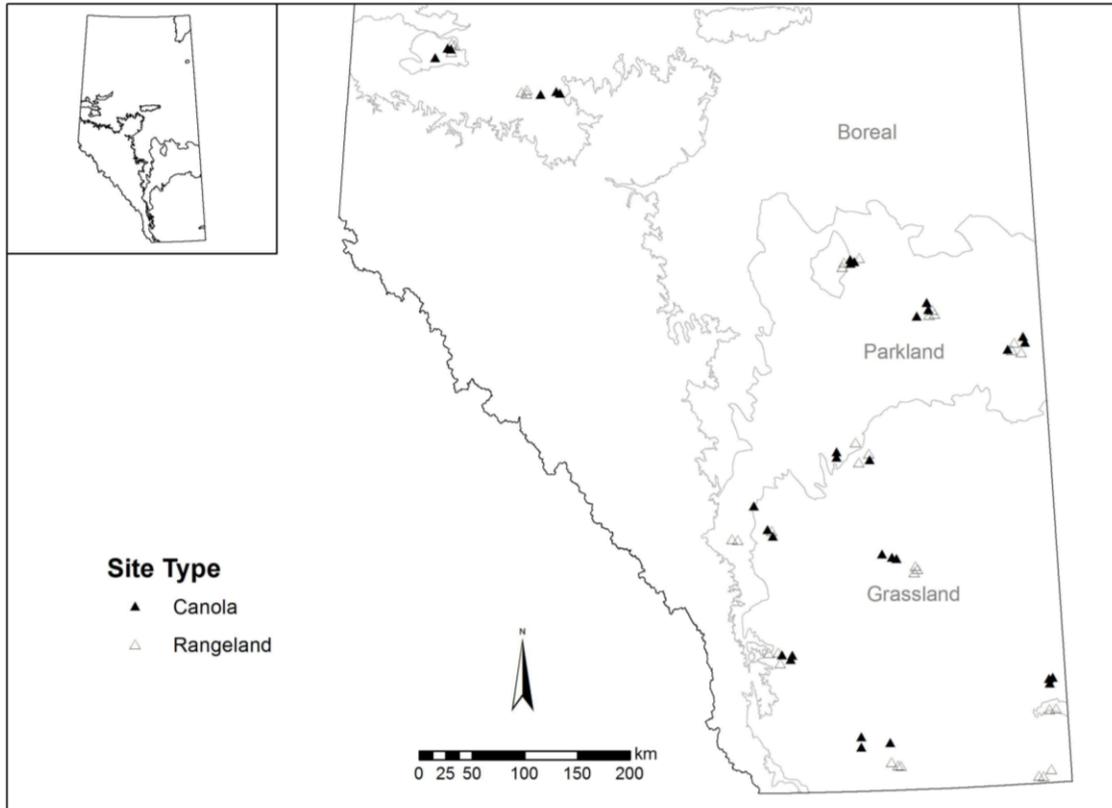


Figure 3. 1. Locations of bee surveys in the agricultural zone of Alberta are shown. Sites occurred in either canola fields (filled in triangle) or native rangelands (open triangle). Sites were surveyed twice for native bees during the summers of 2014 and 2015 using pan traps and netting methods. Exact canola field locations varied slightly between the two seasons but were in the same general area and owned by the same landowners; only 2015 locations are shown here.

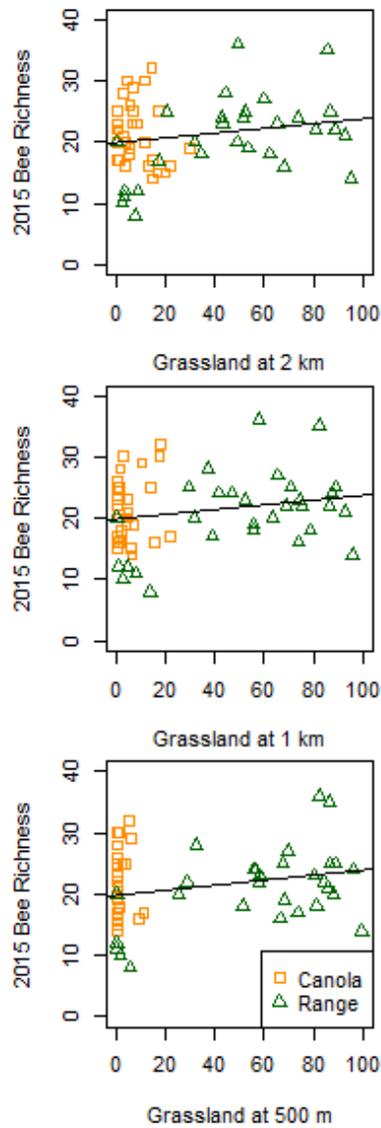


Figure 3. 2. Positive linear relationships between 2015 bee richness and proportion of grassland cover at the 2 km (top), 1 km (middle), and 500 m (bottom) scales across two different land use types—canola (orange squares) and range (green triangles). Relationships were tested using linear mixed effects models that included land use type as a fixed factor and ecoregion as a random factor. Significance was tested using Type III ANOVA Wald’s Tests (See Table 3.1 for statistical results).

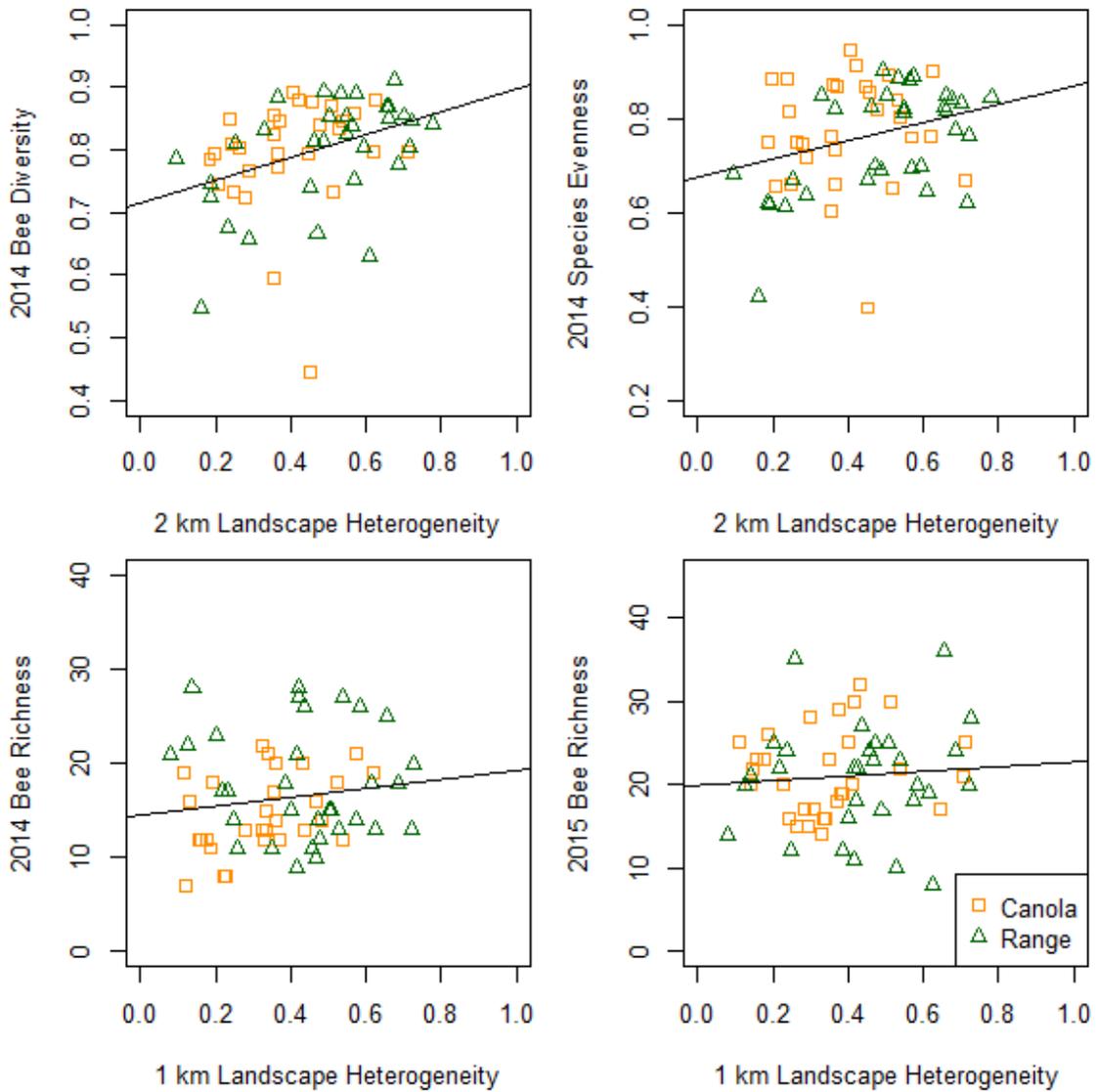


Figure 3. 3. Relationships between metrics of the overall bee community and landscape heterogeneity: A) Relationship between 2014 bee diversity and landscape heterogeneity at the 2 km scale (top left), B) Relationship between 2014 bee species evenness and landscape heterogeneity at the 2 km scale (top right), C) Relationship between 2014 bee richness and landscape heterogeneity at the 1 km scale (bottom left), and D) Relationship between 2015 bee richness and landscape heterogeneity at the 1 km scale (bottom right). Relationships were tested using linear mixed effects models that included land use type as a fixed factor and ecoregion as a random factor. Significance was tested using Type III ANOVA Wald's Tests (See Table 3.2 for statistical results).

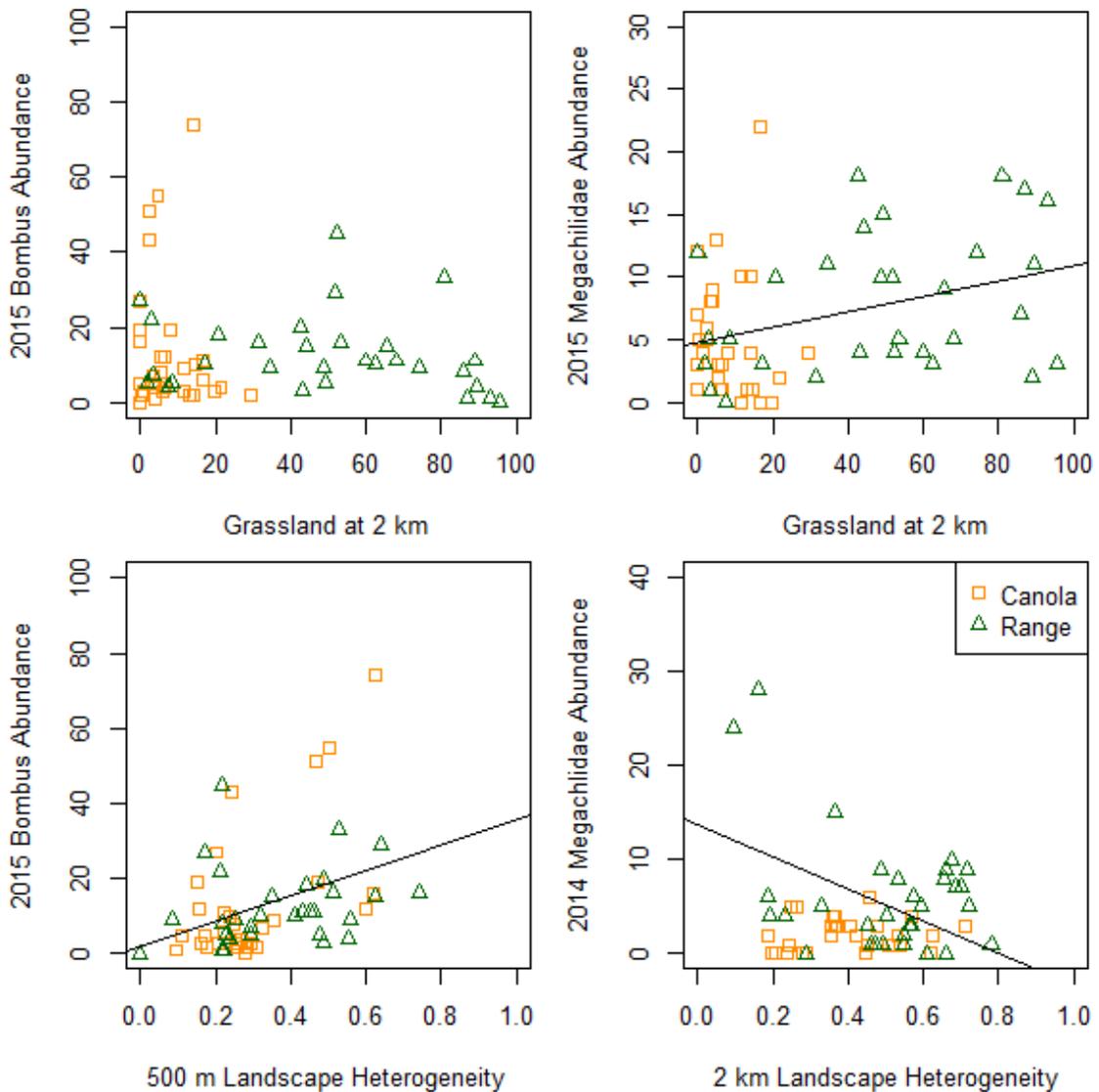


Figure 3. 4. Relationships between targeted taxa of bees and landscape variables. A) Non-significant relationship between 2015 *Bombus* abundance and proportion of grassland cover at the 2 km scale, B) Significant positive relationship between 2015 Megachilidae abundance and proportion of grassland cover at the 2 km scale, C) Significant positive relationship between 2015 *Bombus* abundance and landscape heterogeneity at the 2 km scale, and D) Significant negative relationship between 2014 Megachilidae abundance and landscape heterogeneity at the 2 km scale. Relationships were tested using linear mixed effects models of log-transformed variables that included land use type as a fixed factor and ecoregion as a random factor. Significance was tested using Type III ANOVA Wald’s Tests (See Table 3.3 for statistical results).

