Indicators of native bee communities in Alberta's agricultural zone

by

Ashton Brook Sturm

A thesis submitted in partial fulfillment of the requirements for the degree of

Master of Science
in
Plant Science

Department of Agricultural, Food and Nutritional Science
University of Alberta

Abstract

Bees are a key component of terrestrial ecosystems and provide valuable ecosystem services to both natural and agricultural landscapes. It estimated that 87.5% of native plants benefit from pollination, including 1/3 of global food crops. Additionally, pollination by bees provides maximized yields for commercial pulse crops, which has significant economic benefits. Unfortunately, bees are in decline. With an increasing demand for higher crop production to support the growing human population, the need for conservation efforts to maintain native bee populations is becoming increasingly important. In this study, I investigated how two major agricultural practices (grazing by livestock and production of canola, *Brassica napus*) in Alberta affected native bee pollinators and assessed whether an apex group of the bee community (cleptoparasites) could be used as an indicator taxa to predict the size and species richness of the non-parasitic bee community. I evaluated bee responses to changes in the flowering plant community and land use type, across a large environmental gradient over a two-year study period. I used rangeland health assessments to determine the condition of grasslands from grazing, and compared bee community abundance, richness, diversity and evenness to varying degrees of rangeland health across four study regions. Grazed sites that were considered healthy had higher bee abundance, richness and diversity than grazed sites that were unhealthy, suggesting that grazing can be beneficial to the bee community when managed appropriately. Cleptoparasites were useful for predicting overall bee community abundance in both grasslands and canola fields when environmental conditions were unfavorable, however when floral resources were abundant this relationship was lost. In addition, cleptoparasite richness did not predict bee community richness. Overall, the cleptoparasite guild was not an effective indicator taxa for the larger bee community in this study system. Results from this work suggests that assessing bee communities for conservation, and implementing effective monitoring schemes is a complex task. Finding alternative strategies, including the investigation of prospective indicator taxa is important, but managing for biodiversity through responsible land use is essential. This study demonstrates that cattle producers can aid in conservation efforts for native bee communities through responsible range management.

I dedicate this body of work to myself.

The struggle was real.

Acknowledgements

First and foremost I would like to thank my partner Daniel Golec for all of the love and support you have provided me throughout this experience. I will forever be grateful. Many thanks to my family and friends for their encouragement and excess of motivational speeches, and of course my "bee wife" Monica Kohler. Having the opportunity to collaborate with you on this project has meant so much to me. Thank you to my committee members and supervisors including Cameron Carlyle, Jessamyn Manson, Cory Sheffield and Nadir Erbilgin. Each of you has had such an impact on me as a person and as a scientist. I feel so fortunate to have had such an amazing group of people mentor and inspire me.

I am indebted to the cohort of field assistants and volunteers who generously donated their time, and travelled many hours exploring this beautiful province with me. Jennifer Nichols a.k.a Jenji, you were the best field assistant a human could ask for. Thank you to the U of A for being my home for the last eight years. During that time I not only found my amazing partner but, an unparalleled university family – (Monica Kohler, Angela Phung, Sean Chaun, Monica Higuera, Britney Miller, Jennifer Klutsch, Gisela Stotz, Gregory Peck, Tan Bao, Jennifer Nichols, Jenny Kleininger, Alec Carrigy, Giovanny Fagua Gonzalas, Ronald Batallas, Carly Moore, Lysandra Pyle, Crisia Tabacaru, Michael Foisy, Dylan Sjolie, and of course Cam and Jess- you were excellent academic parents). I have so much love and respect for all of you. Thank you for your friendship and guidance. Thank you to our amazing land owners. Without your participation in this project, it would cease to exist.

Finally, this project would not have been possible without the generous financial and technical support from the following institutions and organizations: the Alberta Livestock and Meat Agency Ltd. (ALMA), the Alberta Biodiversity Monitoring Institute (ABMI), the Alberta

Conservation Association (ACA), the Rangeland Research Institute (RRI) and Alberta Environment and Parks (AEP).

Table of contents

List of figures

List of tables

List of symbols and abbreviations

RHS – Rangeland health scores

FA – Flower abundance

NR - Natural region

FC – Percent forb cover

Clepto(s) – Cleptoparasitic bee guild

Host(s) – Taxa that are known to be parasitized by cleptoparasites

Non-host(s) – Taxa that have no known host: parasite relationships with cleptoparasites

Chapter one: An introduction to the effects of livestock grazing on bees and the importance of monitoring schemes for conservation

Animal-mediated pollination is an essential ecosystem service that contributes to the production of 1/3 of global food crops and is crucial for maintaining diversity and richness of flowering plants (Kremen et al., 2007; Roulston & Goodell 2010; Allsopp, De Lange, & Veldtman 2008). In fact, it is estimated that 87.5% of flowering plants rely on animal pollinators for sexual reproduction (Ollerton et al., 2011), including many fruit and vegetable crops that are essential for maintaining human health (Kremen et al., 2007; Steffan-Dewenter et al., 2005). While animal pollinators include many insects, birds and mammals, bees are among the most efficient at moving pollen between plants and plant populations, which enhances genetic diversity within and between plant communities, and are the primary pollinators of human valued food crops (Roulston & Goodell 2010).

Bees are among the some of the most diverse animal taxa, with an estimated 20,000 bee species globally (Michener 2007). Native bees, which are distinct in North America from the commercialized honey bee (*Apis mellifera*) in their origin and in their management, have diverse life history traits and exhibit a range of behavioural and reproductive strategies including floral specialization, facultative or obligate sociality, and cleptoparasitism. Unfortunately, both commercialized and native bee populations are currently at risk. Bee declines have been reported globally (Potts et al., 2010; Burkle et al., 2013; Goulson et al., 2015), with potential causes including, increased use of agrochemicals (Gill, Ramos-Rodriguez & Raine 2012), habitat loss and fragmentation (Winfree et al., 2009; Potts et al., 2010) and disturbance due to changes in land use (Foley et al., 2005) including grazing by livestock (Kruess & Tscharntke 2002; Xie et al., 2008).

Grazing is one of the most extensive land uses on earth, and affects both plant and animal communities (Eldridge et al., 2016). Impacts of grazers on invertebrate communities can be both direct and indirect. Cattle can directly reduce bee populations through destruction of existing nest sites and trampling of adult bees (Sugden 1985; Black et al., 2011) and indirectly through modifications of the plant community, including removal of floral resources or reduction of competitive non-flowering species, which can increase flowering plant abundance (Vuillamy et al., 2006). There is evidence for positive (Carvell 2002; Vuillamy et al., 2006), negative (Kruess & Tscharntke 2002; Xie et al., 2008) and null effects (Sjodin et al., 2008; Elwell et al., 2016) of livestock grazing on bee communities. These conflicting results are a consequence of variation in four main factors: the type of grazer under investigation (Kimuyu et al., 2014), the intensity of grazing pressure (lunt et al., 2007), the level of plant productivity (Proulx & Mazumder 1998) and the evolutionary history of grazing (Milchunas & Lauenroth 1993). Understanding the effects of grazing within an ecosystem can have significant implications for conservation and management practices.

Grazing is a common practice in Canada's prairie region, where native prairie remnants provide essential ecological goods and services. Unfortunately, only 25-30% of these native areas remain, with much of that designated as rangeland or grazing lands (Hammermeister et al., 2001) and merely 3.5% of the area protected under some form of conservation status (Gauthier & Wiken 2003). Much of the surrounding area has been converted to crop production, and experiences regular disturbance by production practices, including tilling, irrigation, and removal of woody debris, making it difficult for bees to find suitable nesting sites (Kremen et al., 2007).

These remaining prairie grasslands support native bee communities in two key ways. First, they provide a diverse flowering plant community, with a continuous supply of pollen and nectar throughout the growing season, supporting growth and reproduction of bee populations (Black et al., 2011; Sheffield, Frier & Dumesh 2014.) Second, grasslands provide undisturbed nesting habitat, demonstrated as the underlying limiting factor for native bee prevalence (Cane 2001; Cane & Tepedino 2001).

The Canadian prairies have a long evolutionary history of grazing. Disturbance from grazing, fire and drought has shaped the landscape and selected for biota that can withstand frequent perturbation (Anderson 2006). The prairie grasslands are broken up into ecoregions with distinct climatic conditions and corresponding plant communities, including dry mixed grass, mixed grass, parkland, and foothills fescue (Bailey, Schellenberg & McCartney 2010). According to the 2007 global synthesis of plant trait responses to grazing (Diaz et al., 2007), climatic and historical contexts are essential for understanding how grazing affects plant traits and responses are specific to regions with different climate and herbivory history. Therefore, addressing the differences in plant and bee community responses to grazing across a climatic gradient is essential for management implications for grasslands.

In addition to understanding the effects of human mediated disturbance on native species, it is imperative that researchers continue to develop cost- and time-effective strategies for assessing the status of native bee communities. There is little baseline data on bee populations within the Canadian Prairies (Sheffield, Frier & Dumesh 2014), and the impacts of grazing on pollinator diversity has seldom been evaluated in North America (Elwell, Griswold & Elle 2016). Monitoring bees can be difficult and expensive because it requires a large number of sites, multiple site visits, multiple seasons to capture inter-annual variation, and specialized taxonomic training for correct species identification. Traditional survey methods can provide extensive data on bee communities (see Chapter 2), but are incredibly labor intensive. One strategy to surmount the challenge of managing bee biodiversity is to identify an indicator taxa or guild / functional group (Williams, Minckley & Silviera 2001; Cane et al., 2006; Murray, Kuhlmann & Potts 2009; Williams et al., 2010; Sheffield et al., 2013a). Cleptoparasites, which rely on host bees to provide for their offspring, have been proposed as potential indicator guild (Sheffield et al., 2013a). Cleptoparasite abundance is dependent on host bee abundance which is determined by the number of floral and nesting resources available to them in any area. Using this knowledge and focusing monitoring efforts on a specific group to infer the effects of disturbance or habitat quality could be a viable alternative to capturing and identifying whole communities of native bees, provided they act as indicators for the overall bee community. Generating baseline data and developing tools to monitor changes within bee communities in response to human-mediated disturbance is essential for future management of bee biodiversity and the ecological goods and services they provide.

Summary

In the next two chapters, I will investigate i) the effects of grazing on plant and bee communities across a large environmental gradient, and ii) the potential of the cleptoparasitic guild to represent the overall, host and non-host bee community responses to changes in land-use and climate. I will do this by i) evaluating the effects of grazing on plant abundance, richness, percent forb cover and plant productivity; in turn, I examine how the plant community affects bee abundance, richness, diversity and evenness (Chapter 2), and ii) assessing the relationship between cleptoparasite abundance and richness as predictors for overall, host and non-host bee abundance and diversity, and how these relationships change depending on land-use type and region (Chapter 3).

Increasing our understanding of land use change and land management practices on native bee communities, including the use of prospective indicator strategies, will enable researchers to better understand bee responses to two main land-uses across a large scale agro-environmental gradient, feasibly aiding in the conservation of native bee communities.

Chapter two: Evaluating indirect effects of long term grazing on wild bee communities using rangeland health assessments in temperate grasslands

Introduction

Concern over the health and stability of managed pollinators has triggered an increasing interest in native pollinator communities worldwide (Cane & Tepedino 2001; Biesmeijer et al., 2006; Potts et al., 2010; Winfree et al., 2011). Despite their importance as a failsafe to managed bees for pollination in agricultural ecosystems (Morandin & Winston 2005) and their key role in maintaining natural ecosystems, there is limited data available about native bee diversity, abundance or habitat use globally (Potts et al., 2010). Moreover, recent declines in native bees have been attributed to multiple factors including climate change, agricultural intensification, urbanization, and habitat loss (Cane 2001; Goulson et al., 2005; Brown & Paxton 2009; Winfree et al., 2009; Potts et al., 2010), putting their contributions to ecosystem services at risk. Natural areas such as grasslands serve as important habitat reservoirs for native bee communities by providing quality floral and nesting resources (Ockinger & Smith 2006, 2007; Potts et al., 2010; Black et al., 2011). However, extensive conversion of native grasslands for agriculture (Conant et al., 2001; Wright & Wimberly 2013), oil and gas exploration (Braun et al., 2002), and urban development has drastically reduced the area of remaining native grasslands, and the majority of remaining grasslands are used for livestock grazing (Gauthier & Wiken 2003). Grazing can alter grassland ecosystems through changes to the structure and function of the plant community (Potts et al., 2003), but little is known about the consequences of changes in the plant community, due to grazing, on native bee communities in temperate grasslands.

Bees provided critical pollination services that support the productivity and diversity of plant communities. Bees contribute to energy rich food webs (Black et al., 2011) and sustainable food production (Foley et al., 2005) by increasing seed set (Ashman et al., 2004), genetic variation, and overall resiliency of plant populations to disturbance (Hughes and Stachowicz 2004). The health and diversity of bee communities are directly linked to the abundance and richness of the floral community they visit and inhabit (Potts et al., 2003; Vulliamy et al., 2006; Biesmeijer et al., 2006). As bees are reliant on floral resources such as nectar and pollen for reproduction (Michener 2007), the availability and quality of floral resources are fundamental for shaping the structure of native bee communities (Potts et al., 2003). Consequently, if floral resources are reduced the fecundity, fitness, and survival of bees will also decline (Cane & Tepedino 2001; Potts et al., 2003), and can result in local exclusion of rare or uncommon species with small populations or limited diet breadth (Cane & Tepedino 2001; Shavit, Dafni & Ne'eman 2009). Therefore, in order to conserve bee communities it is critical to understand the effect of disturbance on floral resources and subsequently the bee communities themselves.

The grasslands of North America have been shaped by disturbance (Anderson 2006). Fire, grazing, and periodic droughts are essential for the maintenance of grassland ecosystems by inhibiting encroachment of woody species. As a keystone process, grazing by large herbivores has been shown to increase plant diversity (Milchunas et al., 1988; Huntley 1991), aid in nutrient cycling (Haynes & Williams 1993), create landscape heterogeneity and promote the establishment of a plant community that provides floral resources throughout the growing season (Black et al., 2011). Moderate levels of grazing has been shown to increase the production of forb species in fescue grasslands (Willms et al., 1985). Responses of the plant community to grazing are dependent on several factors including climate, topography, nutrient availability, and grazing history (Olff and Ritchie 1998; Anderson 2006). Timing and intensity of grazing can also influence ecosystem function (Willms 1991; Fuhlendorf & Engle 2001; Anser et al., 2004; Hickman et al., 2004). Areas of over grazing can experience significant changes to soil moisture as a result of compacted soils and reduced herbaceous cover, which promotes unstable soil surfaces, increases run off and losses of available soil nutrients (Asner et al., 2004). Excessive grazing can also have deleterious effects on the plant community, reducing species diversity and creating a plant community dominated by only a few grazing tolerant species (Olff & Ritchie 1998), thus potentially reducing the floral resources available to pollinators.

The impact of grazing on grassland ecosystems will vary based on grazing intensity as well as differences in environmental and landscape features. While several studies have examined the impacts of grazing on native bee communities in grasslands (Kruess & Tscharntke 2002a; Kruess & Tscharntke 2002b; Vuilliamy, Potts, & Willmer 2006; Sjodin et al., 2008; Elwell, Griswold & Elle 2016), few of these studies address the impacts of grazing across a large spatial and climatic gradient with various disturbance regimes, features commonly found in North America's vast agricultural areas. In this study, we investigated the response of bees and ecosystem changes caused by cattle grazing across differing ecological regions with varying climatic, soil, and vegetation characteristics. We measured rangeland health (Adams et al., 2005) to determine the effects of livestock grazing on native plant and bee communities.

Specifically, we predict that 1) healthy rangelands will have more floral resources for bees than unhealthy rangelands, 2) as a consequence of increased floral resources, healthy rangelands will have larger and more diverse bee communities than unhealthy rangelands and 3) while bee diversity and abundance will decline in cooler and wetter regions, the overall relationship between rangeland health, floral resources and the bee communities should hold across broad geographic regions.

Methods

Study system

We assessed plant communities and surveyed local bee communities at 35 grassland sites within the prairie ecozone of Alberta, Canada over the 2014 and 2015 growing seasons. This area is part of the Great Plains ecoregion of North America encompassing an area with variable climate regimes that results in different plant communities ranging from semi-arid grasslands to boreal forest. For our study, the maximum distance between sites was over 1000 km in latitudinal spread. As a result of this spatial range, sites fell in a variety of ecotypes (Downing & Pettapiece 2006) with differing climatic, vegetation, and soil characteristics (Table 2.1). Southernmost sites occurred in semi-arid areas with low precipitation and comparatively high annual temperatures, resulting in plant communities that are dominated by native grasses and forbs. Northernmost sites are characterized by lower solar inputs and relatively low annual temperatures, with high annual precipitation allowing for the establishment of mature parkland forests. A transitional aspen parkland zone connects these southern grasslands to northern forested areas. Sites were grouped into four regions based on climate and dominant plant communities (Table 2.1). There was considerable year to year variation in rainfall between survey seasons. All regions had less rainfall in 2015 compared to 2014, with the exception of the boreal which had more rainfall in 2015 than 2014 (Table 2.1).

Floral Surveys

We completed floral surveys twice in both the 2014 and 2015 growing season, on the same day we sampled bees, to get an estimate of resource availability for bee pollinators. We surveyed flowering plants using three 50 m long by 1 m wide belt transects located 5 m immediately adjacent to pan trap transects to avoid disturbing insects that may have been foraging near our traps. We identified and counted the number of individual stems for all flowering forbs and shrubs, and counted the number of open flowers on up to ten individuals for each species at random to get an average estimate of flower abundance. For flowering plants in the Asteraceae we counted number of inflorescences instead of the number of open flowers. Flower abundance and flower richness were measured during bee survey visits to reflect the immediate resource environment for bees captured in the study.