Table 3. 1. Results of linear mixed effects models testing the relationships between proportion grassland cover and land use type at three spatial scales with: overall bee abundance, richness, diversity, and evenness. Model significance was tested using Type III ANOVA Wald's *F* Tests. Abundance data was log-transformed prior to analysis. Significant differences ($p < 0.05$) are bolded; marginally significant differences ($p < 0.10$) are italicized.

Grassland Cover	2 km Grassland Cover			2 km Land Use			1 km Grassland Cover			1 km Land Use			500 m Grassland Cover			500 m Land Use			
	2014	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Richness		1,20	2.87	0.11	1,38	0.06	0.81	<i>1,38</i>	3.6	<i>0.07</i>	1,49	0.01	0.92	1,48	2.41	0.13	1,54	0.17	0.68
Diversity		1,20	2.87	0.11	1,37	0.06	0.81	1,38	0.94	0.34	1,49	0.72	0.4	1,52	0.01	0.92	1,55	0.03	0.86
Abundance		<i>1,57</i>	<i>2.93</i>	<i>0.09</i>	1,58	0.01	0.94	1,58	1.65	0.2	1,58	0.04	0.84	1,58	0.72	0.4	1,58	0.35	0.56
Species Evenness		1,36	2.22	0.15	1,49	0.36	0.55	1,52	1.69	0.2	1,56	0.21	0.65	1,57	0.27	0.61	1,57	0.03	0.87
	2015	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Richness		1,53	4.84	0.03	<i>1,56</i>	<i>3.41</i>	<i>0.07</i>	1,55	8.01	0.01	1,56	5.91	0.02	1,52	12.78	0	1,55	9.63	0
Diversity		1,51	0.87	0.35	<i>1,56</i>	2.8	<i>0.1</i>	1,55	1.46	0.23	<i>1,56</i>	<i>3.45</i>	<i>0.07</i>	<i>1,54</i>	<i>3.55</i>	<i>0.06</i>	1,56	5.74	0.02
Abundance		1,57	0.82	0.37	1,56	4.39	0.04	1,56	0.94	0.34	1,56	4.3	0.04	1,56	0.67	0.42	<i>1,56</i>	<i>3.69</i>	<i>0.06</i>
Species Evenness		1,54	0	0.99	1,57	0	0.99	1,56	0.01	0.93	1,57	0	0.95	1,56	0.54	0.47	1,56	0.33	0.57

Table 3. 2. Results of linear mixed effects models testing the relationships between landscape heterogeneity and land use type at three spatial scales with: overall bee abundance, richness, diversity, and evenness. Model significance was tested using Type III ANOVA Wald’s F Tests. Abundance data was log-transformed prior to analysis. Significant differences ($p<0.05$) are bolded; marginally significant differences ($p<0.10$) are italicized.

	2 km Landscape Heterogeneity			2 km Land Use			1 km Landscape Heterogeneity			1 km Land Use			500 m Landscape Heterogeneity			500 m Land Use			
	2014	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Richness		1,56	0.15	0.70	1,56	5.62	0.02	1,57	0.19	0.66	1,56	4.32	0.04	1,55	0.00	0.95	1,57	4.47	0.04
Diversity		1,56	7.72	0.01	1,56	0.37	0.55	1,57	4.71	0.03	1,56	0.29	0.59	<i>1,55</i>	<i>3.14</i>	<i>0.08</i>	1,57	0.34	0.56
Abundance		1,57	2.46	0.12	1,56	5.18	0.03	1,57	0.38	0.54	<i>1,56</i>	<i>4.00</i>	<i>0.05</i>	1,58	1.12	0.29	1,56	4.74	0.03
Species Evenness		1,58	5.32	0.02	1,56	2.20	0.14	1,58	1.69	0.20	1,56	1.56	0.22	1,58	2.10	0.15	1,56	1.96	0.17
	2015	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
Richness		1,57	1.43	0.24	1,56	0.23	0.63	1,57	4.80	0.03	1,55	0.68	0.41	1,57	0.60	0.44	1,55	0.21	0.65
Diversity		1,53	0.56	0.46	1,55	2.44	0.12	1,54	0.87	0.36	1,55	2.72	0.11	1,54	1.24	0.27	<i>1,55</i>	<i>2.82</i>	<i>0.10</i>
Abundance		1,57	0.00	0.98	1,55	4.27	0.04	1,57	0.43	0.51	1,55	4.84	0.03	1,57	1.53	0.22	1,55	5.53	0.02
Species Evenness		1,53	1.13	0.29	1,55	0.04	0.85	1,53	0.59	0.44	1,55	0.04	0.84	1,52	0.33	0.57	1,55	0.33	0.89

Table 3. 3. Results of linear mixed effects models testing relationships between a) grassland cover (top half of table), b) landscape heterogeneity (bottom half of table) and land use type at three spatial scales on the abundance of *Bombus*, *Lasioglossum*, and Megachilidae. Model significance was tested using Type III ANOVA Wald’s F Tests. Data was log-transformed prior to analysis. Significant differences ($p<0.05$) are bolded; marginally significant differences ($p<0.10$) are italicized

a) Grassland Cover	2 km Grassland Cover			2 km Land Use			1 km Grassland Cover			1 km Land Use			500 m Grassland Cover			500 m Land Use			
	2014	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
<i>Bombus</i> Abundance		1,58	2.56	0.11	1,58	2.80	0.10	1,58	2.65	0.11	<i>1,58</i>	<i>2.90</i>	<i>0.09</i>	1,57	3.22	0.08	1,57	3.31	0.07
Megachilidae Abundance		1,23	0.52	0.48	1,23	2.41	0.13	1,41	0.17	0.68	<i>1,48</i>	<i>3.18</i>	<i>0.08</i>	1,49	0.01	0.92	1,53	4.98	0.03
<i>Lasioglossum</i> Abundance		1,57	6.50	0.01	1,58	0.31	0.58	1,58	5.77	0.02	1,58	0.24	0.63	1,58	2.33	0.13	1,58	0.05	0.83
	2015	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
<i>Bombus</i> Abundance		1,57	0.00	0.97	1,56	0.21	0.65	1,56	0.00	0.99	1,56	0.22	0.64	1,56	0.06	0.80	1,56	0.06	0.81
Megachilidae Abundance		<i>1,56</i>	<i>2.97</i>	<i>0.09</i>	1,56	0.32	0.58	1,56	4.43	0.04	1,56	0.00	0.96	1,56	4.60	0.04	1,56	0.00	0.95
<i>Lasioglossum</i> Abundance		1,57	2.76	0.10	1,57	2.76	0.10	<i>1,57</i>	<i>3.19</i>	<i>0.08</i>	<i>1,57</i>	<i>3.24</i>	<i>0.08</i>	1,57	2.50	0.12	1,57	2.72	0.10
b) Landscape Heterogeneity	2 km Landscape Heterogeneity			2 km Land Use			1 km Landscape Heterogeneity			1 km Land Use			500 m Landscape Heterogeneity			500 m Land Use			
	2014	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
<i>Bombus</i> Abundance		1,57	1.24	0.27	1,56	0.10	0.76	1,57	0.06	0.81	1,56	0.44	0.51	1,58	0.39	0.54	1,56	0.66	0.42
Megachilidae Abundance		1,56	4.14	0.05	1,56	6.18	0.02	<i>1,57</i>	<i>3.33</i>	<i>0.07</i>	1,56	6.08	0.02	1,55	1.37	0.25	1,57	5.10	0.03
<i>Lasioglossum</i> Abundance		1,58	4.70	0.03	1,56	7.92	0.01	1,58	1.89	0.17	1,56	6.73	0.01	1,58	1.43	0.24	1,56	6.54	0.01
	2015	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>	<i>df</i>	<i>F</i>	<i>p</i>
<i>Bombus</i> Abundance		1,57	1.42	0.24	1,55	0.63	0.43	1,57	2.45	0.12	1,55	0.96	0.33	1,57	4.31	0.04	1,55	1.16	0.29
Megachilidae Abundance		1,52	0.29	0.59	1,55	4.75	0.03	1,53	0.75	0.39	1,55	4.14	0.05	1,50	0.01	0.94	1,55	4.92	0.03
<i>Lasioglossum</i> Abundance		1,57	0.15	0.70	1,55	0.74	0.39	1,57	0.32	0.57	1,55	1.10	0.30	1,57	1.66	0.20	1,55	1.49	0.23

Table 3. 4. Post-hoc pairwise comparisons of total bee community composition (perMANOVA) differences for different categories of grassland cover at a 2 km radius buffer: None=no grassland cover, Low=0-30% grassland cover, Medium=30-60% grassland cover, and High=60-90% grassland cover. 2014 results shown above the parallel line (shaded), 2015 results below and unshaded.

Grassland Cover Category	None	Low	Medium	High
None	-	0.288	0.036	0.018
Low	1.000	-	0.216	0.006
Medium	1.000	0.200	-	0.012
High	1.000	0.060	0.300	-

Table 3. 5. Results of indicator species analyses for four categories of grassland habitat cover at a 2 km radius buffer: none, low (0-30%), medium (30-60%), and high (60-100%). All indicator species had $p < 0.05$. Species with p values higher than this are not reported. Categories with indicator species are listed as columns. Groupings of several categories refer to indicators that were identified for combined categories.

Year		2014									
Grassland Cover Category	Low		High		Low-High		None-Med-High		None-Low-Medium		
	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	
Species											
<i>Megachile dentitarsus</i>			0.66	0.00							
<i>Osmia trevoris</i>			0.63	0.02							
<i>Perdita albipennis</i>			0.62	0.00							
<i>Perdita</i> sp			0.58	0.01							
<i>Osmia</i> sp			0.52	0.04							
<i>Eucera</i> sp			0.52	0.02							
<i>Nomada</i> sp 6	0.66	0.01									
<i>Colletes</i> sp					0.79	0.00					
<i>Agapostemon virescens</i>					0.65	0.03					
<i>Anthidium tenuiflorae</i>					0.57	0.03					
<i>Halictus confusus</i>							0.92	0.00			
<i>Halictus</i> sp							0.70	0.04			
Year		2015									
Grassland Cover Category	Low		High		Low-High		Non-Med-High		Non-Low-Medium		
	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	
Species											
<i>Agapostemon texanus</i>			0.93	0.00							
<i>Osmia trevoris</i>			0.75	0.00							
<i>Osmia</i> sp			0.74	0.01							
<i>Agapostemon virescens</i>			0.68	0.02							
<i>Osmia simillima</i>			0.64	0.02							
<i>Dianthidium</i> sp			0.63	0.00							
<i>Melissodes</i> sp			0.63	0.04							
<i>Osmia distincta</i>			0.62	0.01							
<i>Diadasia diminuta</i>			0.62	0.01							
<i>Hoplitis pilosifrons</i>			0.60	0.04							
<i>Osmia tersula</i>			0.52	0.03							
<i>Megachile anograe</i>			0.51	0.04							
<i>Anthidium</i> sp			0.50	0.03							
<i>Osmia morphH</i>			0.49	0.05							
<i>Megachile relativa</i>							0.64	0.01			
<i>Bombus frigidus</i>							0.64	0.01			
<i>Anthidium clypeodentatum</i>							0.59	0.01			
<i>Bombus</i> sp							0.59	0.01			
<i>Bombus flavifrons</i>							0.58	0.04			

<i>Hylaeus modestus</i>	0.57	0.03		
<i>Lasioglossum evylaeus</i> sp	0.82	0.04		
<i>Halictus confusus</i>	0.82	0.01		
<i>Hoplitis producta</i>	0.67	0.02		
<i>Lasioglossum</i> sp	0.61	0.04		
<i>Bombus rufocinctus</i>			0.93	0.01
<i>Bombus fervidus</i>	0.55	0.04		

Chapter Four: Summary and conclusion

Bees are estimated to support the production of over 80 global food crops (Klein et al. 2007), contributing over €150 billion to the global economy yearly (Gallai et al. 2009). At the same time, they are important in natural systems, pollinating 87% of native flowering plants (Ollerton et al. 2011). Given reports of recent global bee declines, broad-scale information on abundance, richness, and composition of native bee communities is required in order to support evidence-based management and mitigation responses (Goulson et al. 2015). The approach used in this study provides comprehensive information on how environmental and disturbance factors are driving responses in bee communities. It presents the first survey of prairie bee communities across a large spatial gradient of latitude and disturbance. Here, I have summarized differences in bee abundance, richness, diversity, and composition in response to differing ecoregions, land use, and elements of landscape structure.

The effect of two differing land uses—rangeland and canola—was evaluated with differing approaches in both Chapters 2 and 3. In Chapter 2, I found differences in bee community composition across both survey years between these two land uses, with several species of cavity nesting bees (Megachilidae) strongly associated with rangelands. However, the effect of land use on abundance and richness was weaker than expected and variable across survey regions and years. In the case of the southern Grasslands region, the effect of land use on abundance was reversed across years—I saw higher bee abundance in rangelands in 2014 and in canola fields in 2015. Weather and floral abundance were quite different between these 2 years, suggesting that response to land use likely interacts with climatic factors (Abrahamczyk et al. 2011). I also saw differing responses between targeted bee taxa in chapter 3—*Lasioglossum* and Megachilidae both responded positively to rangeland (Megachilidae across both years,

Lasioglossum only in 2014), whereas *Bombus* had no response to land use. These results suggest that bee taxa do not all respond consistently to land use change, either within the same year, or across years with variable weather patterns. Differing responses to disturbance across taxa are common (Steffen-Dewenter et al. 2002; Rollin et al. 2003; Hopfenmuller et al. 2014). Across both chapters, I found evidence for cavity-nesting bees (*Megachile*, *Osmia*, and *Hoplitis* in Megachilidae) being strongly associated with rangelands and increasing grassland cover. Previous studies have also found evidence for strong associations between cavity-nesters and undisturbed habitat (Williams et al. 2010; Sheffield et al. 2013; Cusser et al. 2015), suggesting that this group of bees may be sensitive to ongoing loss of this habitat type.

I also explored patterns in bee abundance, richness, diversity, and composition across three ecological regions. I found significant effects of ecoregion on both abundance and composition of bee communities, but few impacts on richness or diversity. Bee abundance followed a latitudinal gradient, with highest abundance in the southern Grasslands region and lowest in the northern Boreal. Regional differences in composition were driven primarily by a unique assemblage of bees existing in the southern Grasslands region; several species in my survey were highly associated with this region, as it represents the northern limit of their current range. Both abundance and composition differences were highly correlated with differences in climate across these regions; factors such as latitude and growing degree days over 18°C were the strongest predictors of differences in bee community composition and bee abundance. Climate change is expected to have negative impacts on native bees through range constrictions (Kerr et al. 2015), phenological mis-matches with flowering plants (Kudo and Ida 2013), and potential drops in richness with temperature rise (Papanikolaou et al. 2017). Documenting

current patterns in response to climatic gradients will be important not only in predicting future changes, but also in developing adaptation options to ensure species persistence over time.

Lastly, I evaluated response of bee abundance, richness, diversity, evenness and composition to two elements of landscape structure—percentage of grassland cover and landscape heterogeneity—across three spatial scales. I found positive impacts of percentage grassland cover on bee species richness, and positive impacts of landscape heterogeneity on richness, diversity, and evenness. When evaluating these responses across three targeted bee taxa (*Bombus*, *Lasioglossum*, and Megachilidae) I saw differing, and in some cases opposing, responses to these two landscape variables. Megachilidae and *Lasioglossum* both responded positively to grassland cover and negatively to landscape heterogeneity, while *Bombus* had no relationship with grassland cover and responded positively to landscape heterogeneity. One possible explanation for differences in response is the degree of specialization of differences species, with generalists responding more favorably to landscape heterogeneity than bees that are strongly associated with a particular habitat type (Steffan-Dewenter 2003; Rollin et al. 2013). Loss of amount and diversity of habitats is an ongoing pressure on bee communities (Winfree et al. 2009; Senapati et al. 2017). Understanding the habitat associations of different species and variability in response to ongoing landscape change is essential in developing management tools that support a range of management goals.

Monitoring strategies that document both the diversity and abundance of bee communities are required in order to identify conservation priorities both globally and regionally (Goulson et al 2015). Overall, these results highlight the range of variability not only in overall bee response metrics, but also variability across different taxa of bees. While bee abundance appears to be driven primarily by climate and ecological gradients, richness and diversity are

more responsive to the proportion of grassland cover and surrounding landscape heterogeneity, and composition appears to vary in response to a combination of these factors (Liow et al. 2001; Grundel et al. 2010). This suggests that not all bees respond consistently to these types of drivers, making it essential to further our biological and ecological understanding of individual bee species. Bee taxonomy is currently understudied, and taxonomic resources like comprehensive identification keys or complete species lists do not exist for the prairies (Sheffield et al. 2014). Investments in this area of study are essential to support robust monitoring programs of bee communities moving forward. Based on my results, subsequent research into the degree of specialization of different species with respect to both floral resources and nesting habitat may identify some of the mechanisms behind variability in species response.

Bee communities are responding to a myriad of drivers, both natural and anthropogenic (Vanbergen et al. 2013). Disentangling the separate and combined effects of these drivers is essential for understanding how anthropogenic impacts such as habitat loss and climate change are influencing different elements of native bee communities. This study provides, for the first time, insight into patterns of abundance, richness, and composition of native bee communities across a broad spatial gradient of Alberta's prairies. The results suggest that there is no "one size fits all" management strategy for native bees, and that monitoring and management activities will vary depending on the desired goal or outcome. Maintaining abundance levels, diversity, or identifying and sustaining species of conservation concern may all require differing monitoring approaches, and differing courses of management action.

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Appendix I: Climate and environmental data for each site. Climate data was extracted with the ClimateNA v5.10 softwarepackage, available at <http://tinyurl.com/ClimateNA>, based on methodology described by Wang et al. (2016).

Site	Land Use	Natural Region	Latitude (°)	Elevation (m)	Mean annual temperature (°C)	Mean warmest month temperature (°C)	Mean coldest month temperature (°C)	Mean annual precipitation (mm)	Frost free days
CNW10	Canola	Boreal	54.57	722	2.7	15.4	-12.2	571	166
CNW11	Canola	Boreal	54.56	757	2.6	15.3	-12.1	572	165
CNW12	Canola	Boreal	54.55	664	3.1	15.8	-11.8	550	169
RCE1	Range	Boreal	53.29	741	2.5	16.1	-13.7	429	171
RCE2	Range	Boreal	53.37	688	2.5	16.4	-13.9	426	172
RNW1	Range	Boreal	54.58	698	3.1	15.7	-11.8	571	170
RNW2	Range	Boreal	54.56	700	3.1	15.7	-11.8	575	170
RNW3	Range	Boreal	54.56	742	3	15.5	-11.6	570	168
CSE20	Canola	Grassland	51.49	846	3.3	17.3	-13.1	416	167
CSE23	Canola	Grassland	50.58	762	4.3	17.9	-11.7	333	171
CSE24	Canola	Grassland	50.58	765	4.3	17.9	-11.7	332	171
CSE25	Canola	Grassland	51	773	3.7	17.5	-12.6	327	166
CSE26	Canola	Grassland	49.5	959	3.6	17.7	-11.5	424	157
CSE27	Canola	Grassland	49.52	926	3.8	17.9	-11.6	447	159
CSE28	Canola	Grassland	49.53	900	3.9	18.1	-11.6	453	159
CSW11	Canola	Grassland	51.14	1105	2.9	15.6	-11.3	376	157
CSW12	Canola	Grassland	51.11	994	3.3	16.2	-11.4	370	160
CSW13	Canola	Grassland	50.1	1062	4.5	16.8	-9.1	412	169
CSW14	Canola	Grassland	50.08	1017	4.7	17.1	-9.1	407	172
CSW15	Canola	Grassland	49.24	1026	5.7	18.2	-7.6	405	181
CSW16	Canola	Grassland	50.1	974	4.8	17.3	-9.2	405	173
CSW17	Canola	Grassland	49.27	1081	5.2	17.5	-8	472	175
CSW18	Canola	Grassland	49.24	996	5.8	18.3	-7.6	405	182
RSE11	Range	Grassland	49.08	882	4.3	19	-12.2	302	160
RSE12	Range	Grassland	49.03	897	4.5	19	-11.6	292	162
RSE13	Range	Grassland	49.03	896	4.6	19	-11.3	293	163
RSE2	Range	Grassland	51.52	861	3.2	17.2	-13.2	421	166
RSE3	Range	Grassland	51.47	803	3.5	17.5	-12.8	398	168
RSE6	Range	Grassland	50.52	718	4.5	18.4	-12.2	322	173
RSE7	Range	Grassland	50.53	722	4.4	18.4	-12.2	322	173
RSE8	Range	Grassland	50.5	696	4.6	18.6	-12.1	322	174
RSW3	Range	Grassland	51.13	1003	3.3	16.1	-11.5	371	160
RSW4	Range	Grassland	50.11	1384	3.3	15	-8.9	428	158
RSW5	Range	Grassland	50.11	1108	4.3	16.5	-9.1	414	168
RSW6	Range	Grassland	50.05	1030	4.7	17	-8.9	421	171
RSW7	Range	Grassland	49.14	1195	5.1	17.3	-7.5	406	175
RSW8	Range	Grassland	49.12	1144	5.3	17.7	-7.5	395	177

RSW9	Range	Grassland	49.12	1115	5.5	17.9	-7.5	393	178
CCE10	Canola	Parkland	53.31	640	2.6	16.7	-14.3	424	172
CCE11	Canola	Parkland	53.29	684	2.6	16.5	-14	429	172
CCE12	Canola	Parkland	53.3	681	2.5	16.4	-14.2	422	171
CCE13	Canola	Parkland	53.01	662	2.4	16.8	-15.1	438	168
CCE14	Canola	Parkland	53.07	670	2.2	16.7	-15.4	456	167
CCE15	Canola	Parkland	53.04	695	2.2	16.6	-15.2	450	167
CCE16	Canola	Parkland	52.47	651	2.3	17.2	-15.8	390	166
CCE17	Canola	Parkland	52.44	623	2.3	17.4	-16	390	167
CCE18	Canola	Parkland	52.41	648	2.3	17.3	-15.9	398	165
CNW13	Canola	Parkland	55.17	674	2.1	15.4	-14.3	470	161
CNW14	Canola	Parkland	55.12	708	2	15.2	-14.1	466	159
CNW15	Canola	Parkland	55.12	684	2.1	15.4	-14.1	466	160
CSE21	Canola	Parkland	51.53	849	3.4	17.2	-12.6	382	166
CSE22	Canola	Parkland	51.47	866	3.4	17.1	-12.6	398	166
CSW10	Canola	Parkland	51.26	1044	3.8	15.9	-9.6	439	163
RCE3	Range	Parkland	53.32	666	2.4	16.5	-14.4	419	170
RCE4	Range	Parkland	53.01	640	2.4	16.9	-15.4	445	167
RCE5	Range	Parkland	53.03	680	2.2	16.7	-15.3	448	166
RCE6	Range	Parkland	53.01	649	2.3	16.8	-15.5	445	167
RCE7	Range	Parkland	52.44	738	2.1	16.7	-15.3	393	164
RCE8	Range	Parkland	52.41	633	2.3	17.4	-16	397	165
RCE9	Range	Parkland	52.39	631	2.3	17.5	-16	390	166
RNW4	Range	Parkland	55.15	651	2.1	15.5	-14.3	466	161
RNW5	Range	Parkland	55.18	554	2.3	16	-14.6	458	164
RNW6	Range	Parkland	55.2	552	2.3	16	-14.6	457	164
RSE1	Range	Parkland	51.58	864	3.3	16.9	-12.8	402	165
RSW1	Range	Parkland	51.09	1113	3.5	15.3	-9.2	449	156
RSW2	Range	Parkland	51.09	1166	3.4	15.2	-9.1	439	157
RSE10	Range	Rocky Mountain	49.37	1419	1.9	15.1	-11.2	374	144
RSE9	Range	Rocky Mountain	49.37	1438	2	14.9	-11	384	145

Appendix II: List of species or taxonomic unit identified, including the number of total individuals identified across both years (2014 and 2015) and survey methods (pan trap and netting) combined.