Grazing and livestock use

To measure the long-term effects of cattle grazing, we used a rangeland health assessment, which is based on a scoring system related to the integrity and ecological status of a site and was specifically developed for managed grasslands (Adams et al., 2005). The assessment determines the similarity of a site to the predicted plant community, which is based on conditions including climate, soil type, topography, and disturbance level. Rangeland health is scored out of 100 possible points and based on five categories including plant community structure, hydraulic function, nutrient cycling, site stability (evidence of erosion), and density of by invasive or weedy species. High scoring sites reflect better range condition and are indicative of high productivity whereas low scoring sites are dominated by an early seral stage community containing disturbance-tolerant plant species are indicative of diminished ecological processes

(Adams et al., 2005). Sites were scored based on the number and type of plant communities found at each transect. Sites with a continuous plant community were given a single score, and sites that had multiple plant communities within the survey area were averaged across transects. Sites were categorized into three standardized levels of rangeland health based on these scores, including unhealthy (RHS <50, n=6), healthy with problems (50 < RHS < 75, n=12) and healthy (RHS >75, n =17; Adams et al., 2005).

Plant community composition

To measure plant community composition, we set up three 100 m long vegetation transects that were placed perpendicular to the nearest access site ~50 m from the fence line and spaced ~100 m apart. We collected plant species cover data from 10 (0.5 x 0.5 m^2) quadrats placed every 10 m alternating along the transect. Live plant biomass and litter were collected from 3 quadrats at 0 m, 50 m, and 100 m along each transect. To assess shrub density we recorded shrub type and distance along the 100 m transect and calculated a total percentage for shrubs for each site. We performed both relative cattle use estimates and rangeland health assessments at the end of the growing season during the second week of August in both 2014 and 2015.

Bee surveys

We surveyed bees (Apoidea: Apiformes) using a combination of pan trapping and focal netting. Pan traps were placed along three 50 m transects spaced 100 m apart. We used a total of 36 pan traps per site (12 along each transect) placed on the ground, 3 m apart alternating in colour (blue, yellow, white). Pan traps (New Horizons Entomology Services ©, Item number P325, Highland Park, IL), constructed from 96 ml bowls, were painted blue and yellow with florescent Silica paint, while white traps were left unpainted. We filled traps 3/4 full with a soapy water solution to reduce surface tension. Traps were set out in the morning between 7:00-10:00 am for a minimum of 5 hours at each site. We collected trap contents at the end of each survey day and pooled specimens by bowl colour within each transect. While pan traps were in place, we concurrently conducted focal netting, with two individuals netting for bees for 30 min between 11:00-16:00, for a total survey time of one hour per survey day at each site. We surveyed up to four sites per day within the same survey area and netted at sites in the same order as the traps were deployed earlier that morning. The maximum difference between netting times for different sites sampled on the same day was 90 min. To avoid disturbing insects foraging near pan traps, we did focal netting along floral patches distributed away from pan trap transects. We identified and counted managed honey bees (*Apis mellifera*) in the field without collecting specimens, but all wild bees were captured for later identification. We sampled each site twice per season, between June 20th-July 31st in 2014 and June 18th-July 26th in 2015, with approximately 2.5 weeks between sample times at each site. Captured insects from both survey methods were stored in 95% ethanol and brought back to the lab, where they were refrigerated at 4°C prior to being cleaned, pinned, identified, and labelled (LeBuhn et al., 2003).

Bee identification

We identified bees to genera using taxonomic keys (Michener et al., 1994; Packer et al., 2007). When identification to finer taxonomic units was possible, we used individual genera keys (Mitchell 1960, 1962; Sheffield et al., 2011.) and online resources (Discover Life). Voucher specimens were sent to C. Sheffield, Assistant Curator of Invertebrate Zoology at the Royal Saskatchewan Museum, for verification. We categorized difficult to resolve taxa to morphospecies when appropriate guides were not available. We therefore report data in terms of unique taxonomic units, which includes identification to the species or morphospecies level, as appropriate. Voucher specimens are stored at the University of Alberta EH Strickland Entomological museum.

Statistical analyses

All statistical analyses were completed using R version 3.2.4. (R Core Team 2016). We used a combination of generalized linear models (GLM) and generalized linear mixed-effects models (GLMM) to compare abundances and species richness indices for plant and bee communities as a result of livestock grazing. Livestock use rates, measured annually as the difference between ungrazed biomass and grazed biomass per site, and rangeland health scores (RHS) were highly correlated (Cor= -0.49, p=0.002) and because rangeland health is a more comprehensive measure of disturbance we focused on RHS in our analyses. We analyzed bee data according to survey method (pan traps vs netting) to account for potential sampling biases that may lead to significant differences in bee community assemblages (Cane, Minckley & Kervin 2000; Popic, Devila & Wardle 2013; Torné-Noguera et al., 2014; Gezon et al., 2015).

We estimated the effects of livestock grazing using RHS on flower abundance, flower richness, forb cover, bee abundance, bee species richness, bee diversity (Simpson's diversity), and bee evenness across sites using generalized linear mixed-effects models (GLMM) with Restricted Maximum Likelihood. The models included region and year as fixed factors and site as a random factor. If necessary, data were log-transformation to meet assumptions of normality. Generalized linear models (GLM) were used to test the importance of region as a predictor of the bee community. Region was assigned to each site based on climate and vegetation variables (Table 2.1). In all analyses, we evaluated model significance using a Type III Anova (car package; John Fox & Sanford Weisberg 2011). Model outputs are available in Appendix A.

Results

We captured 8,344 individual bees over our two survey seasons, representing 31 genera and 144 unique taxonomic units (Appendix A: Table A1). More bees were caught in 2014 compared to 2015, and the majority of bees were captured in bee bowls (85%) than by netting. Bee bowls were dominated by small bodied sweat bees (*Lasioglossum*) from the Halictidae family. Netted bees included larger bodied bees such as bumble bees (*Bombus*) and leaf cutters (*Megachile*). Species represented by single individuals were abundant in our surveys; 25% of species represented by 36 individuals were singletons. Rangeland health scores for our survey sites were normally distributed, ranged from 30 points to the maximum of 100, the mean was 69 and the median 73. As such, our sites represent a broad range of grazing impacts ranging from unhealthy to healthy rangelands and are adequate to evaluate the relationship between rangeland health and bee communities.

Regional and grazing effects on floral resources

Flower abundance was influenced by a three-way interaction between rangeland health score, region and year ($F_{3, 88} = 2.28$, $P = 0.046$), followed by multiple two-way interactions including RHS and year ($F_{1, 88} = 14.73$, $P = <0.001$), RHS and region ($F_{3, 57} = 3.35$, $P = 0.025$). Mean flower abundance across all sites dropped from 24,780 ± 8,999 SE in 2014 to only 6,859 ± 2,612 in 2015. The boreal region had the highest number of flowers in 2014 with a mean of 61, 865 ± 30,154 and was drastically reduced in 2015 with a mean of 5620 ± 4591. Conversely, the grassland region, which had the lowest number of flowers in 2014 (5,105 ± 2,036) had the greatest mean number of flowers in 2015 (8,483 ± 7595), a 60% increase in the number of flowers. The effect of RHS on flower abundance was dependent on a two-way interaction between region and year ($F_{3, 88}$=2.77, P=0.05; Figure 2.2A, 2.2B). During both 2014 and 2015 flower abundance decreased as RHS increased for sites in the Parkland region (2014: R^2= 0.28, P=0.07; 2015: R^2=0.35, P=0.04; Figure 2.2A). We found no significant relationship between RHS and flower abundance for the other regions. We found a trend for flower richness to be positively correlated with RHS ($F_{1, 27}$ = 3.187, P = 0.086). Flower richness was not effected by region ($F_{3, 27}$ = 1.15, P = 0.348), nor were there any interactions between RHS and region ($F_{3, 27}$ = 0.69, P = 0.566). Percent forb cover responded positively to RHS ($F_{1, 21}$ = 7.06, P = 0.015) but was dependent on a two-way interaction with year ($F_{1, 21}$ = 7.07, P = 0.015). In 2015, we found a positive relationship between RHS and percent forb cover (R^2=0.13, P=0.03) (Figure 2.2C); there was no relationship in 2014 (R^2=0.06, P=0.10) (Figure 2.2D). Plant productivity (biomass) was not affected by RHS ($F_{1, 36}$ = 0.04, P = 0.837) or region ($F_{3, 36}$ = 1.11, P = 0.956; Appendix A: Table A2).

Regional effects on bee communities

Regional effects were only found for the bowled bee community. We found no effect for region on the netted bee community (Appendix A: Table A3). The abundance of bees caught in bowls over both years varied across regions ($F_{3,34}$= 2.86, P = 0.051), mean bee abundance was highest in the grassland region (223 ± 27), followed by the foothills fescue (114 ± 29), parkland (67 ± 9) and boreal (51 ± 12). Bee evenness changed according to region, but was dependent on a three-way interaction with RHS and year ($F_{3, 22}$ = 6.93, P = 0.002). Bowled bee evenness was negatively correlated with RHS for the boreal region in 2014 only (R^2 = 0.43, P = 0.045).

Relationship between the floral community and metrics of the bee community

Bees caught in bowls

Bowled bee abundance was influenced by a three-way interaction between flower abundance, natural region and year ($F_{3, 30} = 2.66$, $P = 0.066$). Subsequently, a two-way interaction between year and flower abundance ($F_{1, 35} = 8.08$, $P = 0.007$) revealed that for our 2014 survey year, bowled bee abundance decreased with increasing flower abundance across all regions ($R^2 = 0.13$, $P = 0.04$). A two-way interaction between region and year did not reveal any significant differences between bowled bee abundance across regions in response to flower abundance ($F_{3, 24} = 2.90$, $P = 0.056$).

Flower richness was an important factor for bowled bee abundance (Figure 2.3). Results from mixed effect models show that the relationship between flower richness and bowled bee abundance was dependent on two-way interactions between flower richness and region ($F_{3, 41}=3.42$, $P=0.026$), and natural region and year ($F_{3, 24}=3.84$, $P=0.022$). In 2014, there was a positive relationship between bowled bee abundance and flower richness for the boreal region ($R^2 = 0.75$, $P = 0.004$), and no effect for the other regions (Grassland, Parkland, Fescue) (Figure 2.3) and this relationship was not apparent in 2015 (Figure 2.3). There was no effect of percent forb cover on bowled bee abundance ($F_{1, 37} = 0.11$, $P = 0.743$). Species richness of the bowled bee community differed according to natural region ($F_{3, 37} = 3.99$, $P = 0.015$) when investigating the response of bowled bee richness to flower richness. Mean bee richness bowled was greatest in the grassland (20.83 ± 1.28) followed by the fescue (16.33 ± 1.54), parkland (14.25 ± 1.18) and boreal (10.8 ± 0.97). Flower richness ($F_{1, 44} = 1.19$, $P = 0.282$) and percent forb cover ($F_{1, 42} = 0.002$, $P = 0.968$) had no effect on bowled bee richness. Flower abundance ($F_{1, 37} = 1.13$, $P =$

0.294), flower richness ($F_{1, 44}$ = 0.28, P = 0.033) and percent forb cover ($F_{1, 42}$ = 0.99, P = 0.327) did not influence bowled bee diversity. Evenness of bowled bees responded to flower abundance, and was conditional on a three-way interaction between flower abundance, region and year ($F_{3, 30}$ = 3.03, P = 0.043). There were also two additional two-way interactions between region and year ($F_{3, 28}$ = 4.65, P = 0.009) and flower abundance and year ($F_{1, 35}$ = 9.19, P = 0.005) and a main effect of year ($F_{1, 37}$ = 11.58, P = 0.002). Bowled bee evenness had a positive correlation with flower abundance for the boreal region in 2015 (R^2 = 0.73, P = 0.009). Evenness bowled varied with flower richness, and was dependent on a two-way interaction between flower richness and year ($F_{1, 22}$= 6.09, P=0.022; Figure 2.4). Flower richness ($F_{1, 44}$ = 4.85, P = 0.033) and year had significant main effects ($F_{1, 24}$ = 7.03, P = 0.014). However, linear regressions revealed that although years differed, the result was not significant (2014: R^2 = -0.025, P = 0.599; 2015: R^2 = -0.005, P = 0.364; Appendix A: Table A4).

Bees caught in nets

The abundance of netted bees tended to increase with flower abundance ($F_{1, 28}$=3.68, P=0.07), and the extent of this relationship differed depending on a two-way interaction between flower abundance and year ($F_{1, 35}$ = 5.28, P = 0.028). In 2015, there was a slight trend for increased netted bee abundance with more flowers (Figure 2.5), but was relatively insignificant when we ran our linear regression (R^2 = 0.003, P = 0.309). We found no relationship between flower abundance and netted bee abundance in 2014 (R^2 = -0.039, P = 0.870), (Figure 2.5). There were no main effects for flower richness ($F_{1, 43}$ = 1.14, P = 0.292) or percent forb cover ($F_{1, 42}$ = 0.18, P = 0.671) on netted bee abundance. Netted bee richness did not respond to flower abundance ($F_{1, 32}$ = 0.21, P = 0.650). Netted bee richness tended to increase with flower richness

($F_{1, 44} = 3.67$, $P = 0.062$) ($R^2 = 0.104$, $P = 0.007$) (Figure 2.6) and this response did not change according to region or year. Netted bee richness was unaffected by forb cover ($F_{1, 44} = 0.004$, $P = 0.950$). Netted bee diversity and evenness were both non responsive to flower abundance (Diversity: $F_{1, 34} = 0.09$, $P = 0.768$; Evenness: $F_{1, 33} = 0.02$, $P = 0.903$), flower richness (Diversity: $F_{1, 41} = 1.11$, $P = 0.299$; Evenness: $F_{1, 40} = 0.09$, $P = 0.770$) and percent forb cover (Diversity: $F_{1, 41} = 0.12$, $P = 0.727$; Evenness: $F_{1, 37} = 0.07$, $P = 0.793$) (Appendix A: Table A4).

Impacts of grazing on the bee community

Bees caught in bowls

Rangeland health was an important predictor for metrics of the bee community (Appendix A: Table A3). The abundance of bees caught in bowls positively correlated with RHS ($F_{1, 34} = 4.30$, $P = 0.046$; Figure 2.8). There was no effect of RHS on bowled bee richness ($F_{1, 44}$=0.36, P=0.55). Bowled bee diversity was subject to a three-way interaction ($F_{3,22} = 3.327$, $P = 0.038$) between RHS, natural region and year. In 2014, in the grassland region, there was a positive relationship between RHS and bee diversity in bowls (R^2=0.56, P=0.01) whereas RHS had a negative relationship with bowled bee diversity in the boreal region in 2015 (R^2=0.48, P=0.03), none of the other linear regressions were significant (Figure 2.7A, 2.7B). There were significant two-way interactions between RHS and year ($F_{1,22} = 8.29$, $P = 0.009$). Overall, bee diversity was greater in 2015 (0.73 ± 0.019) than 2014 (0.74 ± 0.019), but this relationship varied by a two-way interaction between year and natural region ($F_{1,22} = 3.23$, $P = 0.042$). The fescue region had the highest bee diversity for both 2014 (0.82 ± 0.01) and 2015 (0.77 ± 0.04), and the boreal region with the lowest bee diversity for both years (2014 = 0.71 ± 0.04; 2015 = 0.70 ± 0.05). Bowled bee evenness was also subject to a three-way interaction ($F_{3, 22} = 6.93$, $P = 0.002$) between RHS, natural region and year (Figure 2.7C, 2.7D). In 2014, there was a negative relationship between RHS and bee evenness in the boreal region (R^2=0.43, P=0.05), but no relationship for the other regions. There was an also a significant two-way interactions between RHS and year ($F_{1, 22}$ = 18.28, P = <0.001) between year and natural region ($F_{3, 22}$ = 6.84, P = 0.002). Bee evenness was lower in 2015 (0.68 ± 0.02) than 2014 (0.72 ± 0.02). The grassland region had the lowest bee evenness for both 2014 (0.62 ± 0.03) and 2015 (0.64 ± 0.02), whereas the fescue region had the highest evenness value for 2014 (0.79 ± 0.02) and the parkland region had the highest evenness (0.71 ± 0.04) in 2015.

Bees caught in nets

Netted bee abundance responses to RHS were dependent on a two-way interactions between survey year and region ($F_{3, 22}$=4.38, P=0.015) and RHS and year ($F_{3, 22}$=9.43, P=0.006). Netted bee abundance increased with higher RHS for the boreal region in 2015 (R^2=0.66, P=0.01). RHS was not a significant predictor for netted bee abundance in the other regions for either sample year. The number of bees caught in nets differed in the two years, the mean number of bees caught in nets in 2014 was 13 ± 2 and 21 ± 3 in 2015. Rangeland health was a significant predictor for netted bee richness ($F_{1, 44}$=4.35, P=0.043; Figure 2.8B) and diversity ($F_{1, 44}$=4.56, P=0.039; Figure 2.8C). Unhealthy, low scoring sites had less rich and less diverse bee communities compared to healthy sites. We found a trend for decreasing bee evenness with increasing RHS ($F_{1, 36}$=3.24, P=0.08) for both survey years.

Discussion

Grasslands are important to biodiversity (Carré et al., 2009; Black et al., 2011), and we have shown that they are likely important habitat for many species of bee, including threatened and endangered species, such as *Bombus occidentalis* and *Bombus terricola*. To our knowledge this was the first systematic sampling of bees in grasslands across a broad climatic gradient in the Northern Great Plains. To determine the indirect effect of livestock use on native bee communities across a large agro-climatic gradient, we examined bee community responses to livestock effects in grasslands over a two year period. Rangeland health, year, and ecological region were all found to be important factors affecting bee communities. Grazing likely affected bees indirectly through changes in the plant community, although the relationship between the plant community and bees was not always as predicted. Flower richness was a better predictor than flower abundance and forb cover for both bowled and netted bees. Additionally, high inter-annual differences in precipitation were likely the primary driver for year effects on the plant community, with flower abundance, flower richness, percent forb cover and productivity (mean biomass) all responding and some of these responses likely affected bees. Flower richness and percent forb cover differed across regions, and bee abundance regardless of survey method also varied according to region. Sites with higher rangeland health were associated with greater bee abundance, species richness and diversity, including higher rates of rare or uncommon bee species. Overall, our study suggests that healthier grasslands support healthier bee communities.

We found patterns of positive bee community response to rangeland health scores, which is likely due to indirect effects of cattle on bees mediated through the plant community (Potts et al., 2003; Vazquez & Simberloff 2004; Potts et al., 2006; Minckley 2014; Lazaro et al., 2016). Rangeland health includes a direct measure of vegetation structure (Adams et al., 2005) in addition to assessing impacts of grazing management and livestock use in grasslands (Miller 2008). Furthermore, rangeland health assessments scored higher when there is a well-developed litter layer and if the present plant community is similar to the expected plant community based on ecological site. In our study, rangeland health positively correlated with the abundance, species richness and diversity of the bee community, and may reflect increasing habitat structure based on the number of plant life form layers present at a site. Indeed, a number of studies have suggested that habitat type and vegetation structure may be more indicative of the bee community than floral resources (Grundel et al., 2010; Zhu et al., 2012; Elwell, Griswold & Elle 2016), including higher bee abundance (Moniera et al., 2017), richness (Grundel et al., 2010) and diversity (Tscharntke et al., 2005) in response to structurally complex landscapes with high potential for nest availability. Krauss & Tscharntke (2002) determined that mean vegetation height was the best predictor for species richness and abundance of solitary non-parasitic bees and wasps when they investigated grazing intensity effects on insect diversity in European grasslands. As nesting habitat is expected to be a strong predictor for bee community assemblages in addition to floral resources (Petanidou & Ellis, 1996; Potts et al., 2003; Potts et al., 2005) and pollinator persistence will depend on the maintenance and quality of habitats remaining in agricultural areas (Kennedy et al., 2013), rangeland health may serve as an ecological tool for assessing habitat quality and potential availability of nest sites.

Bee communities often track the floral community and are thought to be shaped by the availability and diversity of floral resources (Potts et al., 2003; Biesmeijer et al., 2006; Potts et al., 2009). We found mixed support for our hypothesis that areas with abundant floral resources would have larger bee populations and greater diversity. In our study, the bee community responded to the abundance and species richness of the floral community differently across sample year, region and survey method. Both the bowled and netted bee communities responded positively to flower richness. A plant community with greater species richness offers great breadth in the availability and quality of floral resources, which attracts more bees and more species of bees (Potts et al., 2003; Beismeijer et al., 2006; Grundel et al., 2010; Black et al., 2011). Although there is a tendency for bee capture via netting to have observer bias (Cane, Minckley & Kervin 2000), the netted bee community was a good reflection of the plant community and may provide be a better metric of the relationship between floral resource availability and floral resource bees. Percent forb cover had no effect on bee abundance, species richness, diversity or evenness for either year or region. This may have been due to the fact that forb cover is not reflective of immediate floral resources available to bees, and because bees move freely throughout the environment, forbs without flowers would not encourage bees to stop at a site. Flower abundance had a negative relationship with number of bees captured in bee bowls, counter to previous findings (Potts et al., 2003; Blaauw & Isaacs 2014) that only used observer and sample netting techniques. A possible explanation for these results may be due to sampling method. Passive sampling of bees using bee bowls are very useful as they remove the issue of observer bias and experience. However, bee bowl effectiveness may vary with the availability of floral resources (Cane, Minckley & Kervin 2000; Baum & Wallen 2011). As floral resource availability increases, the attractiveness and effectiveness of bee bowls may decrease. When floral resources are abundant bees may not travel as far or spend as much time searching for food and the likelihood of encountering bee bowls is much lower than if floral resources are limited (Baum & Wallen 2011).

Rangeland health was reflective of current and potential floral resources for bees. We found a positive correlation between rangeland health and percent forb cover across all regions in 2015, and rangeland health was a reliable indicator for flower abundance in the grassland region for both years. Previous studies have found that grazing increases landscape heterogeneity and plant diversity, and plant species richness is significantly reduced in the absence of grazing (Hickman 2004; Vuillamy, Potts & Wilmer 2006; Golodets, Kigel & Sternberg 2011; Dorrough et al., 2012). Moderate levels of grazing has been shown to increase flower abundance and percent forb cover (Milchunas & Lauenroth 1993). This pattern is attributed to a reduction in the dominance of more competitive species and increased spatial heterogeneity that enables a more diverse plant community (Huston 1994; Olff & Ritchie 1998). Further, effects of grazing on plant communities is dependent on climate and scale; in arid climate grazing reduced species richness at the local scale, but increased plant species richness in moist environments and at the landscape scale (De Bello, Leps & Sebastia 2007). These differences are likely dependent on the interactions between grazing and pre-existing spatial patterns of the vegetation. In arid landscapes plants tend to be patchily distributed and may lead to increased plant mortality when grazers are present, whereas in moist grasslands there is less of an opportunity for grazers to be as selective (De Bello, Leps & Sebastia 2007). Our results are consistent with these findings. In our study, the plant community responded to rangeland health (livestock use) differently across region and study year, and has been attributed to difference in climate. When moisture was limited rangeland health became an important metric to detect flower abundance and percent forb cover across regions. These differences were less detectable with high rainfall conditions.

Plant communities are shaped by abiotic factors such as climate, soil, moisture and nutrient regimes (Huntley 1991; Anderson 2006), thus studying a large geographic area with variation in these factors allowed us to compare how distinct plant communities influence bee communities (Michener 1979; De Bello, Leps & Sebastia 2007; Carre et al., 2009). We identified four distinct regions as part of our study and found significant differences in flower richness and percent forb cover between these areas for both survey years. This is consistent with previous work done in this geographic area (Downing & Pettapiece 2006) and in similar studies with a large spatial scale (De Bello, Leps & Sebastia 2007; Moretti et al., 2009). Interestingly, flower abundance did not different across regions, but both bee abundance and species richness steadily decreased as we moved north across our study area. Flower abundance has been considered the single best variable in explaining bee abundance (Potts et al., 2003; Roulston & Goodell 2011) because of floral resources such as nectar and pollen, but flower abundance appears to be a poor predictor at the scale of our study. Instead, regional differences were the primary drivers of bee abundance. This is not surprising as bees are most diverse in warm temperate regions with xeric environmental conditions (Michener 1979; Michener 2007), conditions similar to our grassland region, where we found bee abundance and species richness to be the highest. An increase in the number of bees in the south may be caused by the variation in the number of warm days available during the active period for bees. There is evidence that cooler northern temperatures may reduce the number of generations per season, including slower development of northern populations, resulting in fewer overall individuals (Sheffield, Frier & Dumesh 2014). Foraging activity is also heavily influenced by temperature and remains a constraint for bee pollinators (Corbet et al., 1993; Tautz et al., 2003). Small bodied bees have a harder time foraging when ambient temperatures are low (such as early morning) than large bodied bees, even of the same species (Stone 1994). Tunnel temperature was a significant predictor for emergence time for provisioning females and ambient temperature predicted total duration of female flight activity in *Anthophora plumipes* (Stone 1994). The activity periods of female *A. plumipes* on warm weather days averaged to 14.75 hours of activity, whereas on cool days, only averaged 10.5 hours of activity, leading to differences in offspring provisioning and the size of offspring (Stone 1994). Temperature remains to be a constraint for bees and appears to be highlighted in the differences we are seeing in bee communities across regions.

Conclusion

Assessing impacts of livestock use on floral resource availability for bees using rangeland health scores can provide information on multiple site level responses of the plant community including plant community structure, site stability, nutrient cycling and ecological integrity of managed grasslands (Adams et al., 2005). Sites with healthy rangeland assessments provided more diverse floral rewards and greater food availability to bee pollinators than unhealthy sites, and this had a positive effect on the bee community. These findings suggest that measuring rangeland health could be an informative tool for creating a sustainable land management strategy that includes supporting native bee communities.

Table 2.1. Regional characteristics for study sites located throughout Alberta, organized by study region, including climate variables, soil types and dominant vegetation. The mean temperature and mean precipitation were generated from ClimateAB v3.21.

Natural Region	n	2014 rainfall (mm)	2015 rainfall (mm)	MAT (°C)	Elevation (m)	Major soils	Dominant Vegetation
Boreal	8	145.50	219.36	2.49	952	Orthic and Dark gray luvisols	Mix of modified non-native grasses and native shrublands; Modified: *Bromus* and *Po*a; Native shrubland: *Potentilla*, *Danthonia*, *Festuca*
Grassland	10	179.22	133.62	4.08	980	Black, Dark brown, and Brown chernozems	Native grassland: *Calamovilfa*, *Stipa*, *Agropyron, Koeleria*, *Bouteloua*.
Fescue	7	236.97	168.58	3.9	1169	Mainly Black chernozems	Native shrubland mixed with native grassland: *Symphoricarpos*, *Rosa*, *Potentilla*, *Festuca*, *Danthonia*, *Bouteloua*, *Stipa*, *Agropyron*
Parkland	10	173.12	154.02	2.49	805	Mainly Black chernozems with some Dark gray chernozems	Mix of modified non-native grasses and native shrubland; Modified: *Bromus*, *Poa*, *Symphoricarpos*; Native shrubland: *Stipa*, *Agropyron*, *Festuca*, *Koeleria*

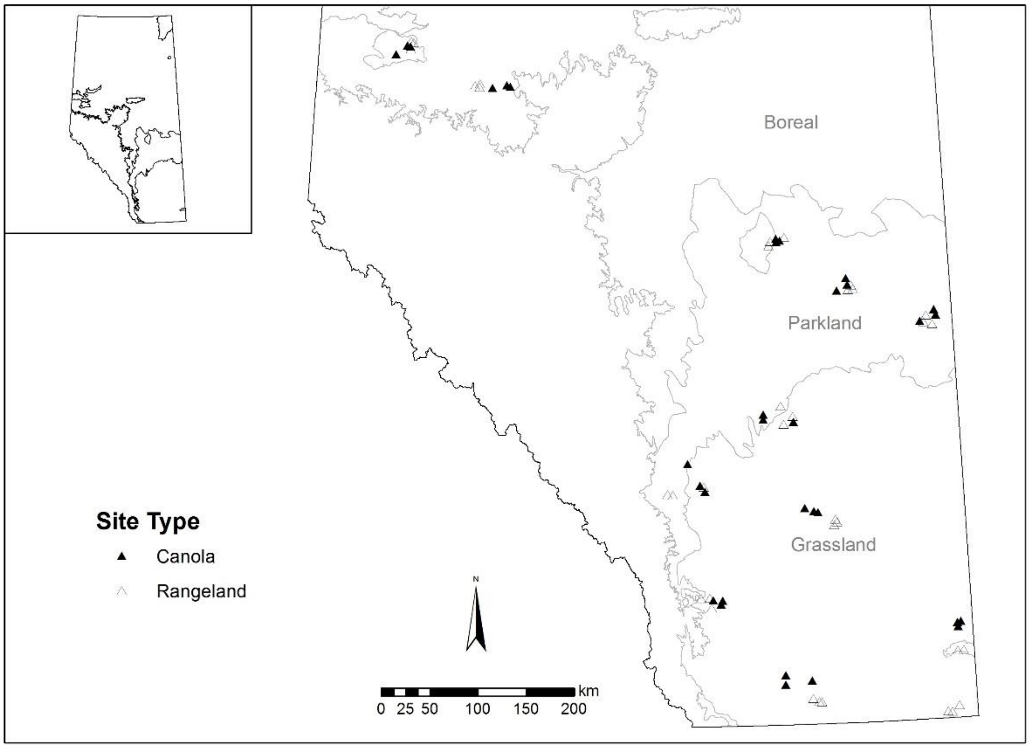

Figure 2.1. Map showing geographic locations of sites sampled throughout the province of Alberta. Sites were organized into four regions (Boreal, Parkland, Fescue and Grasslands) and surveyed during the same week for both survey seasons, weather permitting. Fescue regions were classified using elevation data and dominant plant community types. Fescue sites included a unique area in southeastern Alberta (Cypress Hills), and higher elevation sites in the foothills sub-region occurring along the eastern border of the Rocky Mountains.

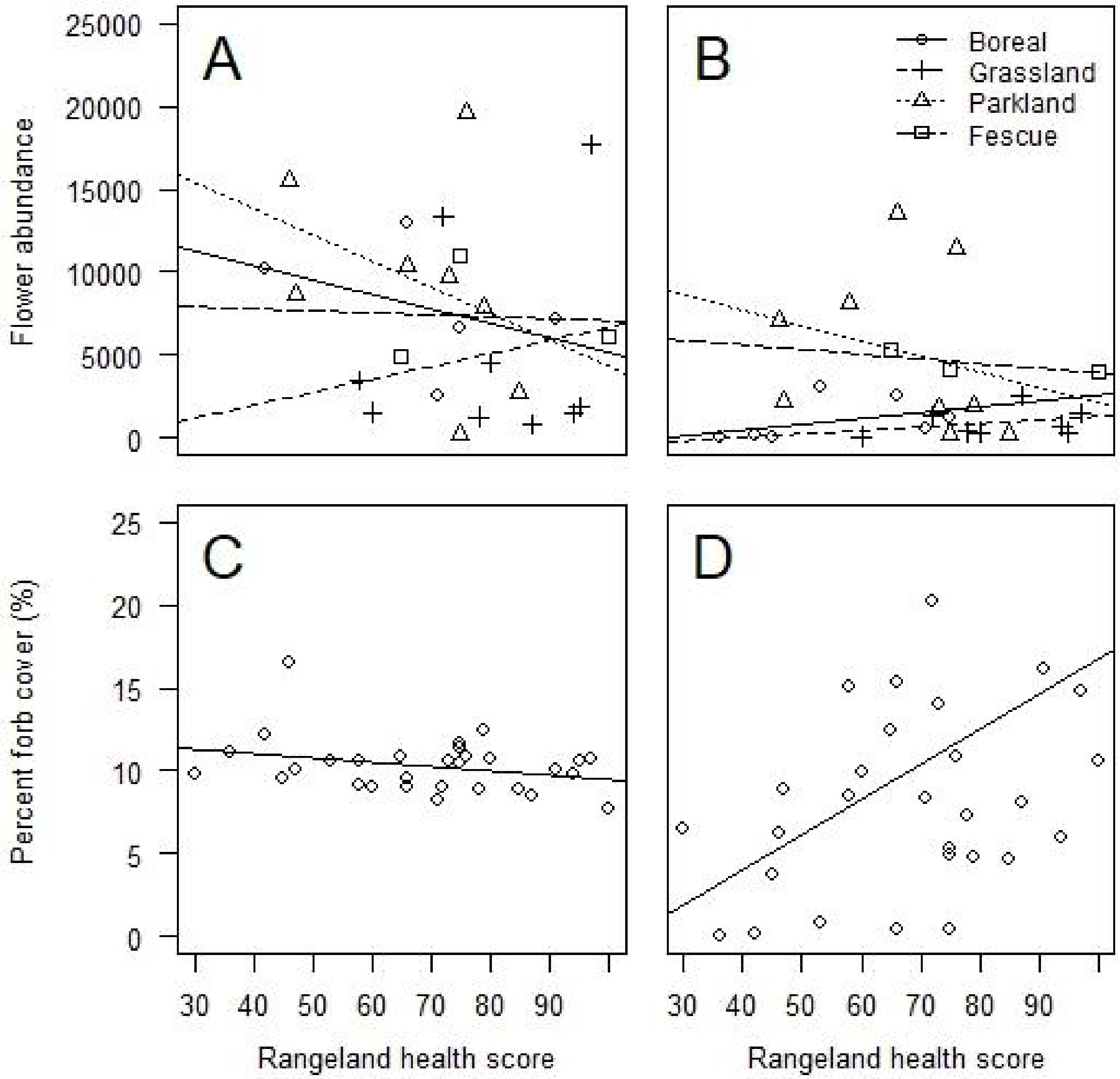

Figure 2.2. Responses of flower abundance and percent forb cover to change in rangeland health score (RHS) in 2014 (A, C) and 2015 (B, D). Multiple linear regression lines for flower abundance reflect differences in flower responses to RHS by study region (A, B), (Boreal, Grassland, Parkland, Fescue). Percent forb cover did not differ according to region regardless of survey year, and is represented by a single regression line (C, D).