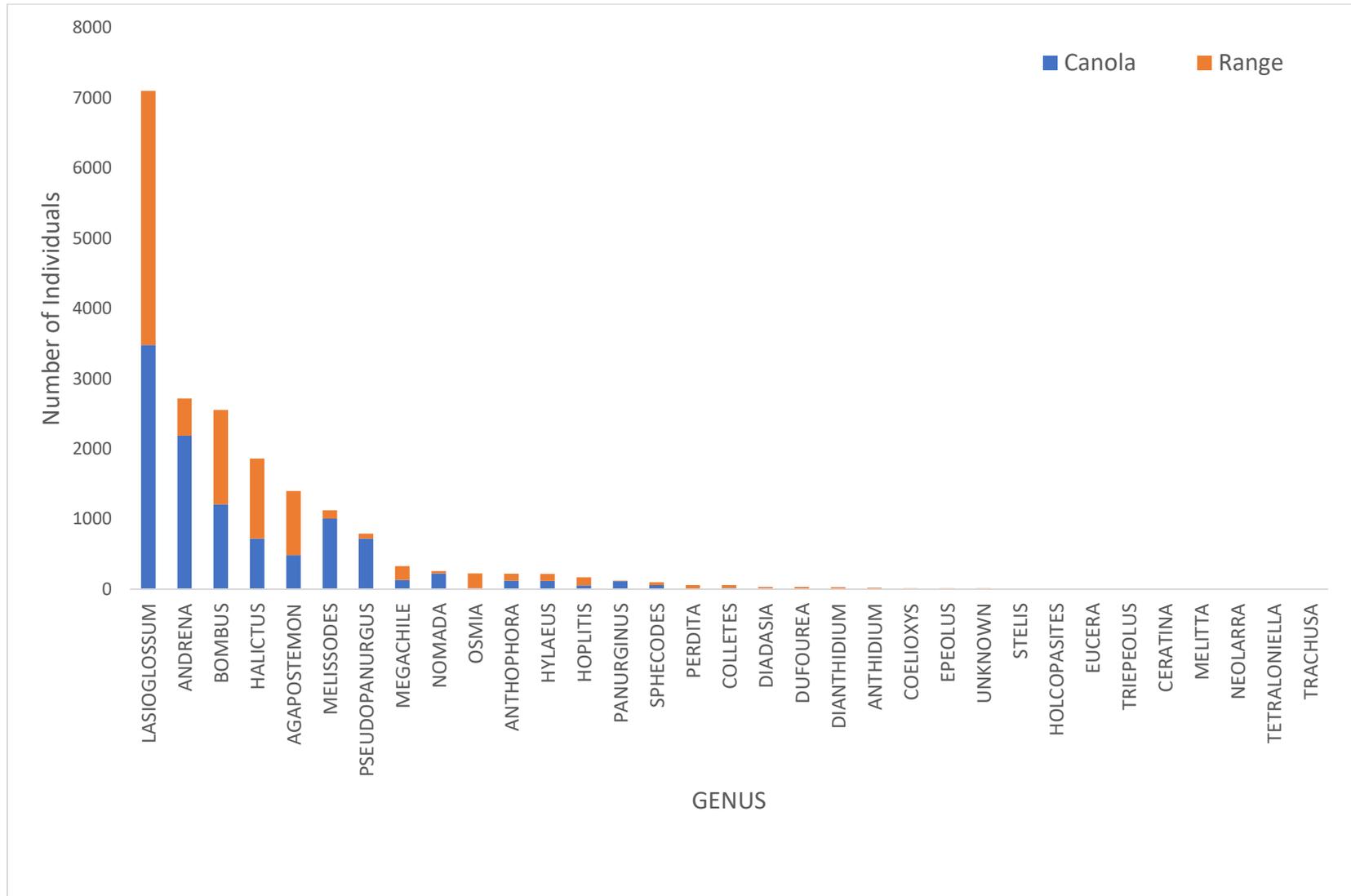
FAMILY	SPECIES	TAXONOMIC RESOLUTION	TOTAL INDIVIDUALS
Andrenidae	<i>Andrena carlini</i> Cockerell	Species	1
Andrenidae	<i>Andrena cyanophila</i> Cockerell	Species	5
Andrenidae	<i>Andrena dunningi</i> Cockerell	Species	4
Andrenidae	<i>Andrena erythrogaster</i> (Ashmead)	Species	1
Andrenidae	<i>Andrena lupinorum</i> Cockerell	Species	346
Andrenidae	<i>Andrena medionitens</i> Cockerell	Species	100
Andrenidae	<i>Andrena prunorum</i> Cockerell	Species	1
Andrenidae	<i>Andrena</i> spp.	Genus	2280
Andrenidae	<i>Andrena trachl</i>	Morphospecies	3
Andrenidae	<i>Andrena transnigra</i> Viereck	Species	7
Andrenidae	<i>Panurginus ineptus</i> Cockerell	Species	119
Andrenidae	<i>Panurginus</i> sp.	Genus	1
Andrenidae	<i>Perdita albipennis</i> Cresson	Species	15
Andrenidae	<i>Perdita</i> spp.	Genus	44
Andrenidae	<i>Pseudopanurgus hefty</i>	Morphospecies	10
Andrenidae	<i>Pseudopanurgus</i> spp.	Genus	781
Apidae	<i>Anthophora bomboides</i> Kirby	Species	4
Apidae	<i>Anthophora occidentalis</i> Cresson	Species	9
Apidae	<i>Anthophora</i> spp.	Genus	2
Apidae	<i>Anthophora terminalis</i> Cresson	Species	208
Apidae	<i>Bombus appositus</i> Cresson	Species	1
Apidae	<i>Bombus bifarius</i> Cresson	Species	22
Apidae	<i>Bombus borealis</i> Kirby	Species	200
Apidae	<i>Bombus centralis</i> Cresson	Species	1
Apidae	<i>Bombus cryptarum</i> (Fabricius)	Species	58
Apidae	<i>Bombus fervidus</i> (Fabricius)	Species	16
Apidae	<i>Bombus flavidus</i> Eversmann	Species	5
Apidae	<i>Bombus flavifrons</i> Cresson	Species	154
Apidae	<i>Bombus frigidus</i> Smith	Species	31
Apidae	<i>Bombus griseocollis</i> (De Geer)	Species	1
Apidae	<i>Bombus huntii</i> Greene	Species	16
Apidae	<i>Bombus insularis</i> (Smith)	Species	34
Apidae	<i>Bombus mixtus</i> Cresson	Species	13
Apidae	<i>Bombus nevadensis</i> Cresson	Species	32
Apidae	<i>Bombus occidentalis</i> Greene	Species	3
Apidae	<i>Bombus perplexus</i> Greene	Species	5
Apidae	<i>Bombus rufocinctus</i> Cresson	Species	612
Apidae	<i>Bombus sandersonii</i> Cresson	Species	12
Apidae	<i>Bombus sitkensis</i> Nylander	Species	3
Apidae	<i>Bombus</i> spp.	Genus	12

Apidae	<i>Bombus sylvicola</i> Kirby	Species	4
Apidae	<i>Bombus ternarius</i> Say	Species	318
Apidae	<i>Bombus terricola</i> Kirby	Species	50
Apidae	<i>Bombus vagans</i> Smith	Species	158
Apidae	<i>Ceratina dupla</i> Say	Species	1
Apidae	<i>Ceratina</i> sp.	Genus	1
Apidae	<i>Diadasia diminuta</i> (Cresson)	Species	20
Apidae	<i>Diadasia morphA</i>	Morphospecies	2
Apidae	<i>Diadasia morphB</i>	Morphospecies	1
Apidae	<i>Diadasia rinconis</i> Cockerell	Species	2
Apidae	<i>Diadasia</i> spp.	Genus	7
Apidae	<i>Epeolus minimus</i> (Robertson)	Species	12
Apidae	<i>Epeolus</i> spp.	Genus	3
Apidae	<i>Eucera</i> spp.	Genus	5
Apidae	<i>Holcopasites heliopsis</i> (Robertson)	Species	10
Apidae	<i>Melecta</i> spp.	Genus	2
Apidae	<i>Melissodes communis</i> Cresson	Species	2
Apidae	<i>Melissodes</i> spp.	Genus	1124
Apidae	<i>Neolarra</i> sp.	Genus	1
Apidae	<i>Nomada lehighensis</i> Cockerell	Species	3
Apidae	<i>Nomada morphA</i>	Morphospecies	2
Apidae	<i>Nomada morphE</i>	Morphospecies	7
Apidae	<i>Nomada morphF</i>	Morphospecies	6
Apidae	<i>Nomada morphI</i>	Morphospecies	1
Apidae	<i>Nomada morphL</i>	Morphospecies	1
Apidae	<i>Nomada morphO</i>	Morphospecies	5
Apidae	<i>Nomada morphP</i>	Morphospecies	1
Apidae	<i>Nomada morphQ</i>	Morphospecies	1
Apidae	<i>Nomada morphR</i>	Morphospecies	1
Apidae	<i>Nomada morphT</i>	Morphospecies	5
Apidae	<i>Nomada morphU</i>	Morphospecies	1
Apidae	<i>Nomada morphW</i>	Morphospecies	2
Apidae	<i>Nomada morphX</i>	Morphospecies	1
Apidae	<i>Nomada morphY</i>	Morphospecies	1
Apidae	<i>Nomada</i> spp.	Genus	30
Apidae	<i>Nomada</i> sp 1	Morphospecies	9
Apidae	<i>Nomada</i> sp 2	Morphospecies	9
Apidae	<i>Nomada</i> sp 3	Morphospecies	12
Apidae	<i>Nomada</i> sp 5	Morphospecies	103
Apidae	<i>Nomada</i> sp 6	Morphospecies	58
Apidae	<i>Nomada waspy</i>	Morphospecies	2
Apidae	<i>Tetraloniella albata</i> (Cresson)	Species	1
Apidae	<i>Triepeolus helianthi</i> (Robertson)	Species	2
Apidae	<i>Triepeolus</i> spp.	Genus	3
Colletidae	<i>Colletes aberrans</i> Cockerell	Species	4