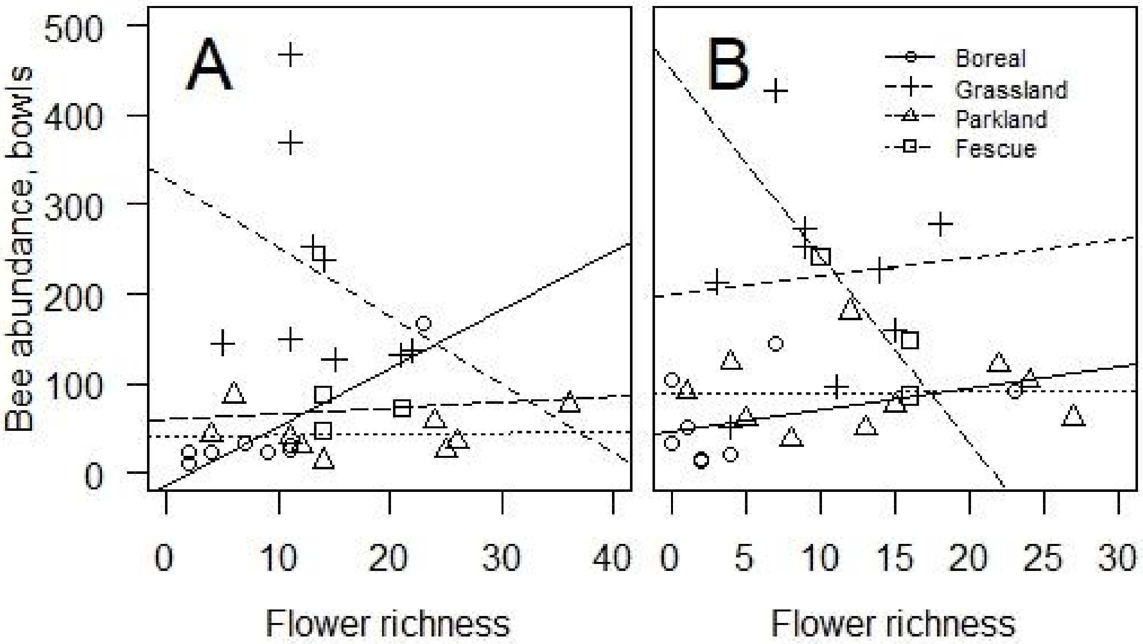

Figure 2.3. The effect of flower richness on bowled bee abundance for both survey years. Effects vary based on region of interest (Boreal, Grassland, Parkland, Fescue) and survey year (2014=A, 2015=B).

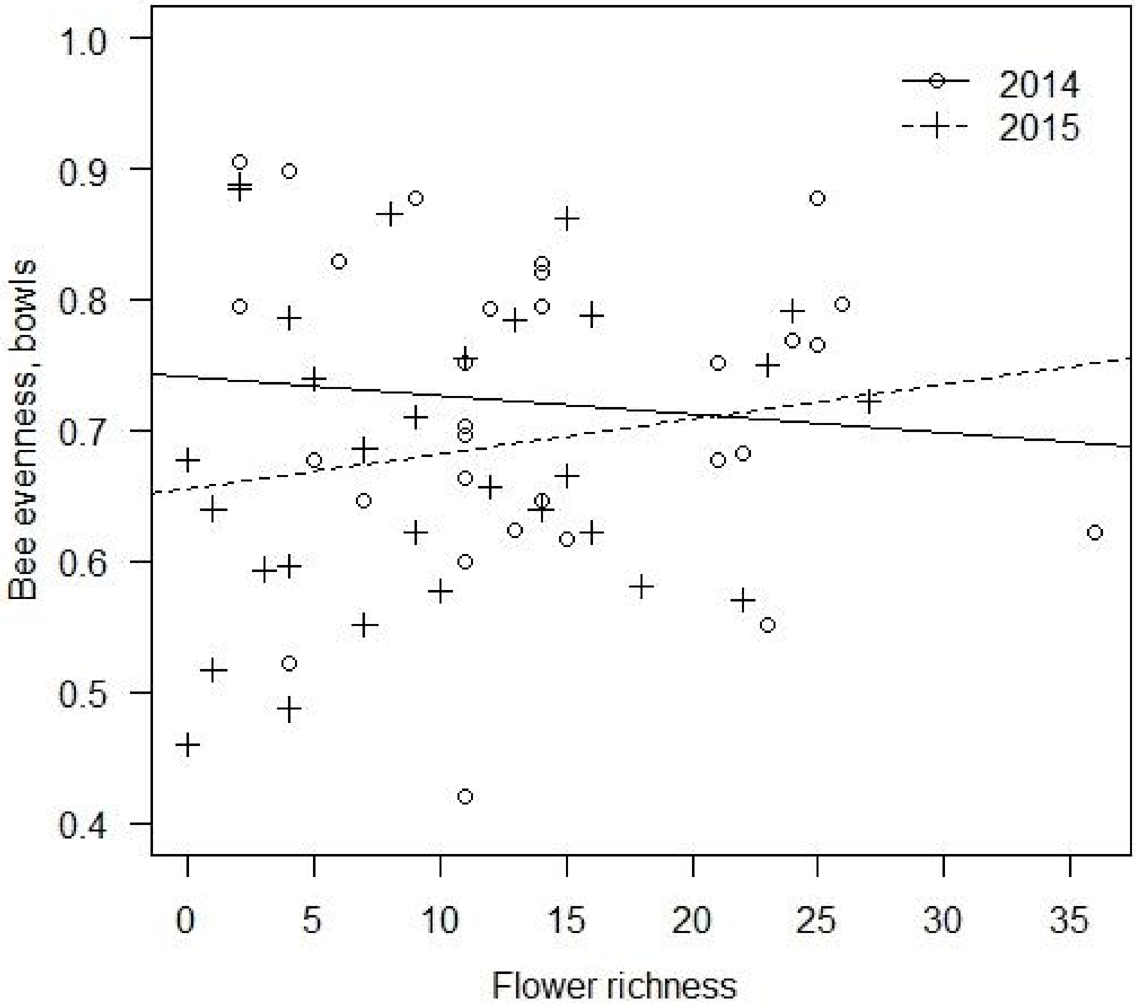

Figure 2.4. Response of bowled bee evenness to flower richness. Lines represent a linear regression between bowled bee evenness and flower richness for each survey year.

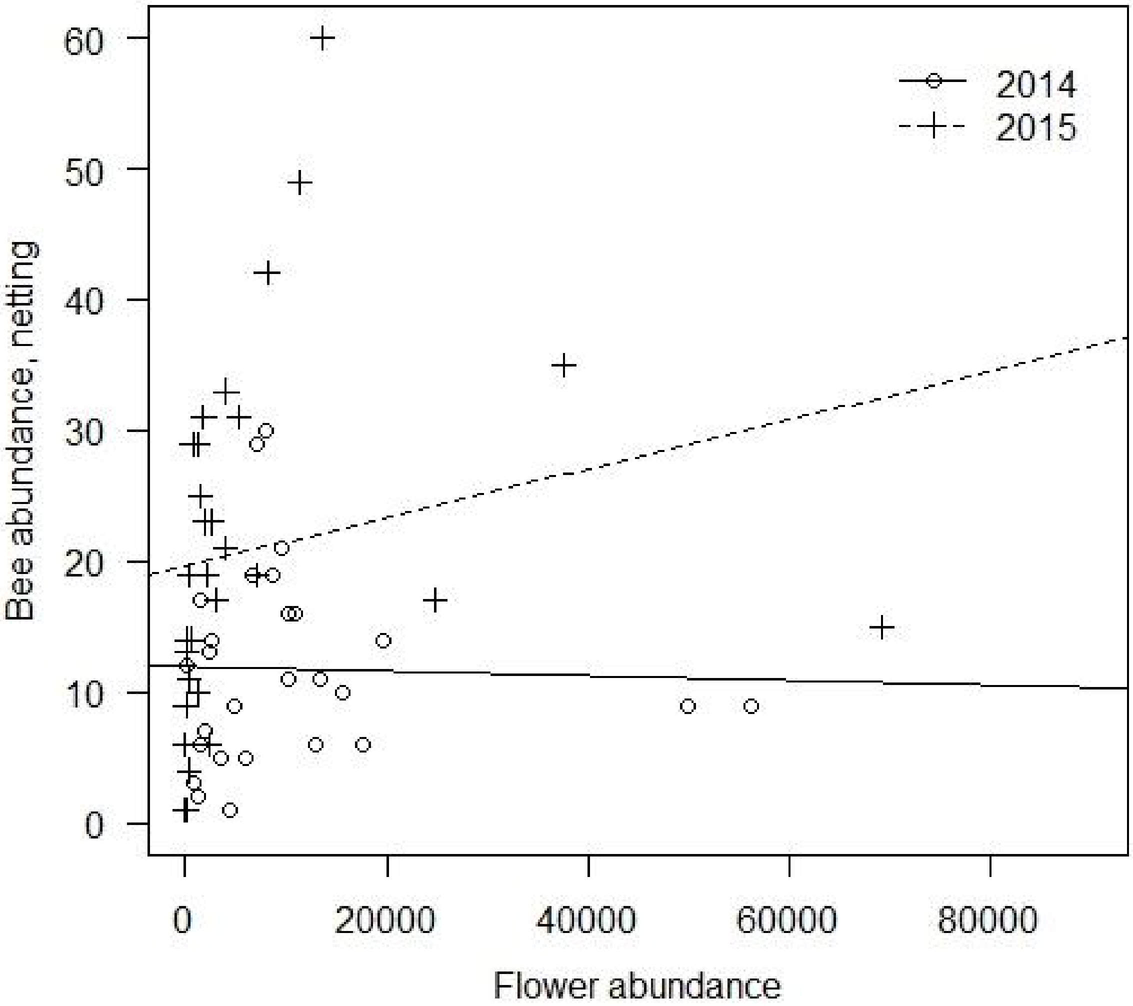

Figure 2.5. Response of netted bee abundance to flower abundance. Lines represent a linear regression between netted bee abundance and flower abundance for each survey year. Flower abundance values that exceeded 90,000 individuals (mean + 2 SD) were removed from the analysis.

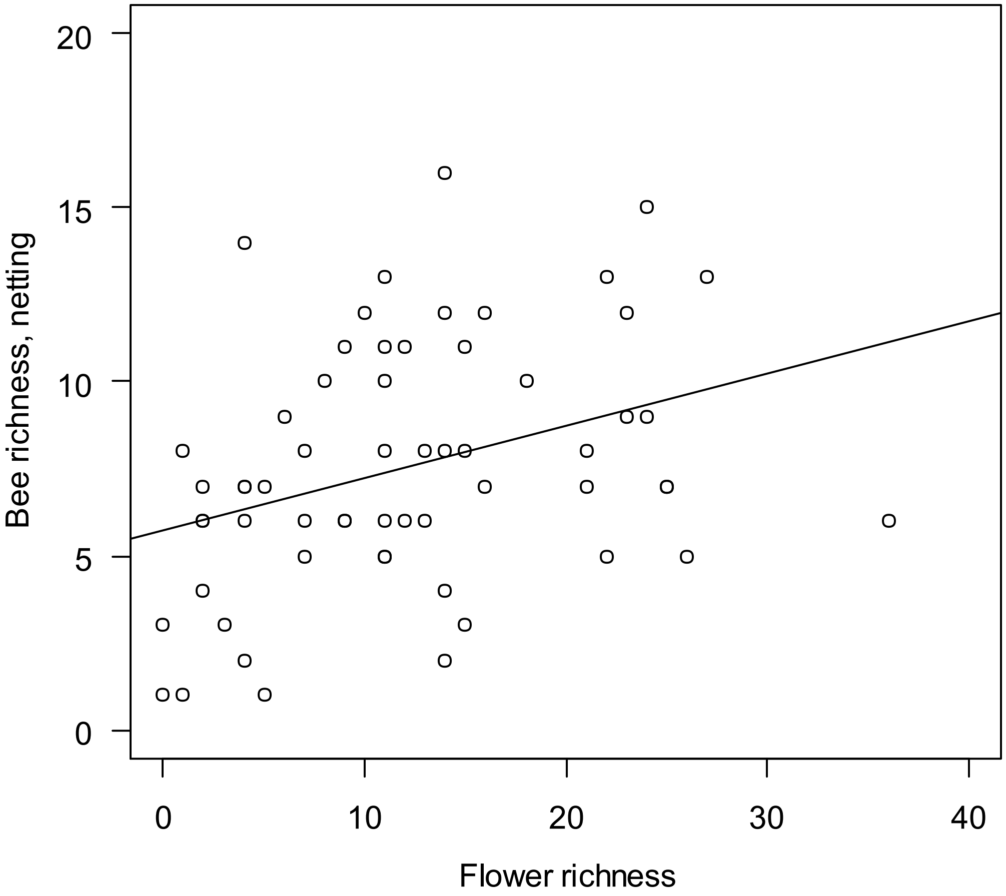

Figure 2.6. Response of netted bee richness to change in flower richness averaged over the two survey years.

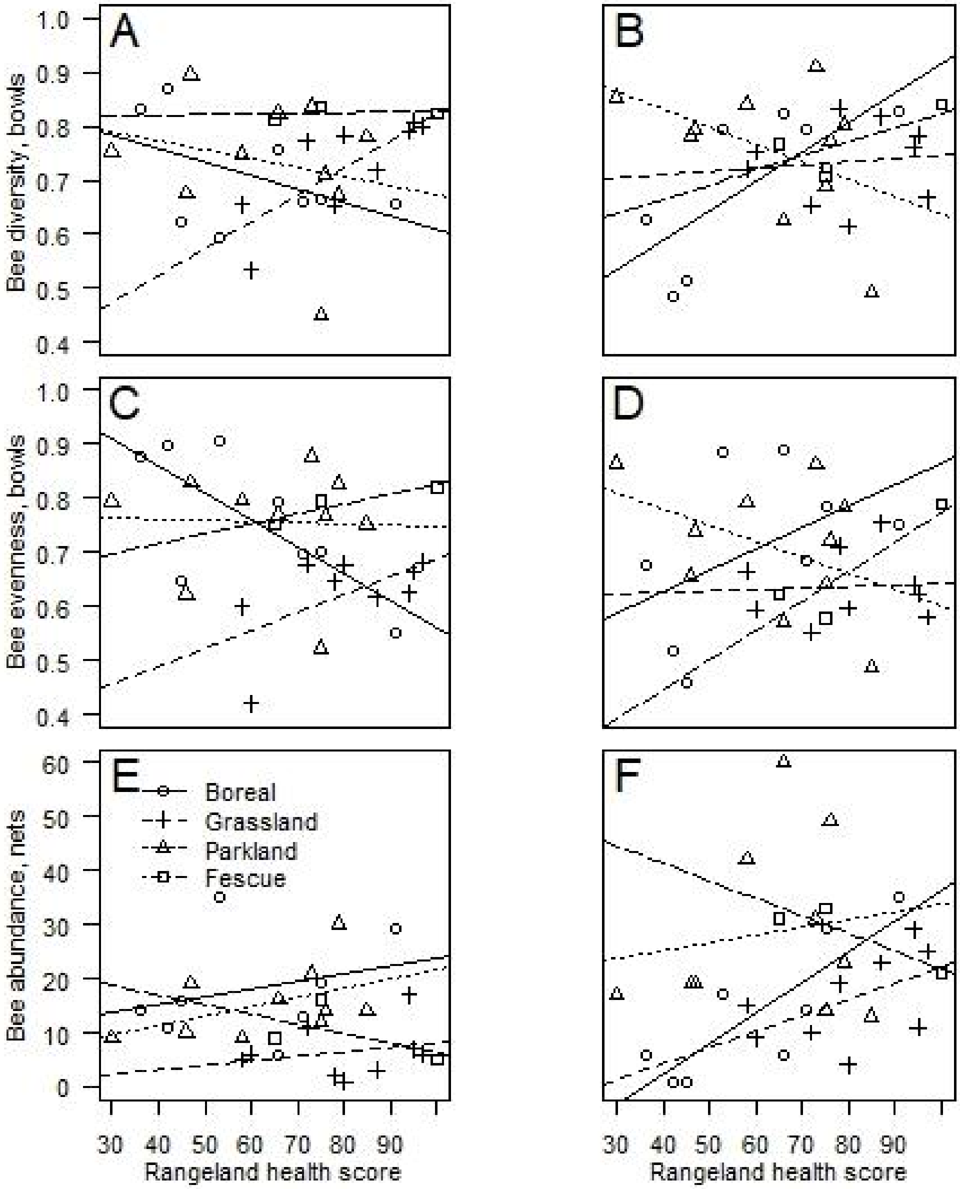

Figure 2.7. Responses of bee diversity, evenness and abundance to change in rangeland health scores (RHS) in 2014 (A,C,E) and 2015 (B,D,F). Lines represent a linear regression between the response variables and RHS for each of the natural regions (Boreal, Grassland, Parkland and Fescue).

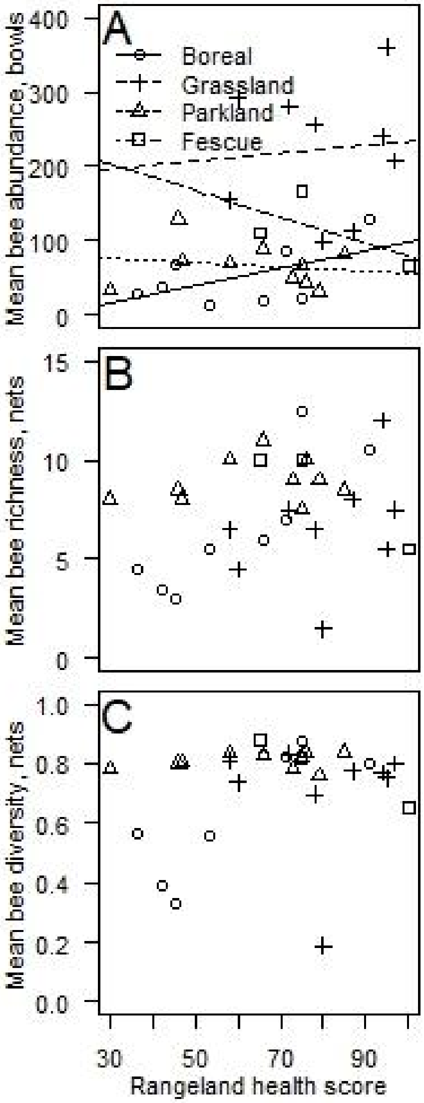

Figure 2.8. Responses of bee abundance (bowls), bee richness (nets) and bee diversity (nets) to changes in rangeland health score (RHS) averaged over the two surveys years. Lines in panel A refer to a linear regression between bowled bee abundance and RHS for each of the natural regions (Boreal, Grassland, Parkland and Fescue).

Chapter three: Cleptoparasitic bees as an indicator taxa for bee communities across a temperate agro-ecosystem

Introduction

Bee pollinators play an essential role in terrestrial ecosystems by providing valuable pollination services for flowering plants. However, declines in both domesticated honey bee and wild bee populations may have serious consequences for ecosystem function (Biesmeijer et., al 2006; Potts et al., 2010). Reduced bee populations, and subsequent loss of pollination services, can lead to declines in the abundance and genetic diversity of wild plant species, and reduced yields in agricultural crops, (Ellstrand 1992; Kremen et al., 2002; Biesmeijer et al., 2006; Klein et al., 2007; Potts et al., 2010) and are expected to have serious negative consequences on food security for both natural and human ecosystems (Foley et al., 2005; Potts et al., 2010). Pollinator declines have been linked to several human induced disturbances including habitat loss and fragmentation, agricultural intensification, increased use of pesticides and herbicides, and climate change (Winfree et al., 2009; Williams et al., 2010). The extent of these losses however, and the imposed effects of anthropogenic disturbance may vary, depending on life history traits of individual bee species. A first line of defense for combating species declines is being able to monitor bee populations and previous studies (Sheffield et al., 2013a) have proposed that cleptoparasites may function as a potential indicator species for native bee communities.

Declines in wild bee populations have not been reported to the same extent as declines in honey bees (*Apis mellifera*), likely because monitoring and identification of these species is difficult. But monitoring to observe declines in wild bee abundance and species extirpation is critical for assessing the impacts of environmental change on bees, and evaluating the effectiveness of conservation strategies (Cane & Tepedino 2001; Williams, Minckley & Silviera 2001; Williams et al., 2010). Monitoring contributes valuable population information for species of interest, aiding in early detection of population declines and allowing researchers to identify practical solutions to prevent losses. The establishment and coordination of systematic monitoring, however, are challenging to implement, especially across large scales or different habitat types. Bees are a very large (>20,000 species) and taxonomically difficult group (Zeil, Kelber & Voss 1996). Many taxa require experts for proper identification to the species level, which can be costly and time consuming. There is the additional issue of poor historic or baseline data for bees in many parts of the world (Sheffield et al., 2013a), making it difficult to differentiate between populations that naturally occur at low densities and populations that are instead in decline.

A potential solution for monitoring wild bee communities is to focus on guilds or functional groups instead of individual taxa (Williams, Minckley & Silviera 2001; Cane et al., 2006; Murray, Kuhlmann & Potts 2009; Williams et al., 2010; Sheffield et al., 2013a). Bees have diverse life history traits, including nest location, nest substrates, floral specializations and lifestyles (solitary, social, parasitic), that can be used to classify species into distinct groups or guilds. Focusing monitoring efforts on specific groups to determine the effects of disturbance, habitat quality, or land use type could be a viable alternative to capturing and identifying whole communities of wild bees, provided they act as indicators for the overall bee community. With a lifestyle that relies on other bee species, cleptoparasitic bee guilds have been suggested as a potential indicator group for assessing disturbance effects on wild bees (Sheffield et al., 2013a). Cleptoparasitism is an ecological interaction in which one species avoids brood care by using the resources obtained by another species for the development of their young, often by laying their eggs in the nests of host bees (Michener 2007; Sheffield et al., 2013a; Alves Dos Santos 2009). Cleptoparasitic bees lack pollen carrying structures necessary to provision developing offspring, and instead have evolved traits such as strong mandibles and shorter development cycles to outcompete, and, in some cases, kill developing host larvae (Michener 2007). Cleptoparasites represent a unique functional guild and form the apex of bee communities through their role as parasites (Combes 1995). As such, they are the first guild to respond to disturbances and the occurrence of cleptoparasites within a community is dependent on host abundance, and resources made available to hosts (Sheffield et al., 2013a; Finke & Denno 2004). Cleptoparasites are also well known, have diverse enough life history traits to complement bee species with variable nesting preferences, and are easily distinguished from host bees based on morphology. Therefore, inferring the effect of habitat disturbances on host bees by measuring the cleptoparasite guild may prove to be useful indicator for assessing bee communities.

In this study, we evaluate the ability of cleptoparasites to predict the abundance and species richness of bee communities in different land-uses across a climatic gradient. Specifically, we will: 1) test the association between cleptoparasites and host bees, 2) determine the reliability of cleptoparasites as indicator species for the overall bee community, the host bee community, and the non-host bee community, and 3) examine how these relationships differ across region and land use type.

Methods

Study system

We surveyed bee populations in two different land-use types across a climatic gradient in the prairie ecozone in Alberta, Canada. We established 35 grassland sites (used for livestock grazing, and herein will be referred to as rangelands) and 33 canola (*Brassica napus*) sites, which were all surveyed during the 2014 and 2015 growing seasons. Our survey covered a large area spanning approximately 250 km east to west and 900 km north to south. As a result of this spatial range, sites fell in a variety of prairie ecotypes (herein referred to as regions; Downing & Pettapiece 2006) with differing climatic, vegetation, and soil characteristics (Appendix B, Table B1). Rangeland sites varied according to region, with respect to topography, moisture regime, and disturbance level. Canola sites were fairly consistent across the landscape due to external inputs common to crop management. Differences in canola sites included timing of bloom and amount of forested areas adjacent to flowering crop. For rangeland sites, those found in the boreal region were dominated by a mix of non-native forage grasses and native shrub-land, typical to this region with high annual precipitation, cool temperatures and high anthropogenic inputs. Sites classified as fescue tended to be high elevation, receiving higher mean annual precipitation and warm temperatures. Sites within the fescue region were among the most diverse and productive in terms of the plant community. Moving southward, precipitation tends to decrease with increasing temperatures, resulting in plant communities that are dominated by native grasses and forbs. A transitional parkland zone connects these southern grasslands to northern boreal areas and is dominated by native shrub-lands. (Downing & Pettapiece 2016; Figure 3.1).

Bee community

We surveyed bees (Apoidea: Apiformes) using a combination of pan trapping and focal netting. Thirty-six pan traps were used at each site (12 along each transect) placed 3 m apart alternating in colour (blue, yellow, white). Pan traps (New Horizons Entomology Services ©, Item number P325, Highland Park, IL) were painted blue and yellow with florescent Silica paint, while white were left plain. We filled traps 3/4 full with a soapy water solution to reduce surface tension. Traps were set out between 7:00 and 10:00 am and were out for a minimum of 5 hours at each site. We collected trap contents at the end of each survey day and pooled specimens by bowl colour within each transect. For pan trap surveys at rangeland sites, we set up three 36 m transects spaced 50 m apart, placed perpendicular to our access point. To avoid disturbing insects foraging near pan traps, we did haphazard focal netting for 1 hour along floral patches distributed away from pan trap transects. In canola fields, we sampled bees visiting canola plants as well as those attracted by non-canola plants in field margins. We placed transects along either a road edge or an interior edge (opposite of another cropped field), where various flowering plants grow in ditches, and one transect placed 5 m into the focal canola field. We used 2 m tall temporary plastic stakes for pan traps placed in the cropped field when crop height was above 100 cm. This was to ensure bees encountered traps at the same level as canola plants when foraging. For netting surveys, we captured bees along transects near the road edge or interior edge of the field and divided up the 30 min period/observer into two 15 min halves. We would net in canola for 15 min and then in the field margin for 15 min. Bees were pooled based on edge of the field and interior edge focus (margin vs. canola). At all sites we identified and counted managed honey bees (*Apis mellifera*) in the field without collecting specimens, but all wild bees were captured for later identification. We sampled each site twice per season between June 20th-July 31st in 2014 and June 18th-July 26th in 2015, with approximately 2.5 weeks between sample times at each site. Captured insects from both survey methods were stored in 95% ethanol and brought back to the lab, where they were refrigerated at 4°C prior to being pinned, cleaned, labelled, and identified (LeBuhn et al., 2003).

Bee identification

We identified non-*Bombus* bees to genera using Michener, McGinley & Danforth (1994) and Packer, Genaro & Sheffield (2007). *Bombus* individuals were further identified to species using the "Bumble bees of North America" taxonomic guide (Williams et al., 2014). Difficult specimens were sent to Dr. Cory Sheffield (Assistant Curator of Invertebrate Zoology at the Royal Saskatchewan Museum) for verification, including a subset of voucher specimens used for all in-house bee identifications. A separate subset of reference specimens, primarily cleptoparasites, were sent to the Canadian Centre for DNA Barcoding to confirm or determine identification.

Statistical analyses

All statistical analyses were completed using R version 3.2.4 (R Core Team 2016). To test the association between cleptoparasites and the overall bee community (host and non-host bees) we looked at all possible species pairs and calculated co-occurrence using the R package "co-occur" (Veech 2013). This approach calculates frequencies of co-occurrence between species pairs based on expected and observed taxon pairings at each site. The expected frequency is based on the distribution of taxa being random and independent of other taxa. The analysis returns the probabilities that species co-occur more or less frequently than predicted by chance.

To evaluate cleptoparasites as indicator species for bee communities across different region and land-use types, we began by assigning solitary bees to one of three "lifestyle" groupings based on genera identification and previous literature for reproductive strategies (Sheffield, Frier & Dumesh 2014; Williams et al., 2010). The groupings are as follows: cleptoparasites, host bees, which are targeted by cleptoparasites, or non-host bees, which are not known to be parasitized (Sheffield, Frier & Dumesh 2014; C. S. Sheffield, personal communication, November 28, 2016). We examined *Bombus* species, and their associated cleptoparasites separately. All known parasites and their host bee relationships are listed in Table 3.1. We examined the abundance and species richness of host bees and the whole bee community using generalized linear models (GLM), with cleptoparasite abundance or richness, region and land-use type as fixed factors with interaction terms (region*land-use type). Because data were not normally distributed, we used a negative binomial probability distribution for bee abundance (mass package; Venables & Ripley 2002) and a quasi-poisson probability distribution for species richness (lme4 package; Bates et al., 2015) to account for overdispersion of our models. We evaluated the models with Type III Anovas (car package; Fox & Weisberg 2011).

Results

Bee community

Over the two sampling years we collected a total of 17,406 individuals, not including commercial bees (*Apis mellifera*; *Megachile rotundata*). We caught more than twice as many individuals in 2015 (11,892) than 2014 (5,514). Over the two sampling years we caught a total of 35 different bee genera, with 28 genera in canola sites and 32 genera in rangeland sites (Appendix B: Tables B2, B3). Our most abundant genera in 2014 were *Lasioglossum, Bombus* and *Agapostemon*. In 2015, a majority of bees caught belonged to *Lasioglossum, Andrena* and *Halictus*. *Lasioglossum* were by far the most abundant genera in both habitat types for both sample years (6,951 in total for both years). In 2014, known host bees were more abundant in rangeland sites (mean= 91 ± 18 SE) than canola (mean= 51 ±7) (Figure 3.2; Appendix B: Table B4); however, this pattern changed the following year and more host bees were found in canola sites (mean= 201 ± 28) than rangelands (mean= 127 ± 17) in 2015. Non-host bees were most abundant in canola sites for both years (2014 mean= 11 ± 2; 2015 mean =25 ± 7). Over the two survey years we collected 437 known cleptoparasites from both canola and rangeland sites. In 2014 and 2015, cleptoparasites were more abundant in canola (2014 mean =7.91 ± 1.61, 2015 mean= 2.67 ± 0.63) than rangeland sites (2014 mean=1.93 ± 0.61 SE, 2015 mean= 1.23 ± 0.22; Appendix B: Table B4). We caught two more cleptoparasitic genera in 2015 (8) than 2014 (6). *Nomada* (44 individuals in 2014, 205 in 2015) were our most abundant cleptoparasitic genera followed by *Sphecodes* (33 in 2014, 63 in 2015), and the social parasite *Bombus* subgenus *psithyrus* (15 in 2014, 23 in 2015). In 2014, 64% of sites had cleptoparasites (found in 32 of 68 sites during visit 1 and 21 of 68 sites during visit 2) and this number increased to 80% of sites in 2015 (42 of 68 sites in visit 1, 33 of 68 sites in visit 2).

Host bees and cleptoparasites

In 2014, there were 276 pair combinations from a total of 24 bee genera (all bees found excluding *Bombus* species), with 19 positive (Observed > Expected) and 5 negative occurrences (Observed < Expected; Figure 3.2). For host bees, *Diadasia* had the highest percentage of positive pairings (26.7%) followed by *Agapostemon* (25.0%) and *Melissodes* (21.1%). There were no pairs generated between hosts and cleptoparasites in the analysis in 2014, with the exception of *Agapostemon* which had a positive pairing with its cleptoparasite *Sphecodes*. Of the four cleptoparasitic species caught in 2014, *Sphecodes* was the only genera with a positive pairing (5.3%), co-occurring with *Agapostemon*, one of its known host bees. *Nomada*, *Coelioxys* and *Stelis* had no significant pairings and all co-occurrences were considered random. Host-host co-occurrences were common for both years. Co-occurrences coincided with genera that were within the same families most often, and was most frequent in the Megachilidae and Halictidae. We found 378 pairings from 28 bee genera in 2015, 27 positive and 4 negative (Figure 3.3). Once again, the highest number of positive pairings were made by host species, with *Agapostemon* (25.0%) co-occurring most often with other host taxa followed by *Colletes* (20.8%) and *Dianthidium* (17.7%). We caught 5 cleptoparasitic taxa and all (with the exception of *Sphecodes*) had higher than expected positive co-occurrences with their known host bees (Figure 3.3). In 2015, the cleptoparasite *Nomada* also co-occurred with non-host bee *Duforea*. There were no positive or negative co-occurrences for bumble bees and their associated nest parasites in either study year; instead, all species pairings were considered random (Appendix B: Table B5; List of cleptoparasite: host relationships in Table 3.1).

Cleptoparasites as indicator species

Cleptoparasite abundance

In 2014, cleptoparasite abundance was predictive of overall bee ($F_{1, 58}$=16.42, P=<0.01) and host bee abundance ($F_{1, 58}$=21.30, P=<0.01; Figure 3.4A, 3.4C; Appendix B: Table B6), but was dependent on a two-way interaction between cleptoparasite abundance and region (Overall bee community: $F_{3, 51}$ = 8.21, P = 0.04; Host bee community: $F_{3, 51}$ = 10.32, P = 0.02). We found a positive relationship between the number of cleptoparasites and non cleptoparasitic bees in the fescue region (overall bee abundance R^2 = 0.38, P = 0.014; host bee abundance R^2 = 0.40, P =

0.013) and null responses for all other regions in 2014. In 2015, cleptoparasite abundance was predictive of overall ($F_{1,52}$ = 25.44, P = <0.01) and host bee abundance ($F_{1,52}$ = 27.69, P = <0.01) regardless of region. Cleptoparasite abundance was positively correlated with bee abundance for the overall and host bee communities (Figure 3.4B, 3.4D). Cleptoparasites were not predictive of non-host bee abundance for either year (2014: $F_{1,56}$=0.32, P=0.57; 2015: $F_{1,56}$ = 1.44, P = 0.23).

Cleptoparasite richness

In 2014 we found a trend for a two-way interaction between cleptoparasite richness and land-use type for predicting overall bee richness ($F_{1,50}$ = 3.72, P = 0.06) (Appendix B: Table B7). Cleptoparasite richness positively correlated with overall bee species richness in canola (R^2=0.21; P=0.01) and rangelands (R^2=0.08; P=0.06; Figure 3.5), but this relationship was more prevalent in canola sites. Cleptoparasite richness was not a predictor for host bee richness (2014 $F_{1,50}$=0.85, P=0.36; 2015 $F_{1,48}$=0.30, P=0.59) or non-host bee richness (2014: $F_{1,50}$=3.09, P=0.09; 2015: $F_{1,48}$=0.27, P=0.61) in either survey year.

Region

In 2014, region was an important predictor for host bee and non-host bee abundance ($F_{3,55}$=8.04, P=0.05; $F_{3,53}$=22.00, P=<0.01), but not overall bee ($F_{3,55}$ = 4.31, P = 0.23) or cleptoparasite abundance ($F_{3,60}$=1.62, P=0.65). The parkland had the highest number of non-host individuals followed by the boreal, fescue and finally the grasslands with the fewest number of non-host individuals. We found the opposite relationship between regions and host bees. Host bees were most abundant in the grasslands and fescue regions, followed by the parkland and boreal (Figure 3.5). In 2015, region was a significant predictor for bee abundance for all lifestyles (*overall* $F_{3,49}$=29.93, P=<0.01; *host* $F_{3,49}$=49.14, P=<0.01; *non-host* $F_{3,53}$=113.43, P=<0.01; *cleptoparasite* $F_{3, 55}$=19.57, P=<0.01). The non-host bee community followed the same abundance distribution of the 2014 non-host community, with the highest number of individuals found in the parkland region and the fewest in the grasslands. Patterns of host bee abundance and region also held up across survey years. In 2015, both the overall bee community and the cleptoparasite community followed the host bee abundance distribution pattern (Figure 3.5). Region was not a significant predictor for bee community richness for any lifestyle across both survey years (Appendix B: Tables B6, B7).

Land-use type

Habitat type was not an important predictor for bee abundance in 2014 regardless of lifestyle (Appendix B: Table B6). Bees were equally abundant in both habitat types (*overall* $F_{1, 54}$=1.02, P=0.31). However, in 2015, both cleptoparasites and non-host bees were more commonly found in canola sites than rangeland sites (*non-host* $F_{1, 52}$=5.92, P=0.02; *cleptoparasites* $F_{1, 54}$=15.73, P=<0.01; Appendix B: Table B7). Land-use type was a significant predictor for cleptoparasite richness in 2015 ($F_{1, 54}$=4.03; P=0.05), with a more species-rich cleptoparasitic community in canola (mean richness=1.97 ± 0.18) than rangelands (mean richness=1.36 ± 0.22). Land use affected no other metrics of bee abundance or richness in either survey year.