Colletidae	<i>Colletes</i> spp.	Genus	53
Colletidae	<i>Hylaeus affinis</i> (Smith)	Species	108
Colletidae	<i>Hylaeus annulatus</i> (Linnaeus)	Species	29
Colletidae	<i>Hylaeus basalis</i> (Smith)	Species	3
Colletidae	<i>Hylaeus cleptocephalus</i> (Fabricius)	Species	1
Colletidae	<i>Hylaeus mesillae</i> (Cockerell)	Species	41
Colletidae	<i>Hylaeus modestus</i> Say	Species	27
Colletidae	<i>Hylaeus</i> spp.	Genus	18
Halictidae	<i>Agapostemon texanus</i> Cresson	Species	1068
Halictidae	<i>Agapostemon virescens</i> (Fabricius)	Species	339
Halictidae	<i>Dufourea fimbriata</i> (Cresson)	Species	1
Halictidae	<i>Dufourea maura</i> (Cresson)	Species	30
Halictidae	<i>Halictus confusus</i> Smith	Species	676
Halictidae	<i>Halictus farinosus</i> Smith	Species	1
Halictidae	<i>Halictus ligatus</i> Say	Species	79
Halictidae	<i>Halictus rubicundus</i> (Christ)	Species	1107
Halictidae	<i>Halictus</i> spp.	Genus	71
Halictidae	<i>Lasioglossum cooleyi</i> (Crawford)	Species	1
Halictidae	<i>Lasioglossum lineatulum</i> (Crawford)	Species	1
Halictidae	<i>Lasioglossum perpunctatum</i> (Ellis)	Species	1
Halictidae	<i>Lasioglossum (Dialictus) red</i>	Morphospecies	24
Halictidae	<i>Lasioglossum (Dialictus) spp.</i>	Subgenus	5071
Halictidae	<i>Lasioglossum (Evylyaeus) spp.</i>	Subgenus	380
Halictidae	<i>Lasioglossum ovaliceps</i> Cockerell	Species	1
Halictidae	<i>Lasioglossum (Sensu stricto) spp.</i>	Subgenus	1894
Halictidae	<i>Lasioglossum</i> spp.	Genus	29
Halictidae	<i>Sphecodes morphL</i>	Morphospecies	1
Halictidae	<i>Sphecodes solonus</i> Latreille	Species	3
Halictidae	<i>Sphecodes</i> spp.	Genus	74
Halictidae	<i>Sphecodes</i> sp 1	Morphospecies	23
Halictidae	<i>Sphecodes</i> sp 3	Morphospecies	4
Megachilidae	<i>Anthidium clypeodentatum</i> Swenk	Species	10
Megachilidae	<i>Anthidium</i> spp.	Genus	4
Megachilidae	<i>Anthidium tenuiflorae</i> Cockerell	Species	9
Megachilidae	<i>Ashmeadiella</i> spp.	Genus	1
Megachilidae	<i>Coelioxys funeraria</i> Smith	Species	2
Megachilidae	<i>Coelioxys rufitarsis</i> Smith	Species	2
Megachilidae	<i>Coelioxys sodalis</i> Cresson	Species	8
Megachilidae	<i>Coelioxys</i> spp.	Genus	3
Megachilidae	<i>Dianthidium curvatum</i> (Smith)	Species	16
Megachilidae	<i>Dianthidium</i> spp.	Genus	13
Megachilidae	<i>Hoplitis albifrons</i> (Kirby)	Species	8
Megachilidae	<i>Hoplitis pilosifrons</i> (Cresson)	Species	70
Megachilidae	<i>Hoplitis producta</i> (Cresson)	Species	53
Megachilidae	<i>Hoplitis robusta</i> (Nylander)	Species	1

Megachilidae	<i>Hoplitis</i> spp.	Genus	12
Megachilidae	<i>Hoplitis spoliata</i> (Provancher)	Species	29
Megachilidae	<i>Megachile anograe</i> Cockerell	Species	6
Megachilidae	<i>Megachile brevis</i> Say	Species	4
Megachilidae	<i>Megachile casadae</i> Cockerell	Species	1
Megachilidae	<i>Megachile centuncularis</i> (Linnaeus)	Species	3
Megachilidae	<i>Megachile dentitarsus</i> Sladen	Species	8
Megachilidae	<i>Megachile frigida</i> Smith	Species	18
Megachilidae	<i>Megachile gemula</i> Cresson	Species	1
Megachilidae	<i>Megachile inermis</i> Provancher	Species	123
Megachilidae	<i>Megachile lapponica</i> Thomson	Species	2
Megachilidae	<i>Megachile latimanus</i> Say	Species	16
Megachilidae	<i>Megachile melanophaea</i> Smith	Species	64
Megachilidae	<i>Megachile montivaga</i> Cresson	Species	5
Megachilidae	<i>Megachile perihirta</i> Cockerell	Species	17
Megachilidae	<i>Megachile pugnata</i> Say	Species	2
Megachilidae	<i>Megachile relativa</i> Cresson	Species	41
Megachilidae	<i>Megachile</i> spp.	Genus	3
Megachilidae	<i>Megachile sublaurita</i> Mitchell	Species	2
Megachilidae	<i>Osmia bucephala</i> Cresson	Species	11
Megachilidae	<i>Osmia distincta</i> Cresson	Species	21
Megachilidae	<i>Osmia morphD</i>	Morphospecies	1
Megachilidae	<i>Osmia morphE</i>	Morphospecies	2
Megachilidae	<i>Osmia morphF</i>	Morphospecies	1
Megachilidae	<i>Osmia morphG</i>	Morphospecies	1
Megachilidae	<i>Osmia morphH</i>	Morphospecies	3
Megachilidae	<i>Osmia morphI</i>	Morphospecies	1
Megachilidae	<i>Osmia simillima</i> Smith	Morphospecies	29
Megachilidae	<i>Osmia</i> spp.	Genus	69
Megachilidae	<i>Osmia</i> sp 1	Morphospecies	5
Megachilidae	<i>Osmia tersula</i> Cockerell	Species	7
Megachilidae	<i>Osmia trevoris</i> Cockerell	Species	75
Megachilidae	<i>Stelis labiate</i> Panzer	Species	1
Megachilidae	<i>Stelis lateralis</i> Cresson	Species	5
Megachilidae	<i>Stelis nitida</i> Cresson	Species	1
Megachilidae	<i>Stelis permaculata</i> Cockerell	Species	2
Megachilidae	<i>Stelis</i> spp.	Genus	2
Megachilidae	<i>Trachusa</i> sp.	Genus	1
Melittidae	<i>Melitta americana</i> (Smith)	Species	1
Unknown	Unknown	Unknown	20
Grand Total			19, 142

Appendix III: Raw abundance data for all bee genera observed. Data are compiled from both survey years and separated based on land use, with bees collected from canola fields in blue and rangela*nds in orange.



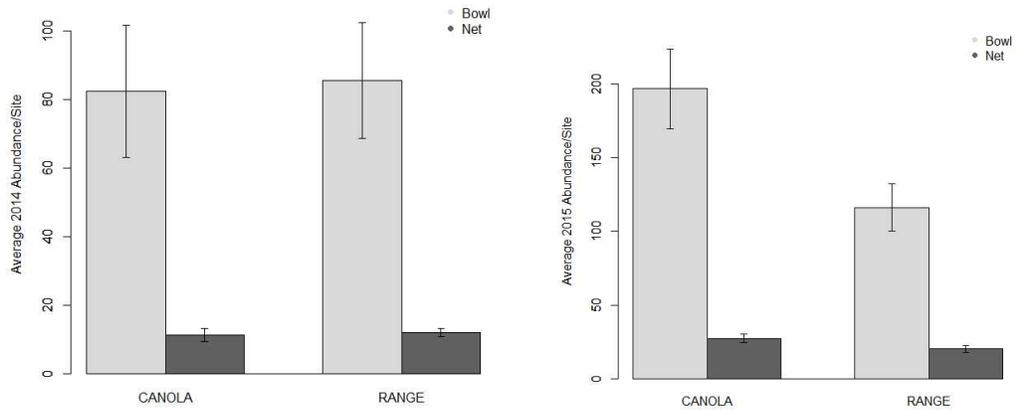
Appendix IV: Summary of honeybee observations. Total honeybees visually observed during field work are provided for each site an survey year. Canola sites begin with “C” and rangeland sites begin with “R.”

Site	2014	2015	Total
CCE1	27	NA	27
CCE10	NA	59	59
CCE11	NA	193	193
CCE12	NA	5	5
CCE14	NA	3	3
CCE15	NA	1	1
CCE2	2	NA	2
CCE3	16	NA	16
CCE6	1	NA	1
CNW1	14	NA	14
CNW10	NA	125	125
CNW11	NA	170	170
CNW12	NA	289	289
CNW14	NA	8	8
CNW15	NA	1	1
CNW2	21	NA	21
CNW3	7	NA	7
CNW5	1	NA	1
CNW6	3	NA	3
CSE11	1	NA	1
CSE20	NA	34	34
CSE21	NA	30	30
CSE22	NA	22	22
CSE23	NA	13	13
CSE24	NA	9	9
CSE26	NA	1	1
CSE3	7	NA	7
CSE4	6	NA	6
CSE5	10	NA	10
CSE6	4	NA	4
CSE7	23	NA	23
CSE8	8	NA	8
CSW10	NA	1	1
CSW11	NA	41	41
CSW12	NA	82	82
CSW13	NA	9	9
CSW14	NA	36	36
CSW15	NA	2	2
CSW16	NA	62	62
CSW17	NA	7	7

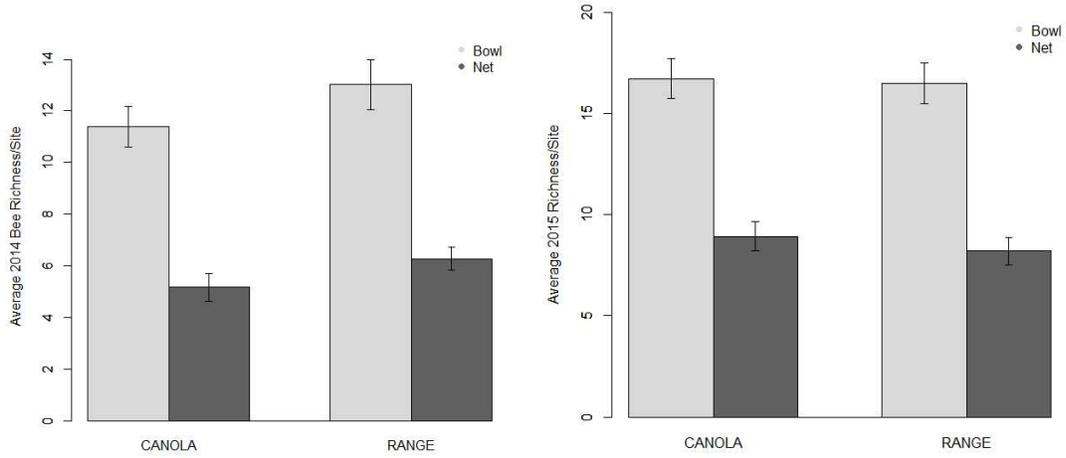
CSW18	NA	25	25
CSW2	6	NA	6
CSW3	4	NA	4
CSW4	5	NA	5
CSW9	19	NA	19
RCE1	7	7	14
RCE2	1	0	1
RCE3	0	1	1
RCE6	0	1	1
RNW1	16	1	17
RNW2	19	0	19
RNW3	3	1	4
RNW4	0	1	1
RNW5	18	3	21
RNW6	2	18	20
RSE2	16	73	89
RSE3	0	1	1
RSE6	1	0	1
RSE7	5	5	10
RSE8	1	75	76
RSW1	6	0	6
RSW2	8	6	14
RSW3	29	33	62
RSW4	1	0	1
RSW5	0	1	1
RSW6	0	1	1
RSW7	1	0	1
RSW8	4	15	19
RSW9	1	4	5
Total	358	1475	1833

Appendix V: Differences in bee abundance, richness, and composition across two survey methods: pan traps and netting.

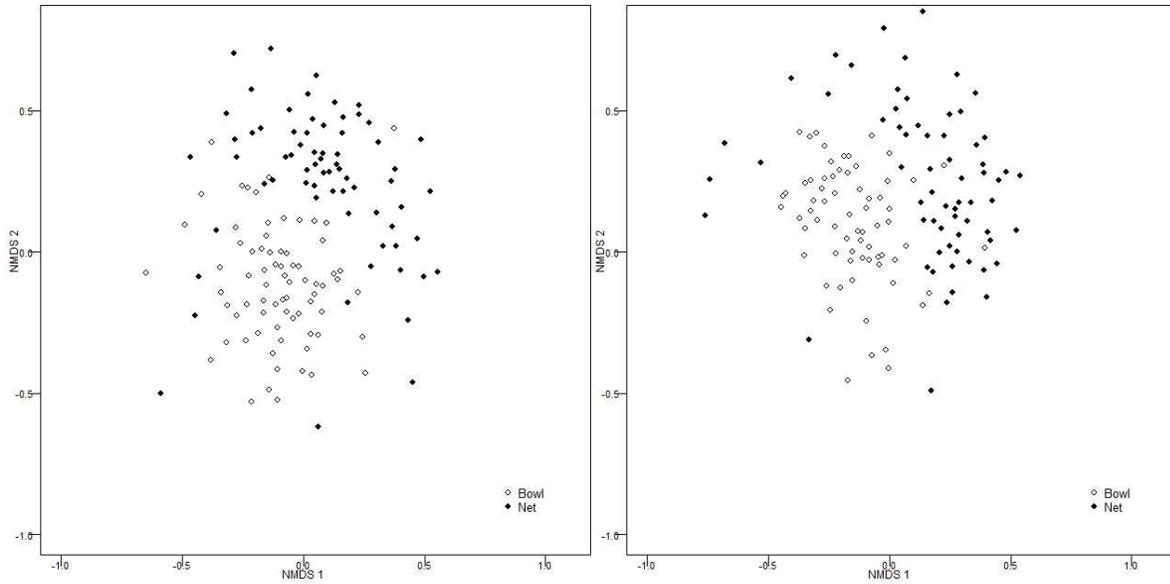
- a) Average bee abundance (\pm SE) caught in pan traps (“Bowls”=light shading) vs netting (“Net”=dark shading) across two land use types, canola fields and native rangelands. Separated by survey year (2014 on the left, 2015 on the right).



b) Average bee richness (\pm SE) caught in pan traps (“Bowls”=light shading) vs netting (“Net”=dark shading) across two land use types, canola fields and native rangelands. Separated by survey year (2014 on the left, 2015 on the right).



- c) Nonmetric multidimension scaling (NMDS) ordination showing differences in community composition between bees caught in pan traps (“Bowl”=open circle) and nets (“Net”=closed circle). Done separately for two survey years: 2014 on the left, and 2015 on the right.



- d) Results of 2015 indicator species analysis identifying species that tended to be caught in pan traps vs by netting. All listed species had a p -value < 0.05. Species with p values higher than this are not reported.

Method	Netting		Pan Traps	
Species	R^2	p	R^2	p
<i>Bombus ternarius</i>	0.605	0.001		
<i>Megachile inermis</i>	0.527	0.003		
<i>Megachile melanophaea</i>	0.464	0.008		
<i>Lasioglossum dialictus</i> sp			0.989	0.001
<i>Lasioglossum sensu stricto</i> sp			0.916	0.001
<i>Halictus rubicundus</i>			0.865	0.001
<i>Halictus confusus</i>			0.86	0.001
<i>Lasioglossum evylaeus</i> sp			0.752	0.001
<i>Agapostemon texanus</i>			0.694	0.001
<i>Andrena lupinorum</i>			0.689	0.001
<i>Melissodes</i> sp			0.642	0.001
<i>Hylaeus affinis</i>			0.611	0.001
<i>Halictus</i> sp			0.601	0.001
<i>Sphecodes</i> sp			0.569	0.001
<i>Andrena medionitens</i>			0.548	0.001
<i>Agapostemon virescens</i>			0.512	0.001
<i>Hoplitis pilosifrons</i>			0.493	0.002
<i>Nomada</i> sp 5			0.485	0.002
<i>Hylaeus mesillae</i>			0.474	0.002
<i>Hoplitis producta</i>			0.466	0.002
<i>Sphecodes</i> sp 1			0.454	0.001
<i>Halictus ligatus</i>			0.401	0.024
<i>Hylaeus modestus</i>			0.361	0.018
<i>Dianthidium curvatum</i>			0.332	0.018
<i>Nomada</i> sp 3			0.321	0.011
<i>Osmia</i> sp			0.321	0.015
<i>Osmia trevoris</i>			0.312	0.05
<i>Nomada</i> sp			0.306	0.045
<i>Perdita</i> sp			0.297	0.036

Appendix VI: Results of indicator species analyses for all combinations of ecoregion (Grassland, Parkland, Boreal), and land use (canola, rangeland). All species listed had a p -value of <0.05 . Species with p values higher than this are not reported. Where species were identified as indicators for two or more combined regions, the same stats are provided multiple times under each region.

a) 2014

Year	2014											
	Grassland Range		Grassland Canola		Parkland Range		Parkland Canola		Boreal Range		Boreal Canola	
Region and Land Use	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p
Species	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p
<i>Bombus cryptarum</i>											0.886	0.001
<i>Bombus</i> sp											0.633	0.017
<i>Psuedopanurgus</i> sp							0.624	0.04				
<i>Osmia bucephala</i>									0.618	0.019		
<i>Hoplitis spoliata</i>									0.555	0.024		
<i>Agapostemon virescens</i>	0.789	0.002										
<i>Hoplitis pilosifrons</i>	0.619	0.027										
<i>Colletes aberrans</i>	0.535	0.042										
<i>Dianthidium</i> sp	0.512	0.036										
<i>Bombus sandersonii</i>									0.623	0.021	0.623	0.021
<i>Bombus terricola</i>					0.763	0.002					0.763	0.002
<i>Agapostemon texanus</i>	0.907	0.001	0.907	0.001								
<i>Hylaeus affinis</i>					0.697	0.009	0.697	0.009				
<i>Bombus flavifrons</i>							0.634	0.021	0.634	0.021	0.634	0.021
<i>Anthophora terminalis</i>					0.733	0.002	0.733	0.002			0.733	0.002
<i>Megachile inermis</i>					0.644	0.019	0.644	0.019	0.644	0.019		
<i>Lasioglossum</i> sp	0.598	0.048			0.598	0.048			0.598	0.048		
<i>Lasioglossum evylaeus</i> sp	0.846	0.011	0.846	0.011					0.846	0.011	0.846	0.011
<i>Bombus vagans</i>					0.905	0.001	0.905	0.001	0.905	0.001	0.905	0.001
<i>Lasioglossum sensu-stricto</i> sp	0.924	0.005	0.924	0.005	0.924	0.005	0.924	0.005				
<i>Halictus confusus</i>	0.826	0.004			0.826	0.004	0.826	0.004	0.826	0.004		
<i>Andrena</i> sp	0.912	0.016	0.912	0.016	0.912	0.016	0.912	0.016			0.912	0.016

b) 2015

Year	2015											
Region and Land Use	Grassland Range		Grassland Canola		Parkland Range		Parkland Canola		Boreal Range		Boreal Canola	
Species	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p	R^2	p
<i>Bombus cryptarum</i>											0.932	0.001
<i>Psuedopanurgus</i> sp							0.897	0.001				
<i>Agapostemon virescens</i>	0.866	0.001	0.866	0.001								
<i>Bombus terricola</i>											0.915	0.001
<i>Agapostemon texanus</i>	0.944	0.001	0.944	0.001								
<i>Bombus flavifrons</i>									0.96	0	0.96	0.001
<i>Anthophora terminalis</i>					0.81	0.002	0.81	0.002	0.81	0	0.81	0.002
<i>Megachile inermis</i>					0.762	0.005	0.762	0.005			0.762	0.005
<i>Bombus vagans</i>									0.825	0	0.825	0.002
<i>Lasioglossum sensu-stricto</i> sp	0.948	0.011	0.948	0.011	0.948	0.011	0.948	0.011				
<i>Andrena</i> sp	0.975	0.001	0.975	0.001	0.975	0.001	0.975	0.001			0.975	0.001
<i>Megachile frigida</i>											0.659	0.005
<i>Coelioxys funeraria</i>											0.527	0.025
<i>Megachile lapponica</i>											0.527	0.025
<i>Bombus perplexus</i>											0.488	0.049
<i>Osmia trevoris</i>	0.627	0.012										
<i>Osmia</i> sp	0.588	0.017										
<i>Perdita albipennis</i>	0.577	0.025										
<i>Diadasia</i> sp	0.5	0.038										
<i>Nomada</i> sp 6			0.72	0.012			0.72	0.012				
<i>Nomada</i> sp 5			0.69	0.04			0.69	0.04				
<i>Andrena medionitens</i>	0.798	0.002	0.798	0.002								
<i>Halictus ligatus</i>	0.677	0.047	0.677	0.047								
<i>Andrena lupinorum</i>	0.876	0.003	0.876	0.003			0.876	0.003				
<i>Bombus ternarius</i>					0.795	0.002	0.795	0.002	0.795	0	0.795	0.002
<i>Megachile relativa</i>					0.669	0.018	0.669	0.018	0.669	0.02	0.669	0.018
<i>Bombus rufocinctus</i>	0.902	0.026			0.902	0.026	0.902	0.026			0.902	0.026
<i>Halictus rubicundus</i>	0.889	0.036	0.889	0.036	0.889	0.036	0.889	0.036	0.889	0.04		

Appendix VII: Regressions results for relationships between environmental variables and NMDS ordination. Climate data was extracted with the ClimateNA v5.10 softwarepackage, available at <http://tinyurl.com/ClimateNA>, based on methodology described by Wang et al. (2016) for the following variables: MAT=Mean annual temperature, MWMT=Mean warmest month temperature, MCMT=mean coldest month temperature, TD=temperature difference between mean January and July temperatures, MAP=mean annual precipitation, MSP=mean summer precipitation, AHM=annual heat to moisture index, SHM=summer heat to moisture index, DD<0=number of degree days below 0°C, DD>5°C =degree days above 5°C, DD<18=degree days below 18°C, DD>18=degree days above 18°C, NFFD=number of frost free days, FFP=frost free period. Analyses conducted separately for 2 years of survey (2014 and 2015), and across two methods: pan traps and netting.

Environmental Variable	2014 Pan Trap		2014 Nets		2014 Total		2015 Pan Trap		2015 Nets		2015 Total	
	<i>R</i> ²	<i>p</i>										
Latitude	0.531	0.001	0.336	0.001	0.684	0.001	0.767	0.001	0.608	0.001	0.787	0.001
Elevation	0.107	0.037	0.079	0.104	0.162	0.006	0.294	0.001	0.291	0.001	0.361	0.001
MAT	0.245	0.001	0.195	0.002	0.463	0.001	0.420	0.001	0.423	0.001	0.525	0.001
MWMT	0.517	0.001	0.415	0.001	0.628	0.001	0.519	0.001	0.386	0.001	0.586	0.001
MCMT	0.066	0.132	0.089	0.080	0.166	0.002	0.188	0.003	0.253	0.001	0.244	0.001
TD	0.006	0.820	0.087	0.089	0.018	0.599	0.028	0.434	0.058	0.198	0.030	0.425
MAP	0.253	0.002	0.315	0.001	0.225	0.001	0.250	0.001	0.012	0.718	0.174	0.005
MSP	0.276	0.001	0.270	0.001	0.199	0.002	0.258	0.001	0.029	0.462	0.170	0.005
AHM	0.359	0.001	0.405	0.001	0.462	0.001	0.447	0.001	0.147	0.019	0.368	0.001
SHM	0.311	0.001	0.342	0.001	0.260	0.002	0.304	0.001	0.048	0.274	0.205	0.003
DD<0	0.093	0.047	0.097	0.062	0.221	0.001	0.239	0.001	0.291	0.001	0.300	0.001
DD>5	0.314	0.001	0.319	0.001	0.362	0.001	0.290	0.001	0.174	0.006	0.340	0.001
DD<18	0.235	0.001	0.179	0.005	0.450	0.001	0.401	0.001	0.417	0.001	0.508	0.001
DD>18	0.473	0.001	0.479	0.001	0.693	0.001	0.613	0.001	0.477	0.001	0.684	0.001
NFFD	0.035	0.348	0.017	0.615	0.046	0.235	0.129	0.019	0.089	0.085	0.146	0.009
FFP	0.038	0.319	0.038	0.354	0.079	0.091	0.164	0.006	0.144	0.017	0.198	0.002

Appendix VIII: Generalized linear model results between bee abundance, richness, and diversity and four environmental variables: a) Latitude, b) Annual heat to moisture index (AHM), c) Mean annual precipitation (MAP), and d) Degree days over 18°C. Analyses were conducted separately across two years of survey. Abundance variables were tested using a negative binomial distribution and Wild's chi-square test, whereas richness and diversity followed a normal distribution and were tested using Type III ANOVA. Significant ($p < 0.05$) values are bolded; marginally significant ($p < 0.10$) are italicized.