Discussion

Effectively estimating population dynamics of bee communities is an important step in the conservation of pollinators. Bees are highly mobile, and interpreting census data can be difficult as surveys tend to have high spatiotemporal variability and a large proportion of singletons (usually rare species), leading to inconsistencies in community data. The use of functional groups, or indicators to assess the effects of land use change on wild bees is potentially a more cost effective and efficient means to infer habitat quality and availability for bee pollinators (Williams et al., 2010). In this study we were able to demonstrate co-occurrence patterns between cleptoparasites and known host bees at our study sites, including the predictive ability of the cleptoparasite group as indicator taxa for the overall bee and host-bee community. In addition to confirming known host bee relationships, we found support for a possible unreported cleptoparasitic relationship. Results from our investigation of cleptoparasite abundance and richness revealed that cleptoparasite abundance was positively correlated with host bee abundance, however, this relationship differed by years, and in 2014 was dependent on region. Cleptoparasite richness was not consistently indicative of host bee richness, and differs with previous findings assessing diversity (Sheffield et al., 2013a, b). Both ecological region and survey year had a significant influence on the cleptoparasite: host bee interaction, suggesting that climatic and inter-annual variation can influence the strength of these relationships. Contrary to our expectations, land-use type had no effect on the cleptoparasite and overall bee or host bee associations, regardless of region or study year. Taken together, our study suggests that there may be merit in further exploring the use of cleptoparasites in determining the abundance of host bees.

The effectiveness of cleptoparasites as indicator species relies on a predictable relationship between the occurrences of these parasitic species with host bees. In natural community assemblages, co-occurrence between species is usually less than expected by chance (Gotelli & McCabe 2002), and is likely driven by environmental filters and ecological interactions. For bee communities, species traits such as physiological tolerances, foraging ranges and preferences in floral and nesting resources are all factors that contribute to the probabilities of species co-occurrences (Gotelli & McCabe 2002). In our study, we predicted that cleptoparasites would co-occur in the same habitats as their host bees, as cleptoparasitic bees are completely reliant on host bees for reproduction. This hypothesis was supported by a positive correlation between cleptoparasite and host bee abundance, and co-occurrence patterns between hosts and cleptoparasites, notably, positive pairings between the host bee genus *Agapostemon* and its cleptoparasites *Nomada* and *Sphecodes*. *Nomada* are primarily cleptoparasites of *Andrena* (Andrenidae), although incidents of parasitism for other genera have been found, including increased nest parasitism of the Halictidae, among them *Agapostemon*, *Halictus*, and *Lasioglossum* (Michener 2007). In 2015, we found *Nomada* had positively paired with a non-host bee *Dufourea* more than expected. *Dufourea* is another member of the Halictidae family, and our finding may indicate *Dufourea* as an unreported host bee of *Nomada*. Interestingly, we had higher than expected positive and negative taxa pairings between the non- parasitic bee *Agapostemon* and other genera. *Agapostemon* are typical of the grasslands, and in a paired study have been identified as indicator taxa for this region (Kohler unpublished data). Pairings between *Agapostemon* and other bee taxa appear to reflect similar or dissimilar habitat needs. For example, this taxa was positively associated with "miner bees" that are known ground nesters, whereas negative taxa pairings were made with cavity nesting bees that require woody substrates, which are often infrequent in the grasslands region.

Our results for testing the predictability of cleptoparasites as an indicator taxa showed that cleptoparasite abundance was a significant predictor for both overall bee abundance and host bee abundance in 2014 and 2015. However, further investigation revealed that although cleptoparasite abundance was positively correlated with overall and host bee abundance in 2015, the relationship between cleptoparasites and non-parasitized bees in 2014 was driven entirely by a positive relationship in the fescue region (Figure 3.4). We believe the differences in effect between years is due to changes in temperature and precipitation. The 2014 season was considerably wet compared to the hot and dry season that followed, and the change in climate resulted in noticeably fewer floral resources in 2015 (Sturm unpublished data). The lack of floral resources may have directly reduced the number of provisioned host nests available to cleptoparasites (Wcislo & Cane 1996), increasing competition for nests, and resulting in a greater effect of cleptoparasite abundance on overall and host bee abundance. This inference is also a possible explanation for the differences in patterns in co-occurrence between years. Competitive interactions are recognized as one of the primary causes for non-random co-occurrence patterns (Gotelli & McCabe 2002) and the number of positive pairings between cleptoparasites and hosts were significantly higher when floral resources were low. Competition for nesting sites and lack of floral resources during short temperate summers has been hypothesized as an explanation for the prevalence of the parasitic lifestyle in northern latitudes by Michener (2007). However, since we did not test this hypothesis directly, more data and either mechanistic experiments or predictive models would be required to evaluate this further.

Variation in habitat productivity, resource availability, and bee preferences contribute to differences in host-parasite relationships (Michener 1979; Sheffield et al., 2013a) and are reflected in the abundance and richness patterns of bee communities (Michener 1979; Potts et al., 2005; Moretti et al., 2009; Ebeling 2012). Land use was shown to have minimal effects on the bee community, but this was dependent on floral resource availability and guild of interest. When floral resources were low (Sturm unpublished data), land use type was a significant predictor for the non-host and cleptoparasite communities, both of which occupied canola sites more than rangeland sites. A possible explanation for higher non-host bee occupancy in canola may be that non-hosts are better able to take advantage of mass flowering crops in adjacent habitats farther away from nesting sites, whereas host bees may alter their foraging behavior to minimize unguarded nest entrances from potential attackers, decreasing their chance of parasitism (Mikat, Cerna & Straka 2016). A study by Abrams & Eickwort (1979) found that communal nest aggregations of *Agapostemon virescens* with nest guarding females were protected from the cleptoparasitic bee *Nomada articulata* and nests that were unguarded by solitary females were successfully attacked. More recently, Mikat, Cerna & Straka (2016) experimentally removed female *Ceratina* bees from nests to determine the importance of nest guarding. In control nests of *Ceratina cucurbitina* the mortality rate for offspring was 21.6% compared to 81.4% of nests where females were removed, and in nests of *Ceratina chalybea* 3.9% of offspring deaths occurred in control nests compared to 53.1% in removal nests. Therefore, it is reasonable to predict that known host females may be exhibiting some kind of risk aversion behaviour, which may in turn be linked to habitat use.

Exploring the use of cleptoparasites as indicator taxa for the overall bee community revealed some interesting general patterns. Although cleptoparasites were indicative of overall bee community abundance and richness, our results varied across year and study region. These inconsistencies challenge the general effectiveness of cleptoparasites as indicator species. We propose that cleptoparasites may be indicative of bee abundance, especially when floral resources are low, or habitat quality is poor, but making predictions about species richness or overall diversity of the bee community from cleptoparasite data alone may be difficult. Instead, the use of cleptoparasite data in combination with census data may yield more interpretable information about the status of wild bee populations. As an apex guild, cleptoparasites provide early detection into habitat change and disturbance effects by being the first group to respond to these changes (Combes 1996). Further, previous studies conducted in managed and abandoned apple orchards found cleptoparasites to be highly effective at assessing habitat quality of intensively managed agricultural areas with very few cleptoparasitic individuals present at sites lacking vegetation structure and diversity (Sheffield et al., 2013a; Sheffield et al., 2013b). Inter-annual differences in bee communities, survey methods or analytical approaches may explain these differences, but do highlight that cleptoparasites may not be effective indicators in all environments.

One drawback to our study may have been our approach to classify host and non-host categories based on taxonomic resolution to genera, as there are behaviors that cannot be overgeneralized across this broad taxonomic classification. However, variation in species responses due to life history traits, the lack of (and sometimes overly complicated) taxonomic species keys available, and the absence of natural history information for many species left us with limited options in terms of classifying different bee taxa for our analyses. Interestingly, although the percentage of cleptoparasites that made up the overall total of bees captured were low, we were surprised to find that the few numbers of cleptoparasitic individuals did not have an effect on the results of the both the co-occur analysis and GLM testing. Positive pairings resulted between cleptoparasites and hosts that were both common (>200 individuals) and rare (10-15 individuals) in our surveys.

Conclusion

Ecosystems are highly variable, and finding cost effective means for evaluating wildlife does not always lead to a one size fits all solution. Although cleptoparasites were not strong indicators of land use change, cleptoparasite abundance still correlated with host bee abundance and provided valuable insight into habitat quality and resource availability. Because there are so few studies that have looked at these particular interactions, and our methods and results differed from previous findings, the use of cleptoparasites as indicator taxa warrants further investigation.

Table 3.1. List of known cleptoparasitic relationships for bees found in our study region.

Cleptoparasite	Known host bee genera
Coelioxys	*Megachile*
Epeolus	*Colletes*
Holcopasites	*Calliopsis*
	Pseudopanurgus
	Panurginus
Melecta	*Anthophora*
	Habropoda
Neolarra	*Perdita*
Nomada	*Andrena*
	Agapostemon
	Halictus
	Lasioglossum
	Panurgus
	Melitta
	Eucera
Sphecodes	*Agapostemon*
	Halictus
	Lasioglossum
Stelis	*Anthidium*
	Hoplitis
	Megachile
	Osmia
Triepeolus	*Eucera*
	Melissodes
Xeromelecta	*Habropoda*
Zacosmia	*Anthophora* subgenus *Heliophila*
Social parasites (*Psithyrus*)	Known host species
Bombus flavidus	*Bombus appositus*
	Bombus occidentalis
	Bombus rufocinctus
Bombus insularis	*Bombus appositus*
	Bombus fervidus
	Bombus nevadensis
	Bombus occidentalis
	Bombus rufocinctus
	Bombus terricola
Bombus suckleyi	*Bombus appositus*
	Bombus fervidus
	Bombus nevadensis
	Bombus occidentalis
	Bombus rufocinctus
	Bombus terricola

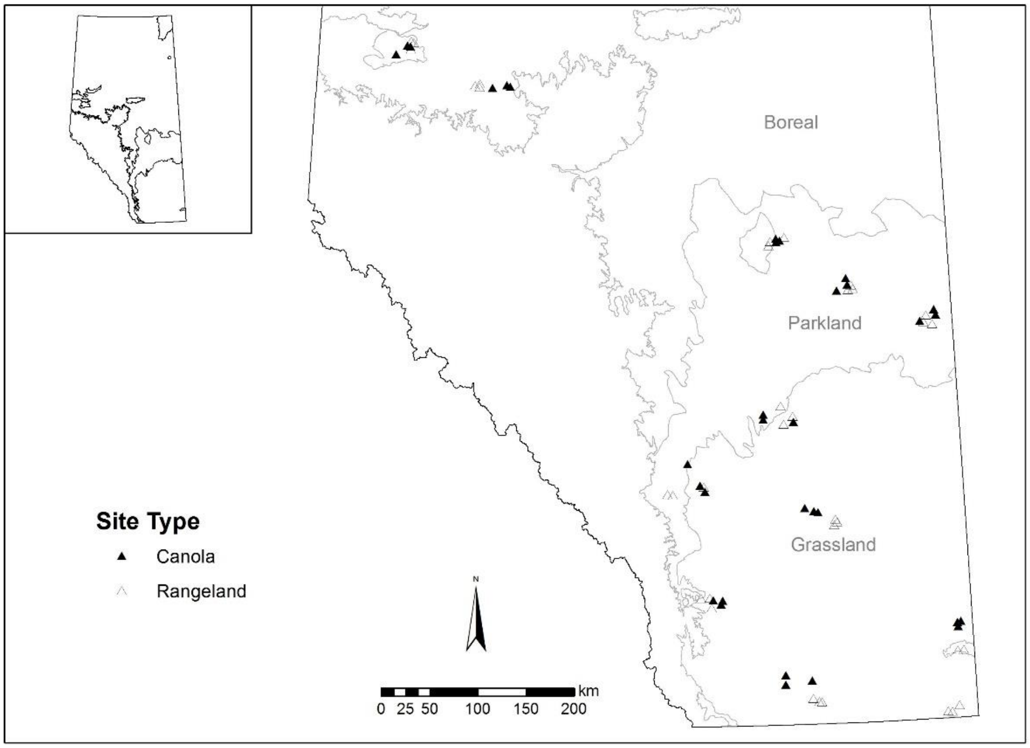

Figure 3.1. Map showing geographic locations of sites sampled throughout the province of Alberta. Sites were organized into four regions (Boreal, Parkland, Fescue and Grasslands) and surveyed during the same week for both survey seasons, weather permitting. Fescue regions were classified using elevation data and dominant plant community types. Fescue sites included a unique area in southeastern Alberta (Cypress Hills), and higher elevation sites in the foothills subregion occurring along the eastern border of the Rocky Mountains.

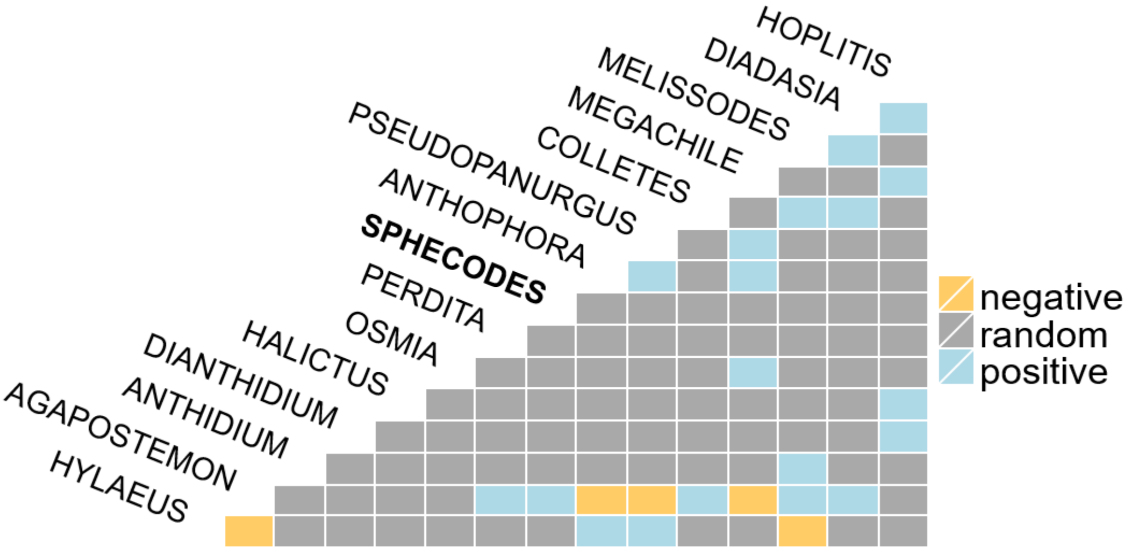

Figure 3.2. Results from co-occurrence analysis for 2014 taxa pairs. Plot summarizes positive, random and negative taxon pairings. Based on identification to genera. Cleptoparasites are bolded.

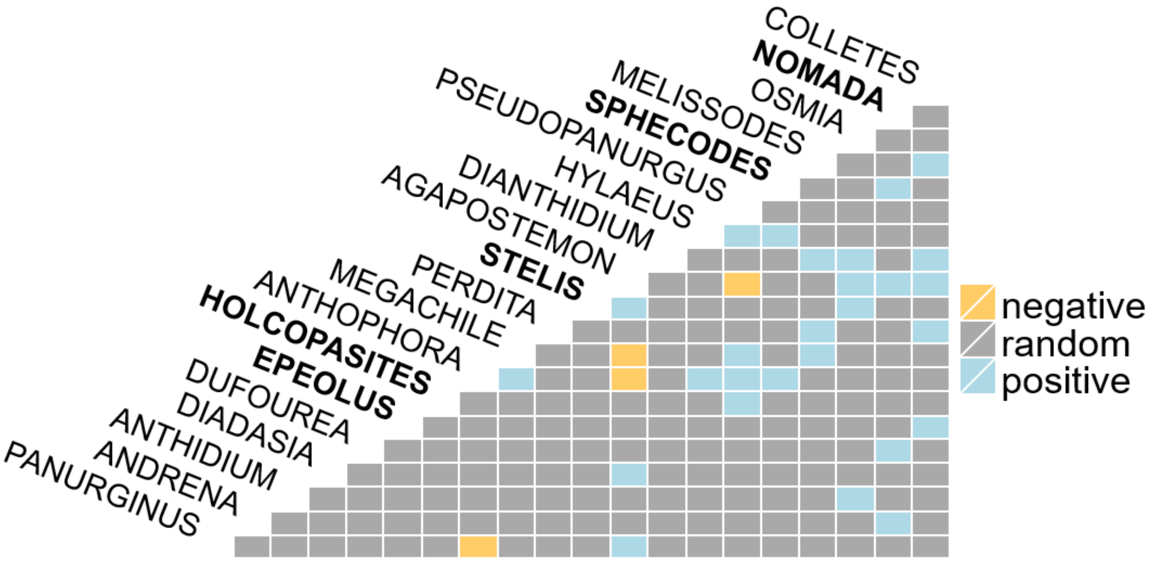

Figure 3.3. Results from co-occurrence analysis for 2015 taxa pairs. Plot summarizes positive, random and negative taxon pairings. Based on identification to genera. Cleptoparasites are bolded.