A)		Latitude			Land Use Type			Latitude~Land Use		
Year	Variable	<i>df</i>	X^2/F	<i>p</i>	<i>df</i>	X^2/F	<i>p</i>	<i>df</i>	X^2/F	<i>p</i>
2014	Total Abundance	1,59	70.93	0.00	1,58	69.99	0.33	1,57	64.92	0.02
	Total Richness	1,57	1.20	0.28	1,57	5.52	0.02	1,57	5.12	0.03
	Total Diversity	1,57	1.35	0.25	1,57	0.00	0.98	1,57	0.00	1.00
2015	Total Abundance	1,58	74.68	0.00	1,57	62.36	0.00	1,56	62.36	0.98
	Total Richness	1,56	0.04	0.84	1,56	5.96	0.02	1,56	6.08	0.02
	Total Diversity	1,56	0.55	0.46	1,56	0.56	0.46	1,56	0.65	0.42

B)		AHM			Land Use Type			AHM~Land Use		
Year	Variable	<i>df</i>	X^2/F	<i>p</i>	<i>df</i>	X^2/F	<i>p</i>	<i>df</i>	X^2/F	<i>p</i>
2014	Total Abundance	1,59	76.75	0.00	1,58	75.79	0.33	1,57	64.71	0.00
	Total Richness	1,57	2.44	0.12	1,57	3.09	<i>0.08</i>	1,57	4.68	0.03
	Total Diversity	1,57	0.12	0.73	1,57	1.82	0.18	1,57	1.75	0.19
2015	Total Abundance	1,58	75.99	0.00	1,57	63.75	0.00	1,56	63.01	0.39
	Total Richness	1,56	0.03	0.86	1,56	13.01	0.00	1,56	13.01	0.00
	Total Diversity	1,56	0.08	0.78	1,56	5.50	0.02	1,56	4.29	0.04

C)		MAP			Land Use Type			MAP~Land Use		
Year	Variable	<i>df</i>	X^2/F	<i>p</i>	<i>df</i>	X^2/F	<i>p</i>	<i>df</i>	X^2/F	<i>p</i>
2014	Total Abundance	1,49	72.29	0.02	1,58	70.01	0.13	1,57	65.24	0.03
	Total Richness	1,57	0.89	0.35	1,57	3.50	<i>0.07</i>	1,57	2.35	0.13
	Total Diversity	1,57	0.28	0.60	1,57	0.50	0.48	1,57	0.55	0.46
2015	Total Abundance	1,58	72.68	0.02	1,57	63.98	0.00	1,56	63.47	0.47
	Total Richness	1,56	0.11	0.74	1,56	7.98	0.01	1,56	9.07	0.00

Total Diversity	1,56	0.14	0.71	1,56	10.28	0.00	1,56	12.93	0.00
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D)		DD over 18°C			Land Use Type			DD~Land Use		
Year	Variable	df	X ² /F	p	df	X ² /F	p	df	X ² /F	p
2014	Total Abundance	1,59	69.45	0.00	1,58	69.38	0.80	1,57	64.10	0.02
	Total Richness	1,57	0.74	0.39	1,57	0.94	0.34	1,57	5.48	0.02
	Total Diversity	1,57	0.51	0.48	1,57	0.27	0.61	1,57	0.06	0.81
2015	Total Abundance	1,58	76.83	0.00	1,57	62.86	0.00	1,56	62.86	0.93
	Total Richness	1,56	0.24	0.63	1,56	2.42	0.13	1,56	1.74	0.19
	Total Diversity	1,56	0.00	0.97	1,56	0.45	0.50	1,56	0.03	0.87

Appendix IX: Description of land cover variables. Taken from ABMI (2010).

Final Variable	Original Variable(s)	Description
Water	Water	Lakes, lagoons, rivers, canals, and artificial water bodies. Shallow open water is included in this category, unless there is more than 20% vegetation cover, in which case it belongs to the relevant vegetated class.
Crop	Agriculture	Annually cultivated cropland, tame pastures (fields planted or sown with non-native grasses/legumes where livestock is directly grazing on them), forage crops (same as tame pasture, but instead cut for hay) and woody perennial crops (fruit orchards and vineyards). Includes annual field crops, vegetables, summer fallow, orchards and vineyards. Bare agricultural soil (i.e., tilled) belongs to this class.
Grassland	Grassland	Predominantly native grasses and other herbaceous vegetation with a minimum of 20% ground cover; may include some shrub cover (but less than a third of the vegetated area) or a few trees (but the tree cover cannot exceed 10%). Land used for range or native unimproved pasture (e.g., rough fescue) is included in this class. Alpine meadows fall into this class. Marshes and other non-woody wetlands with at least 20% vegetation cover (sedges, cattails, or moss) belong to this class.
Shrubland	Shrubland	At least 20% ground cover which is at least one-third shrub, with no or little presence of trees (<10% crown closure). Examples of plants belonging to this class are alder, willow, juniper, and sagebrush. Shrubby fens and other non-treed woody wetlands, usually associated with floodplains and the shores of lakes and streams, belong to this class.
Developed	Developed	Urban and built-up areas (including industrial sites), impervious artificial surfaces (e.g. airport runways), railways and roads. Acreages and farmsteads are included in this class. Oil and gas well pads are included in this class if connected to a road and not abandoned or under reclamation. Urban terrain under development is included in this class, even if the land is exposed. Urban green areas are excluded from this class if larger than 2 ha and if they have less than 2 buildings per hectare.
Forest	Broadleaf Forest	Treed areas with at least a 10% crown closure of trees, where broadleaf trees (trembling aspen, balsam poplar and white birch) are 75% or more of the crown closure. Providing crown closure is more than 10% and dominated by broadleaf trees, young plantations or regenerating cutblocks, and treed swamps along floodplains or wetlands are included in this class providing mean tree height exceeds 2 m.
	Conifer Forest	Treed areas with at least a 10% crown closure of trees, where coniferous trees (spruce, pine, fir, larch) are 75% or more of the crown closure. Providing crown closure is more than 10% and dominated by conifers, young plantations or regenerating cutblocks, and treed wetlands (e.g. black spruce bogs and fens) are included in this class providing mean tree height exceeds 2 m.
	Mixed Forest	Treed areas with at least a 10% crown closure of trees, where neither coniferous nor broadleaf trees account for 75% or more of crown closure.
Bare Ground	Exposed Land	Bare soil (barren, non-agricultural), river sediments and cut banks, pond or lake sediments, reservoir margins, beaches, landings, recently burned areas, mudflat sediments, surface mining, or other non-vegetated (less than 6% trees, or less than 20% shrub/herb) surfaces.

Appendix X: General summary of land cover variables across range and canola sites. Values provide the range (minimum value and maximum value) and average percent of each cover type found in rangeland and canola, across two buffered scales: 2 km, 1 km, or 500 m radius.

Land Cover Category	Minimum Value	Maximum Value	Rangeland Average	Canola Average
Forest 2 km	0	50.47	15.58	9.38
Forest 1 km	0	38.20	13.13	3.33
Forest 500 m	0	21.15	8.28	1.74
Crop 2 km	0	92.50	27.42	73.45
Crop 1 km	0	94.03	25.61	79.85
Crop 500 m	0	90.99	26.25	82.99
Developed 2 km	1.06	21.74	6.57	6.89
Developed 1 km	0	19.84	8.23	8.35
Developed 500 m	0	27.80	10.48	9.77
Grassland 2 km	0	95.79	44.31	7.56
Grassland 1 km	0	96.03	47.62	6.25
Grassland 500 m	0	99.87	49.23	4.52
Shrubland 2 km	0	53.85	4.37	0.85
Shrubland 1 km	0	49.97	4.33	1.09
Shrubland 500 m	0	38.59	5.2	0.68
Water 2 km	0	28.67	1.66	1.84
Water 1 km	0	13.74	1.04	1.11
Water 500 m	0	8.73	0.56	0.29

Appendix XI: Results of *stepAIC* model selection process. Model selection was done 36 times across combinations of year, land use type, and landscape scale (a 2 km, 1 km, or 500 m radius buffer around each site). Within each data subset, I conducted model selection using the *stepAIC* function in R for bee abundance, richness, and diversity. Within each instance of model selection, I selected final model parameters based off of the *stepAIC* output for significance testing. Equally likely models (within 2 AIC counts of the lowest AIC score) were all evaluated for variable significance; in all cases, significance did not change across models. Models with the lowest number of parameters were selected as the final models. Significance testing was conducted using the *lmer* function with ecological region as a random factor. Abundance variables were log-transformed prior to analysis, and all models were tested using Type III Analysis of Variance (ANOVA) Wald's F tests. Final parameters for each model are listed, significant ($p < 0.05$) variables are bolded, marginally significant ($p < 0.10$) variables are italicized.

			Range		Canola		
		Bee Richness	Bee Diversity	Bee Abundance	Bee Richness	Bee Diversity	Bee Abundance
2 km	2014	Forest	Forest, Crop, Developed, Grassland, Shrubland, Water	Forest, Crop, Developed, <i>Shrubland</i>	Developed	Forest, Shrubland, Developed	<i>Forest</i> , Developed
	2015	Forest, Crop, Shrubland, Water	Forest, Crop, Developed, Grassland, Shrubland	Forest, Crop, Developed, <i>Shrubland</i>	Crop, <i>Developed</i> , Grassland	Crop	<i>Crop</i> , Grassland, Shrubland
1 km	2014	<i>Grassland</i> , Crop	Grassland	Forest, Crop, Developed, Grassland, Shrubland	Shrubland , <i>Grassland</i>	Crop, Developed, Grassland	Forest
	2015	Forest, Crop, Developed, Shrubland	<i>Crop, Developed, Grassland</i> , Shrubland , Water	Forest, Crop, Developed, <i>Grassland</i> , Shrubland	Water	<i>Developed</i>	Crop, Developed
500 m	2014	Shrubland	Water	Forest, Crop, Shrubland, Water	Shrubland	Grassland	Forest, Crop, Developed, Grassland, Shrubland, Water
	2015	Crop, Shrubland	<i>Forest, Crop, Developed, Grassland</i> , <i>Shrubland</i> , Water	Forest, Crop, <i>Shrubland</i> , Water	Developed	Crop	<i>Crop</i> , Developed, Grassland, Shrubland , Water

Appendix XII:

a) Results of linear mixed effects models testing the relationships between landscape variables, land use type, and their interaction at three spatial scales with: bee abundance, richness, diversity, and evenness. Landscape heterogeneity model results are shown in the top half, while results for percentage grassland cover are shown in the bottom half. Model significance was tested using Type III ANOVA Wald's F Tests. Abundance was log-transformed prior to analysis. Significant differences ($p < 0.05$) are bolded; marginally significant differences ($p < 0.10$) are italicized.

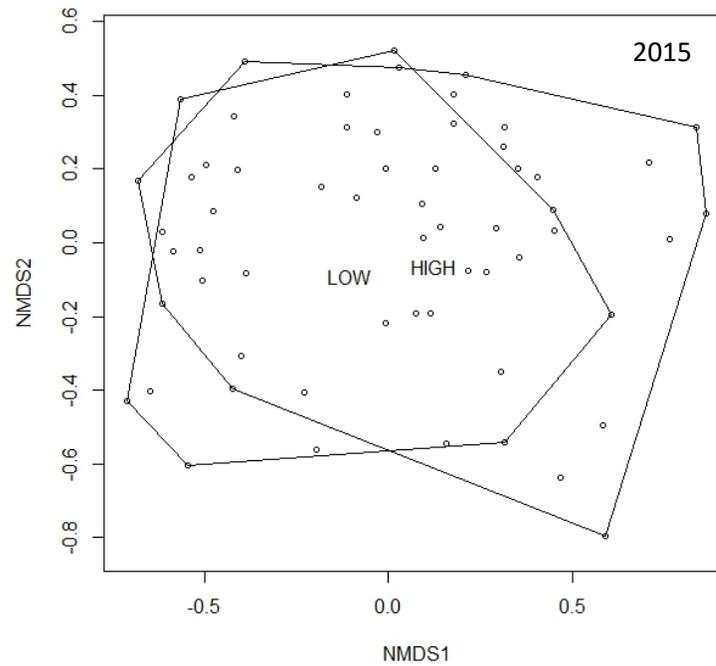
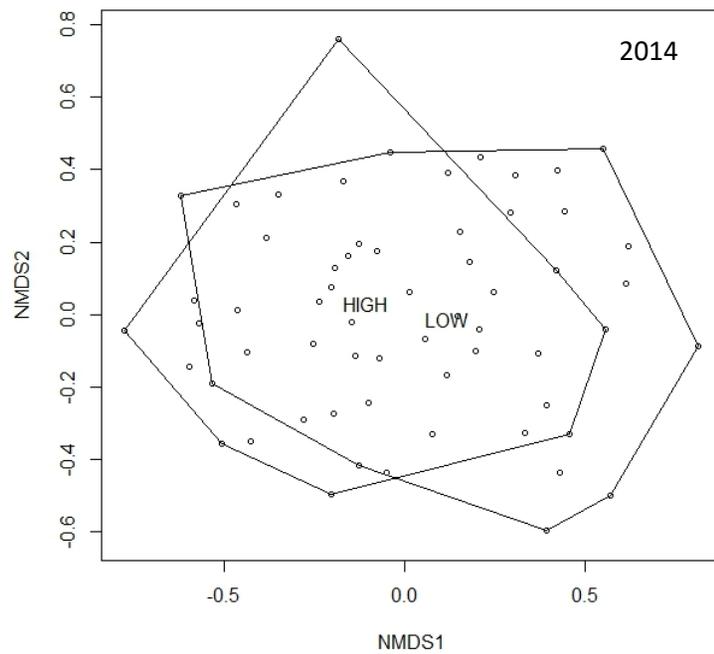
	2 km landscape heterogeneity			2 km Land Use			2 km Landscape*Land Use			1 km Landscape Heterogeneity			1 km Land Use			1 km Landscape*Land Use			500 m Landscape Heterogeneity			500 m Land Use			500 m Landscape*Land Use			
	2014	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Richness		1,57	0.58	0.45	1,56	3.94	0.05	1,56	1.52	0.22	<i>1,57</i>	<i>2.94</i>	<i>0.09</i>	1,56	6.48	0.01	<i>1,56</i>	<i>3.43</i>	<i>0.07</i>	1,57	0.72	0.40	<i>1,56</i>	<i>3.56</i>	<i>0.06</i>	1,56	1.06	0.31
Diversity		1,57	0.98	0.33	1,56	1.00	0.32	1,56	0.71	0.40	1,57	0.40	0.53	1,56	1.05	0.31	1,56	0.78	0.38	1,57	0.45	0.50	1,56	0.30	0.59	1,56	0.10	0.75
Abundance		1,56	0.27	0.60	1,55	6.43	0.01	<i>1,55</i>	<i>3.38</i>	<i>0.07</i>	1,55	0.93	0.34	1,55	5.85	0.02	<i>1,55</i>	<i>3.07</i>	<i>0.09</i>	1,56	0.02	0.88	1,55	2.30	0.13	1,55	0.32	0.58
Species Evenness		1,56	0.00	0.97	1,55	4.49	0.04	<i>1,55</i>	<i>2.89</i>	<i>0.09</i>	1,56	0.42	0.52	1,55	5.08	0.03	<i>1,55</i>	<i>3.61</i>	<i>0.06</i>	1,57	0.00	0.95	1,56	2.61	0.11	1,56	1.17	0.28
	2015	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Richness		1,56	0.35	0.56	1,54	0.18	0.67	1,54	0.07	0.79	<i>1,56</i>	<i>3.15</i>	<i>0.08</i>	1,54	0.01	0.94	1,54	0.19	0.67	1,56	0.19	0.66	1,54	0.07	0.79	1,54	0.01	0.93
Diversity		1,56	0.69	0.41	1,54	0.02	0.89	1,54	0.21	0.65	1,56	0.77	0.38	1,54	0.10	0.76	1,54	0.13	0.72	1,56	0.89	0.35	1,54	0.21	0.65	1,54	0.09	0.77
Abundance		1,55	1.06	0.31	1,54	4.29	0.04	1,54	1.99	0.16	1,55	0.02	0.89	1,54	2.51	0.12	1,54	0.60	0.44	1,56	0.01	0.92	<i>1,54</i>	<i>3.52</i>	<i>0.07</i>	1,54	0.88	0.35
Species Evenness		1,55	2.04	0.16	1,54	0.72	0.40	1,54	0.98	0.33	1,54	0.91	0.35	1,54	0.23	0.63	1,54	0.38	0.54	1,54	0.55	0.46	1,55	0.15	0.70	1,54	0.25	0.62
	2014	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Richness		1,53	0.28	0.60	1,54	0.04	0.84	1,57	0.00	0.99	1,57	1.31	0.26	1,50	0.08	0.78	1,56	0.17	0.68	1,57	0.32	0.58	1,53	0.12	0.73	1,57	0.01	0.94
Diversity		1,53	0.00	0.99	1,54	1.15	0.29	1,57	0.17	0.68	1,57	0.08	0.78	1,50	0.64	0.43	1,56	0.01	0.91	1,56	0.12	0.73	1,54	0.00	0.99	1,57	0.11	0.74
Abundance		1,56	0.03	0.87	1,57	0.08	0.77	1,55	0.17	0.68	1,55	0.12	0.73	1,57	0.01	0.94	1,55	0.04	0.85	1,55	0.04	0.83	1,57	0.06	0.81	1,56	0.39	0.54
Species Evenness		1,57	0.07	0.79	1,56	0.40	0.53	1,56	0.05	0.82	1,56	0.68	0.41	1,55	0.06	0.81	1,56	0.10	0.75	1,56	0.44	0.51	1,56	0.13	0.72	1,56	0.24	0.63
	2015	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
Richness		1,56	1.34	0.25	1,56	6.91	0.01	<i>1,55</i>	<i>3.36</i>	<i>0.07</i>	1,55	1.29	0.26	<i>1,53</i>	<i>3.02</i>	<i>0.09</i>	1,54	0.30	0.59	1,56	0.06	0.81	1,50	8.64	0.00	1,55	0.00	0.95
Diversity		1,56	0.00	0.95	1,56	2.44	0.12	1,55	0.11	0.75	1,55	0.19	0.66	1,53	2.23	0.14	1,56	0.03	0.86	1,56	0.11	0.74	1,51	4.75	0.03	1,56	0.03	0.87
Abundance		1,55	0.01	0.92	<i>1,54</i>	<i>3.52</i>	<i>0.07</i>	1,54	0.88	0.35	1,55	0.38	0.54	1,56	4.84	0.03	1,55	0.72	0.40	1,55	0.38	0.54	<i>1,56</i>	<i>4.11</i>	<i>0.05</i>	1,55	0.48	0.49
Species Evenness		1,55	0.30	0.59	1,56	0.11	0.74	1,55	0.33	0.57	1,55	0.22	0.64	1,54	0.03	0.87	1,56	0.21	0.65	1,56	0.06	0.81	1,54	0.23	0.64	1,56	0.03	0.85

b) Results of linear mixed effects models testing the relationships between landscape variables, land use type, and their interaction at three spatial scales with: *Bombus* abundance, Megachilidae abundance, and *Lasioglossum* abundance. Model results for percentage grassland cover are shown in the top half of the table, while results for landscape heterogeneity are shown in the bottom half. Model significance was tested using Type III ANOVA Wald's F Tests. Data was log-transformed prior to analysis. Significant differences ($p < 0.05$) are bolded; marginally significant differences ($p < 0.10$) are italicized.

Grassland Cover	2 km Grassland Cover			2 km Land Use			2 km Grassland X Land Use			1 km Grassland Cover			1 km Land Use			1 km Grassland X Land Use			500 m Grassland Cover			500 m Land Use			500 m Grassland X Land Use			
	2014	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
<i>Bombus</i> Abundance	1,5	0.0	0.9	1,5	2.95	0.0	1,5	0.3	0.5	1,5	0.3	0.5	1,5	4.68	0.0	1,5	1.89	0.1	1,5	0.0	0.8	1,5	4.4	0.0	1,5	1.1	0.2	
Megachilidae Abundance	1,5	0.1	0.7	1,5	0.94	0.3	1,5	0.4	0.5	1,5	0.0	0.9	1,5	2.23	0.1	1,5	0.02	0.8	1,5	0.0	0.7	<i>1,5</i>	<i>3.6</i>	<i>0.0</i>	1,5	0.0	0.7	
<i>Lasioglossum</i> Abundance	1,5	0.9	0.3	1,5	0.16	0.6	1,5	0.0	0.8	1,5	1.0	0.3	1,5	0.16	0.6	1,5	0.00	0.9	1,5	0.0	0.8	1,5	0.0	0.9	1,5	0.2	0.6	
	6	3	4	7		9	5	2	8	5	4	1	7		9	5	4	7	4	7	0	9	6	2	4			
	2015	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
<i>Bombus</i> Abundance	1,5	0.0	0.7	1,5	0.04	0.8	1,5	0.0	0.7	1,5	0.2	0.6	1,5	0.40	0.5	1,5	0.21	0.6	1,5	0.0	0.8	1,5	0.0	0.7	1,5	0.0	0.8	
Megachilidae Abundance	1,5	1.1	0.2	1,5	0.19	0.6	1,5	2.5	0.1	1,5	1.1	0.2	1,5	0.12	0.7	1,5	0.38	0.5	1,5	0.0	0.9	1,5	0.0	0.9	1,5	0.0	0.8	
<i>Lasioglossum</i> Abundance	1,5	2.7	0.1	1,5	6.88	0.0	1,5	4.7	0.0	1,5	1.4	0.2	1,5	5.62	0.0	1,5	2.61	0.1	1,5	1.0	0.3	1,5	3.8	0.0	1,5	1.4	0.2	
	5	2	1	5		1	4	2	3	5	2	4	6		2	6	2	1	5	9	0	6	1	6	6	1	4	
	2015	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
<i>Bombus</i> Abundance	1,5	2.1	0.1	1,5	1.13	0.2	1,5	1.0	0.3	1,5	0.0	0.8	1,5	0.04	0.8	1,5	0.00	0.9	1,5	1.1	0.2	1,5	0.1	0.7	1,5	0.7	0.3	
Megachilidae Abundance	1,5	0.0	0.9	1,5	5.70	0.0	1,5	2.5	0.1	1,5	0.0	0.8	1,5	6.87	0.0	<i>1,5</i>	<i>3.12</i>	<i>0.0</i>	1,5	0.1	0.7	1,5	4.3	0.0	1,5	1.3	0.2	
<i>Lasioglossum</i> Abundance	1,5	0.6	0.4	1,5	12.9	0.0	1,5	7.4	0.0	1,5	2.5	0.1	1,5	16.6	0.0	1,5	10.4	0.0	1,5	0.8	0.3	1,5	8.7	0.0	<i>1,5</i>	3.8	0.0	
	6	8	1	5		7	0	5	8	1	6	0	2	5		4	0	5	6	0	7	6	7	0	6	2	6	
	2015	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p	df	F	p
<i>Bombus</i> Abundance	<i>1,5</i>	3.6	0.0	1,5	1.23	0.2	1,5	2.2	0.1	1,5	4.8	0.0	1,5	1.04	0.3	1,5	2.38	0.1	1,5	0.1	0.7	1,5	4.3	0.0	1,5	1.3	0.2	
Megachilidae Abundance	<i>1,5</i>	3.4	0.0	1,5	7.30	0.0	<i>1,5</i>	4.0	0.0	1,5	4.3	0.0	1,5	7.51	0.0	1,5	4.27	0.0	1,5	0.1	0.7	1,5	1.7	0.1	1,5	0.1	0.6	
<i>Lasioglossum</i> Abundance	1,5	1.3	0.2	1,5	2.06	0.1	1,5	1.4	0.2	1,5	0.3	0.5	1,5	0.03	0.8	1,5	0.06	0.8	1,5	2.1	0.1	1,5	0.0	0.8	1,5	0.7	0.4	
	6	2	5	4		6	4	5	3	6	2	8	4		6	4	0	6	8	5	4	5	3	4	0	1		

Appendix XIII:

- a) Non-metric multidimensional scaling (NMDS) ordination of bee communities. Differences in bee community composition were assessed using Bray-Curtis distance estimation method across two survey years: 2014 (left), and 2015 (right). Differences were assessed across two categories of landscape heterogeneity—high vs low. Hulls were plotted using the *ordihull* function in R. These results represent a 2-dimensional solution, with final stress values of 0.263 for the 2014 ordination, and 0.235 for the 2015 ordination.



b) Non-metric multidimensional scaling (NMDS) ordination of bee communities. Differences in bee community composition were assessed using Bray-Curtis distance estimation method across two survey years: 2014 (left), and 2015 (right). Differences were assessed across four categories of percentage grassland cover: None (0%), Low (0-30%), Medium (30-60%), and High (60-100%). Hulls were plotted using the *ordispider* function in R. These results represent a 2-dimensional solution, with final stress values of 0.263 for the 2014 ordination, and 0.235 for the 2015 ordination.