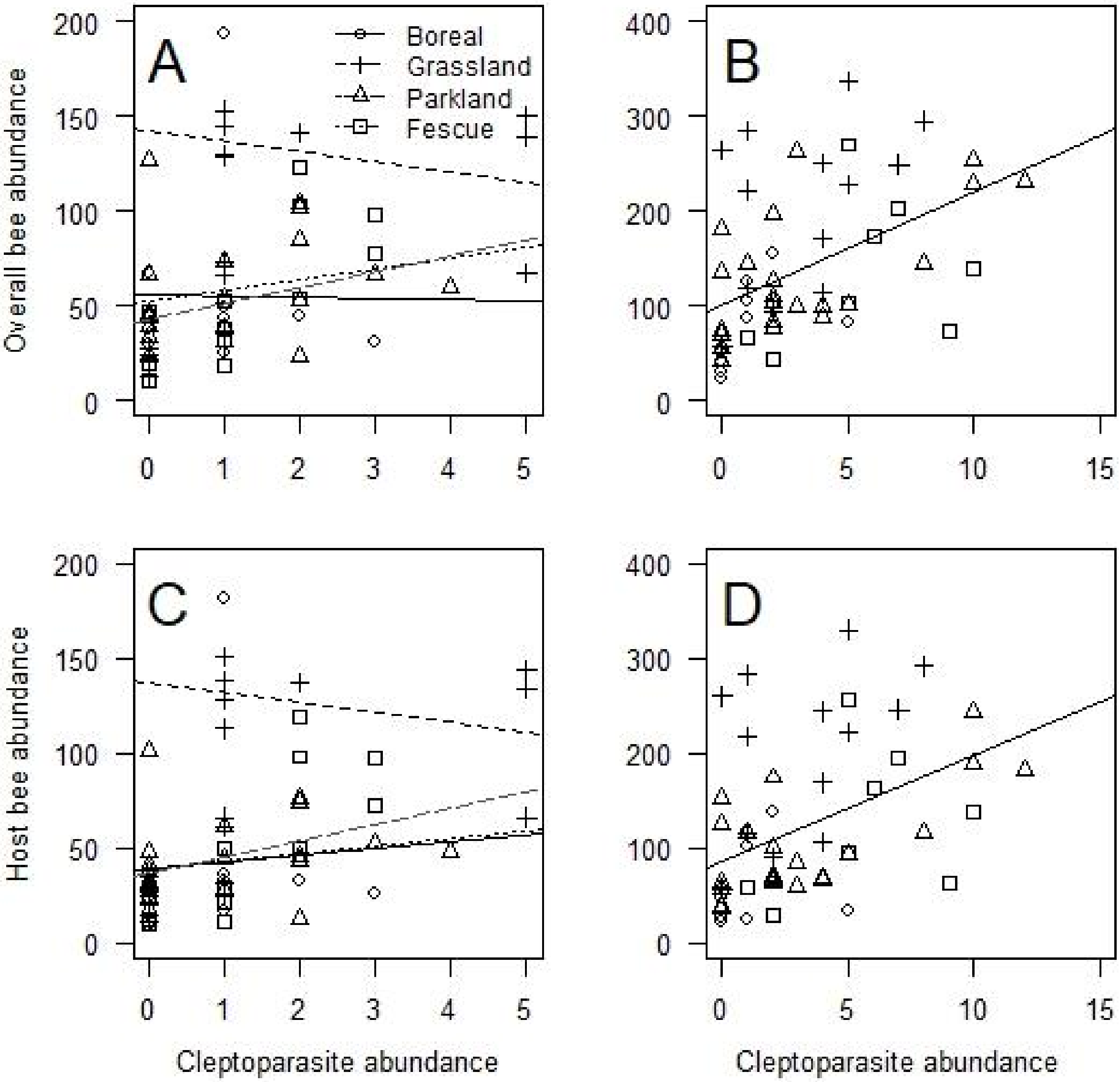

Figure 3.4. Responses of overall bee and host bee abundance to cleptoparasite abundance in 2014 (A,C) and 2015 (B,D). Lines represent a linear regression between the response variables and cleptoparasite abundance for all regions combined (B,D) and natural regions independently (A,C) (Boreal, Grassland, Parkland and Fescue).

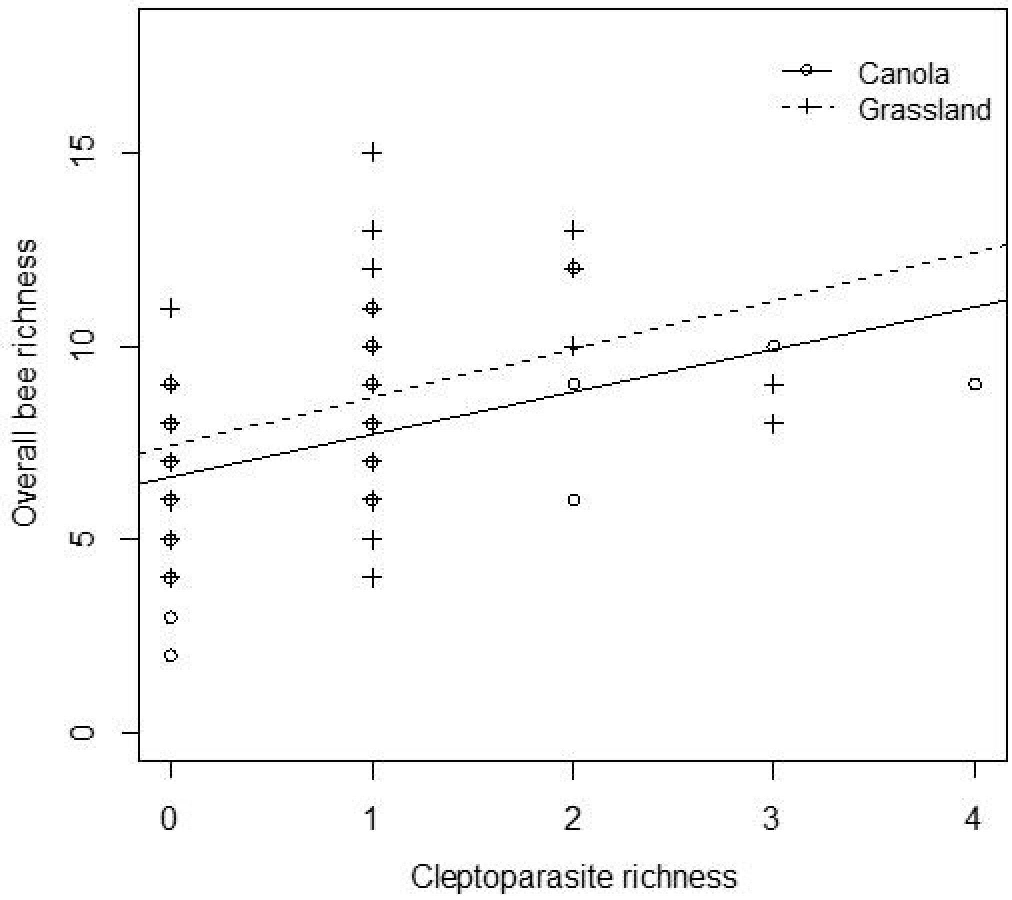

Figure 3.5. Relationship between cleptoparasite richness and the richness of the overall bee community in 2014 in both canola and grassland locations.

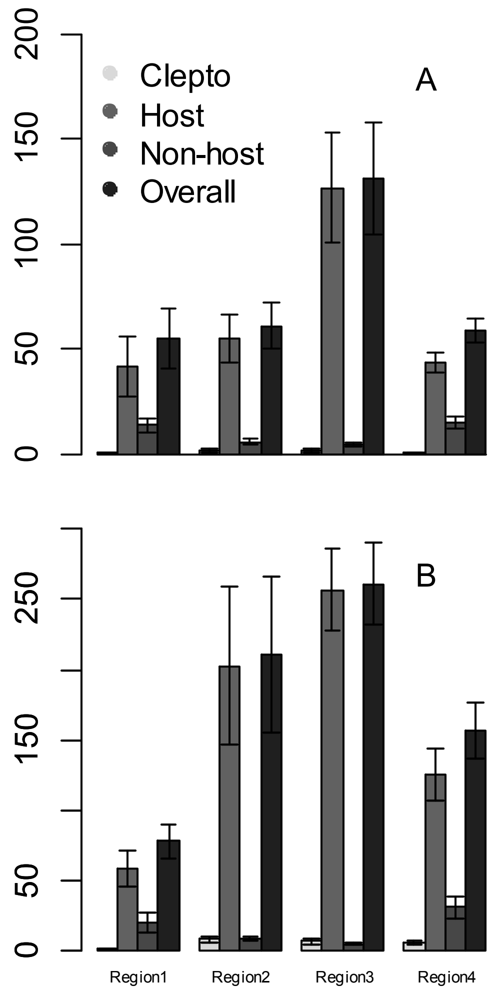

Figure 3.6. Mean (plus/minus SE) bee abundances across regions for the 2014 (A) and 2015 (B) survey years. (Region 1: Boreal, Region 2: Fescue, Region 3: Grassland, Region 4: Parkland).

Chapter four: Conclusion

The threat of ongoing bee declines have negative consequences for ecosystem biodiversity, pollination services and global food production (Kremen et al., 2007; Winfree et al., 2009; Potts et al., 2010). Understanding the effects of land-use and management strategies that will allow for bee conservation is therefore essential to conservation efforts. This body of work contributes valuable biodiversity information for a large portion of the Prairies, and to our knowledge, is one of the first studies to assess native bee communities across a broad latitudinal gradient for two main agricultural land-use types. Here, I have presented two different approaches to evaluating the effects of grazing, land-use, and regional differences on native bee communities across a large environmental gradient.

First, I evaluated the effects of long term grazing on both plant and bee communities using rangeland health scores (Chapter 2). I found that rangeland health score was positively correlated with bee abundance, diversity and richness, even though it was not predictive of overall flower abundance, flower richness or plant productivity. Floral resources are important for bees, and the size and diversity of bee communities often positively correlates with the size and diversity of plant communities (Potts et al., 2003; Biesmeijer et al., 2006; Potts et al., 2009). However, the fact that rangeland health scores predict the bee community but not the plant community suggests that range health captures another site metric that is important to bees. Several studies have suggested that vegetation structure, which is more reflective of potential nesting sites, is a better measure for the bee community than floral resources (Tscharntke et al., 2005; Grundel et al., 2010; Zhu et al., 2012; Elwell, Griswold & Elle 2016; Moniera et al., 2017), and these scores may therefore reflect other habitat requirements for native bees. Ultimately, healthier rangelands were predictive of healthier bee communities and rangeland health assessments may therefore be a valuable ecological tool connecting bee conservation and land management goals.

I also evaluated the potential use of cleptoparasites as an indicator group to predict bee abundance and richness for host, non-host and overall bee communities (Chapter 3). Although cleptoparasitic bees were found to consistently co-occur with their host bees, metrics of the cleptoparasite community had limited predictive abilities for the overall and host bee communities in all regions and between survey years. We tested the effectiveness of the cleptoparasite guild to predict bee abundance and richness in a landscape comprised of both semi-natural and cropped sites. In this study system we did not find that cleptoparasites were reliable indicators for bee abundance and richness, possibly due to the relatively low number of cleptoparasitic individuals captured compared to non-cleptoparasitic bees. The lack of effect by land-use type implies that cleptoparasites were unaffected by the intense management found in canola fields relative to grasslands. This is in contrast to a previous study that found a higher proportion of the cleptoparasitic guild in low vs. high disturbance areas (Sheffield et al., 2013a). One explanation for these conflicting findings is that the overabundance of floral resources in canola fields may have drawn cleptoparasites in from neighboring grasslands, where host bees are more likely to nest and where we predicted to see higher cleptoparasite density. Despite their promise as an indicator species, our results don't strongly support using cleptoparasites as a means of monitoring overall bee populations

Work from this thesis has contributed valuable baseline information for native bees across a large scale, and from two of the main land-use types in the region. We found that with proper management, cattle producers can help sustain native bee populations, and that effectively capturing bee diversity still requires extensive surveying, at least in our study region.

Addressing the issue of biodiversity loss is an important step to sustaining ecosystem services and conservation of species at risk (Thrupp 2000; Gauthier & Wilken 2003; Potts et al., 2010). However, monitoring of biodiversity is needed to aid conservation efforts as it provides valuable population information that supports earlier detection of population declines, allowing researchers to identify practical solutions to prevent losses. Research from monitoring not only provides information about the status of the organism or ecosystem of interest but is also essential for providing information and guidance to decision makers and land stewards to influence policy and management for meeting conservation objectives. Although the cleptoparasitic guild was not found to correlate with overall bee abundance and richness in our study, improving our knowledge of the relationship between potential indicators and bee biodiversity across differing agro-environments is essential. Future work should include strategies to help make the identification process of native bees a simpler process or, alternatively, to identify effective indicator taxa. For example, identification guides that classify individuals to a functional group based on morphological characters, rather than to species, may prove to be more useful for conservation purposes, although there will be exceptions. When these tools are available it will be easier to assess which functional groups or species may be at risk due to different land-use or disturbances, which will allow monitoring efforts to focus primarily on these subgroups of bees rather than the whole bee community. This will also enable researchers to prioritize conservation efforts for bees that may be experiencing greater losses due to these changes.

Our use of rangeland health assessments to determine habitat suitability for bees is just one of the ways that we can integrate land management tools that are already in place to help mitigate species losses. Additional information on how habitat structure influences bees could also help to formulate effective management strategies for growers, landowners and other stakeholders. Grassland habitat across the Prairie ecozone represent some of the last remaining remnants of natural ecosystems in this area, therefore advocating for sustainable use on these areas is of the utmost importance. Grazing is a keystone process in the prairies and, with responsible management, cattle producers can help to maintain these areas as habitat for other native prairie species.

Summary

My study has provided a comprehensive look at the diversity of bee communities in rangelands across Alberta and identified differing patterns in bee community assemblages across a latitudinal gradient. The scale of the study, combined with the investigation of cleptoparasites as a potential strategy for monitoring native bee communities, provides new insight into the impacts of major agricultural use on native bee communities. Declines in native bee populations have increased the need for understanding how human-induced change on ecosystems affect bee communities (Winfree et al., 2009; Potts et al., 2010; Cameron et al., 2011) and the availability of semi-natural habitat is critical for the survival and reproduction of bee populations, especially in areas with intensive agriculture (Kremen, Williams & Thorp 2002; Klein et al., 2007). My results support previous studies that suggest grasslands play an important role in supporting bees by providing valuable nesting habitat and abundant floral resources throughout the growing season (Kwaiser & Hendrix 2008; Black et al., 2011). Managing and conserving these systems for both sustainable agriculture and bee pollinators is therefore essential for conservation.

Literature cited

Adams, B. W., Ehlert, G., Stone, C., Lawrence, D., Alexander, M., Willoughby, M., Carlson, J. (2005). Rangeland health assessment for grassland, forest and tame pasture. *Public Lands and Forests Division, Alberta Sustainable Resource Development.*

Allsopp, M. H., De Lange, W. J., & Veldtman, R. (2008). Valuing insect pollination services with cost of replacement. *PLoS One, 3*(9), e3128.

Anderson, R. C. (2006). Evolution and origin of the central grassland of North America: Climate, fire, and mammalian grazers. *Journal of the Torrey Botanical Society, 133*(4), 626-647. doi:10.3159/1095-5674(2006)133[626:EAOOTC]2.0.CO;2

Ascher, J., & Pickering, J. (2014). Discover life bee species guide and world checklist (hymenoptera: Apoidea: Anthophila). *Draft-35 Http://www.Discoverlife.org/mp/20q,*

Ashman, T., Knight, T. M., Steets, J. A., Amarasekare, P., Burd, M., Campbell, D. R., Mitchell, R. J. (2004). Pollen limitation of plant reproduction: Ecological and evolutionary causes and consequences. *Ecology, 85*(9), 2408-2421.

Asner, G., Elmore, A., Olander, L., Martin, R., & Harris, A. (2004). Grazing systems, ecosystem responses, and global change. *Annual Review of Environment and Resources, 29*, 261-299. doi:10.1146/annurev.energy.29.062403.102142

Bailey, A. W., Schellenberg, M. P., & McCartney, D. (2010). *Management of Canadian prairie rangeland* Agriculture and Agri-Food Canada Ottawa, Canada.

Bates, D., Maechler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models using lme4, *Journal of statistical software*. 67(1), 1-48. Doi:10.18637/jss.v067.i01.

Baum, K. A., & Wallen, K. E. (2011). Potential bias in pan trapping as a function of floral abundance. *Journal of the Kansas Entomological Society, 84*(2), 155-159.

Biesmeijer, J. C., Roberts, S. P., Reemer, M., Ohlemuller, R., Edwards, M., Peeters, T., Kunin, W. E. (2006). Parallel declines in pollinators and insect-pollinated plants in britain and the netherlands. *Science (New York, N.Y.), 313*(5785), 351-354. doi:313/5785/351 [pii]

Blaauw, B. R., & Isaacs, R. (2014). Flower plantings increase wild bee abundance and the pollination services provided to a pollination-dependent crop. *Journal of Applied Ecology, 51*(4), 890-898.

Black, S. H., Shepherd, M., & Vaughan, M. (2011). Rangeland management for pollinators. *Rangelands, 33*(3), 9-13.

Braun, C. E., Oedekoven, O. O., & Aldridge, C. L. (2002). Oil and gas development in western North America: Effects on sagebrush steppe avifauna with particular emphasis on sage grouse. *Transactions of the North American Wildlife and Natural Resources Conference, 67* 337-349.

Brown, M. J., & Paxton, R. J. (2009). The conservation of bees: A global perspective. *Apidologie, 40*(3), 410-416.

Burkle, L. A., Marlin, J. C., & Knight, T. M. (2013). Plant-pollinator interactions over 120 years: Loss of species, co-occurrence, and function. *Science), 339*(6127), 1611-1615. doi:10.1126/science.1232728

Cameron, S. A., Lozier, J. D., Strange, J. P., Koch, J. B., Cordes, N., Solter, L. F., & Griswold, T. L. (2011). Patterns of widespread decline in North American bumble bees. *Proceedings of the National Academy of Sciences of the United States of America, 108*(2), 662-667. doi:10.1073/pnas.1014743108

Cane, J. H., Minckley, R. L., & Kervin, L. J. (2000). Sampling bees (hymenoptera: Apiformes) for pollinator community studies: Pitfalls of pan-trapping. *Journal of the Kansas Entomological Society,* 225-231.

Cane, J. H., Minckley, R. L., Kervin, L. J., & Williams, N. M. (2006). Complex responses within a desert bee guild (hymenoptera: Apiformes) to urban habitat fragmentation. *Ecological Applications, 16*(2), 632-644.

Cane, J. H. (2001). Habitat fragmentation and native bees: A premature verdict? *Conservation Ecology, 5*(1), 3.

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

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

Carvell, C. (2002). Habitat use and conservation of bumblebees (*bombus* spp.) under different grassland management regimes. *Biological Conservation, 103*(1), 33-49.

Combes, C. (1996). Parasites, biodiversity and ecosystem stability. *Biodiversity and Conservation, 5*(8), 953-962.

Conant, R. T., Paustian, K., & Elliott, E. T. (2001). Grassland management and conversion into grassland: Effects on soil carbon. *Ecological Applications, 11*(2), 343-355.

Corbet, S. A., Fussell, M., Ake, R., Fraser, A., Gunson, C., Savage, A., & Smith, K. (1993). Temperature and the pollinating activity of social bees. *Ecological Entomology, 18*(1), 17-30.

Danforth, B. (2007). Bees. *Current Biology, 17*(5), R156-R161.

De Bello, F., Leps, J., & Sebastia, M. (2007). Grazing effects on the species-area relationship: Variation along a climatic gradient in NE Spain. *Journal of Vegetation Science, 18*(1), 25-34. doi:10.1658/1100-9233(2007)18[25:GEOTSR]2.0.CO;2

Diaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. G., NOY-MEIR, I. (2007). Plant trait responses to grazing–a global synthesis. *Global Change Biology, 13*(2), 313-341.

Dorrough, J., Mcintyre, S., Brown, G., Stol, J., Barrett, G., & Brown, A. (2012). Differential responses of plants, reptiles and birds to grazing management, fertilizer and tree clearing. *Austral Ecology, 37*(5), 569-582. doi:10.1111/j.1442-9993.2011.02317.x

Dos-Santos, I. A. (2009). Cleptoparasite bees, with emphasis on the oil-bees hosts. *Acta Biológica Colombiana, 14*(2), 107-114.

Downing, D., & Pettapiece, W. (2006). Natural Regions and Sub-regions of Alberta. Government of Alberta. *Pub,*

Ebeling, A., Klein, A., Weisser, W. W., & Tscharntke, T. (2012). Multitrophic effects of experimental changes in plant diversity on cavity-nesting bees, wasps, and their parasitoids. *Oecologia, 169*(2), 453-465.

Eldridge, D. J., Poore, A. G., Ruiz-Colmenero, M., Letnic, M., & Soliveres, S. (2016). Ecosystem structure, function, and composition in rangelands are negatively affected by livestock grazing. *Ecological Applications, 26*(4), 1273-1283.

Ellstrand, N. C. (1992). Gene flow by pollen: Implications for plant conservation genetics. *Oikos,* 77-86.

Elwell, S. L., Griswold, T., & Elle, E. (2016). Habitat type plays a greater role than livestock grazing in structuring shrub-steppe plant-pollinator communities. *Journal of Insect Conservation, 20*(3), 515-525. doi:10.1007/s10841-016-9884-8

Finke, D. L., & Denno, R. F. (2004). Predator diversity dampens trophic cascades. *Nature, 429*(6990), 407.

Foley, J. A., Defries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., F., Chapin, S., Coe1, M., Daily, G. C., Gibbs, H., Helkowski, J .H., Holloway, T., Howard, E. A., Kucharik, C J., Monfreda, C., Patz, J. A., Prentice, C., Ramankutty, N., Snyder, P. K. (2005). Global consequences of land use. *Science, 309*(5734), 570-574. doi:309/5734/570 [pii]

Fox, J., Friendly, G. G., Graves, S., Heiberger, R., Monette, G., Nilsson, H., Suggests, M. (2011). Companion to Applied Regression, 2nd. Ed. *Sage*.

Fuhlendorf, S. D., & Engle, D. M. (2001). Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. *Bioscience, 51*(8), 625-632. doi:10.1641/0006-3568(2001)051[0625:RHOREM]2.0.CO;2

Garibaldi, L. A., Steffan-Dewenter, I., Winfree, R., Aizen, M. A., Bommarco, R., Cunningham, S. A., Klein, A. M. (2013). Wild pollinators enhance fruit set of crops regardless of honey bee abundance. *Science, 339*(6127), 1608-1611. doi:10.1126/science.1230200 [doi]

Gauthier, D. A., & Wiken, E. B. (2003). Monitoring the conservation of grassland habitats, prairie ecozone, Canada. *Environmental Monitoring and Assessment, 88*(1), 343-364.

Gezon, Z. J., Wyman, E. S., Ascher, J. S., Inouye, D. W., & Irwin, R. E. (2015). The effect of repeated, lethal sampling on wild bee abundance and diversity. *Methods in Ecology and Evolution, 6*(9), 1044-1054.

Gill, R. J., Ramos-Rodriguez, O., & Raine, N. E. (2012). Combined pesticide exposure severely affects individual-and colony-level traits in bees. *Nature, 491*(7422), 105-108.

Golodets, C., Kigel, J., & Sternberg, M. (2011). Plant diversity partitioning in grazed mediterranean grassland at multiple spatial and temporal scales. *Journal of Applied Ecology, 48*(5), 1260-1268. doi:10.1111/j.1365-2664.2011.02031.x

Gotelli, N. J., & McCabe, D. J. (2002). Species co-occurrence: A meta-analysis of jm diamond's assembly rules model. *Ecology, 83*(8), 2091-2096.

Goulson, D., Lye, G. C., & Darvill, B. (2008). Decline and conservation of bumble bees. *Annual Review of Entomology, 53*, 191-208.

Goulson, D., Nicholls, E., Botias, C., & Rotheray, E. L. (2015). Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. *Science, 347*(6229), 1255957. doi:10.1126/science.1255957 [doi]

Grundel, R., Jean, R. P., Frohnapple, K. J., Glowacki, G. A., Scott, P. E., & Pavlovic, N. B. (2010). Floral and nesting resources, habitat structure, and fire influence bee distribution across an open-forest gradient. *Ecological Applications, 20*(6), 1678-1692. doi:10.1890/08-1792.1

Hammermeister, A., Gauthier, D., & McGovern, K. (2001). Saskatchewan's native prairie: Taking stock of a vanishing ecosystem and dwindling resource. *Native Plant Society of Saskatchewan.*

Haynes, R., & Williams, P. (1993). Nutrient cycling and soil fertility in the grazed pasture ecosystem. *Advances in Agronomy, 49*, 119-199.

Henderson, A. E., & Davis, S. K. (2014). Rangeland health assessment: A useful tool for linking range management and grassland bird conservation? *Rangeland Ecology and Management, 67*(1), 88-98.

Hickman, K. R., Hartnett, D. C., Cochran, R. C., & Owensby, C. E. (2004). Grazing management effects on plant species diversity in tallgrass prairie. *Journal of Range Management, 57*(1), 58-65.

Hughes, A. R., & Stachowicz, J. J. (2004). Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proceedings of the National Academy of Sciences of the United States of America, 101*(24), 8998-9002. doi:10.1073/pnas.0402642101 [doi]

Huntley, B. (1991). How plants respond to climate change: Migration rates, individualism and the consequences for plant communities. *Annals of Botany, 67*(supp1), 15-22.

Huston, M. A., & Huston, M. A. (1994). Biological diversity: The coexistence of species. *Cambridge University Press*.

Kearns, C. A., Inouye, D. W., & Waser, N. M. (1998). Endangered mutualisms: The conservation of plant-pollinator interactions. *Annual Review of Ecology and Systematics, 29*(1), 83-112.

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

Kimoto, C., DeBano, S. J., Thorp, R. W., Taylor, R. V., Schmalz, H., DelCurto, T., Rao, S. (2012). Short-term responses of native bees to livestock and implications for managing ecosystem services in grasslands. *Ecosphere, 3*(10), UNSP 88. doi:10.1890/ES12-00118.1

Kimuyu, D. M., Sensenig, R. L., Riginos, C., Veblen, K. E., & Young, T. P. (2014). Native and domestic browsers and grazers reduce fuels, fire temperatures, and acacia ant mortality in an African savanna. *Ecological Applications, 24*(4), 741-749.

Kipyatkov, V., Lopatina, E., Imamgaliev, A., & Shirokova, L. (2004). Effect of temperature on rearing of the first brood by the founder females of the ant *lasius niger* (hymenoptera, formicidae): Latitude-dependent variability of the response norm. *Journal of Evolutionary Biochemistry and Physiology, 40*(2), 165-175.

Klein, A. M., Vaissiere, B. E., Cane, J. H., Steffan-Dewenter, I., Cunningham, S. A., Kremen, C., & Tscharntke, T. (2007). Importance of pollinators in changing landscapes for world crops. *Proceedings. Biological Sciences, 274*(1608), 303-313. doi:8W42N6V08K761023 [pii]

Kremen, C., Williams, N. M., & Thorp, R. W. (2002). Crop pollination from native bees at risk from agricultural intensification. *Proceedings of the National Academy of Sciences of the United States of America, 99*(26), 16812-16816. doi:10.1073/pnas.262413599 [doi]

Kremen, C., Williams, N. M., Aizen, M. A., Gemmill-Herren, B., LeBuhn, G., Minckley, R., Ricketts, T. H. (2007). Pollination and other ecosystem services produced by mobile organisms: A conceptual framework for the effects of land-use change. *Ecology Letters, 10*(4), 299-314. doi:10.1111/j.1461-0248.2007.01018.x

Kruess, A., & Tscharntke, T. (2002). Contrasting responses of plant and insect diversity to variation in grazing intensity. *Biological Conservation, 106*(3), 293-302.

Kruess, A., & Tscharntke, T. (2002). Grazing intensity and the diversity of grasshoppers, butterflies, and trap-nesting bees and wasps. *Conservation Biology, 16*(6), 1570-1580.

Kwaiser, K. S., & Hendrix, S. D. (2008). Diversity and abundance of bees (hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. *Agriculture, Ecosystems & Environment, 124*(3), 200-204.

Lazaro, A., Tscheulin, T., Devalez, J., Nakas, G., & Petanidou, T. (2016). Effects of grazing intensity on pollinator abundance and diversity, and on pollination services. *Ecological Entomology, 41*(4), 400-412.

LeBuhn, G., Griswold, T., Minckley, R., Droege, S., Roulston, T., Cane, J., Williams, N. (2003). A standardized method for monitoring bee populations–the bee inventory (BI) plot. *Available at Http://online.Sfsu.edu/b eeplot/pdfs/Bee% 20Plot% 202003.Pdf,*

Lunt, I. D., Eldridge, D. J., Morgan, J. W., & Witt, G. B. (2007). A framework to predict the effects of livestock grazing and grazing exclusion on conservation values in natural ecosystems in Australia. *Australian Journal of Botany, 55*(4), 401-415.

Michener, C. D. (1979). Biogeography of the bees. *Annals of the Missouri Botanical Garden*, 66(3), 277-347.

Michener, C. D. (2007). *The bees of the world*. 2nd. Ed. Johns Hopkins, Baltimore.

Michener, C. D., McGinley, R. J., & Danforth, B. N. (1994). *The bee genera of North and Central America (hymenoptera: Apoidea).* Smithsonian Institution Press.

Mikat, M., Cerna, K., & Straka, J. (2016). Major benefits of guarding behavior in subsocial bees: Implications for social evolution. *Ecology and Evolution, 6*(19), 6784-6797. doi:10.1002/ece3.2387

Milchunas, D. G., & Lauenroth, W. K. (1993). Quantitative effects of grazing on vegetation and soils over a global range of environments. *Ecological Monographs, 63*(4), 327-366.

Milchunas, D., Sala, O., & Lauenroth, W. (1988). A generalized model of the effects of grazing by large herbivores on grassland community structure. *The American Naturalist, 132*(1), 87-106.

Miller, M. E. (2008). Broad-scale assessment of rangeland health, grand Staircase–Escalante national monument, USA. *Rangeland Ecology & Management, 61*(3), 249-262.

Minckley, R. L. (2014). Maintenance of richness despite reduced abundance of desert bees (hymenoptera: Apiformes) to persistent grazing. *Insect Conservation and Diversity, 7*(3), 263-273.

Mitchell, T. B. (1960). Bees of the eastern United States.vol 1. *North Carolina Agricultural Experiment Station Technologies Bulletin,* 141.1-538.

Mitchell, T. (1962). Bees of the eastern united states. vol. 2. *North Carolina Agricultural Experiment Station Technologies Bulletin,* 152.1-557.

Morandin, L. A., & Winston, M. L. (2005). Wild bee abundance and seed production in conventional, organic, and genetically modified canola. *Ecological Applications, 15*(3), 871-881.

Moreira, E. F., da Silva Santos, R. L., Silveira, M. S., Boscolo, D., das Neves, E. L., & Viana, B. F. (2017). Influence of landscape structure on euglossini composition in open vegetation environments. *Biota Neotropica, 17*(1), e20160294. doi:10.1590/1676-0611-BN-2016-0294

Moretti, M., De Bello, F., Roberts, S. P., & Potts, S. G. (2009). Taxonomical vs. functional responses of bee communities to fire in two contrasting climatic regions. *Journal of Animal Ecology, 78*(1), 98-108.

Murray, T. E., Kuhlmann, M., & Potts, S. G. (2009). Conservation ecology of bees: Populations, species and communities. *Apidologie, 40*(3), 211-236.

Öckinger, E., & Smith, H. G. (2006). Landscape composition and habitat area affects butterfly species richness in semi-natural grasslands. *Oecologia, 149*(3), 526-534.

Öckinger, E., & Smith, H. G. (2007). Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. *Journal of Applied Ecology, 44*(1), 50-59.

Olff, H., & Ritchie, M. E. (1998). Effects of herbivores on grassland plant diversity. *Trends in Ecology & Evolution, 13*(7), 261-265.

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

Osborne, J. L., Williams, I. H., & Corbet, S. A. (1991). Bees, pollination and habitat change in the european community. *Bee World, 72*(3), 99-116.

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

Petanidou, T., & Ellis, W. (1996). Interdependence of native bee faunas and floras in changing mediterranean communities. *Linnean Society. Symposia Series,* 18 201-226.

Popic, T. J., Davila, Y. C., & Wardle, G. M. (2013). Evaluation of common methods for sampling invertebrate pollinator assemblages: Net sampling out-perform pan traps. *PLoS One, 8*(6), e66665.

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

Potts, S. G., Vulliamy, B., Dafni, A., Ne'eman, G., & Willmer, P. (2003). Linking bees and flowers: How do floral communities structure pollinator communities? *Ecology, 84*(10), 2628-2642.

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

Proulx, M., & Mazumder, A. (1998). Reversal of grazing impact on plant species richness in nutrient-poor vs. nutrient-rich ecosystems. *Ecology, 79*(8), 2581-2592.

Roulston, T. H., & Goodell, K. (2011). The role of resources and risks in regulating wild bee populations. *Annual Review of Entomology, 56*, 293-312.

Shavit, O., Dafni, A., & Ne'eman, G. (2009). Competition between honeybees (*apis mellifera*) and native solitary bees in the Mediterranean region of Israel—Implications for conservation. *Israel Journal of Plant Sciences, 57*(3), 171-183.

Sheffield, C. S., Frier, S. D., & Dumesh, S. (2014). The bees (hymenoptera: Apoidea, apiformes) of the prairies ecozone, with comparisons to other grasslands of Canada. *Arthropods of Canadian Grasslands, 4*, 427-467.

Sheffield, C. S., Kevan, P. G., Pindar, A., & Packer, L. (2013). Bee (hymenoptera: Apoidea) diversity within apple orchards and old fields in the Annapolis valley, Nova Scotia, Canada. *The Canadian Entomologist, 145*(01), 94-114.

Sheffield, C. S., Pindar, A., Packer, L., & Kevan, P. G. (2013). The potential of cleptoparasitic bees as indicator taxa for assessing bee communities. *Apidologie, 44*(5), 501-510.

Sheffield, C. S., Ratti, C., Packer, L., & Griswold, T. (2011). Leafcutter and mason bees of the genus *Megachile latreille* (hymenoptera: Megachilidae) in Canada and Alaska. *Canadian Journal of Arthropod Identification, 18*, 1-107.

Sjödin, N. E., Bengtsson, J., & Ekbom, B. (2008). The influence of grazing intensity and landscape composition on the diversity and abundance of flower-visiting insects. *Journal of Applied Ecology, 45*(3), 763-772.

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

Steffan-Dewenter, I., & Tscharntke, T. (1999). Effects of habitat isolation on pollinator communities and seed set. *Oecologia, 121*(3), 432-440.

Stone, G. (1994). Activity patterns of females of the solitary bee *Anthophora plumipes* in relation to temperature, nectar supplies and body-size. *Ecological Entomology, 19*(2), 177-189. doi:10.1111/j.1365-2311.1994.tb00408.x

Sugden, E. A. (1985). Pollinators of *Astragalus monoensis barneby* (fabaceae): New host records; potential impact of sheep grazing. *The Great Basin Naturalist*, 30, 299-312.

Tautz, J., Maier, S., Groh, C., Rossler, W., & Brockmann, A. (2003). Behavioral performance in adult honey bees is influenced by the temperature experienced during their pupal development. *Proceedings of the National Academy of Sciences of the United States of America, 100*(12), 7343-7347. doi:10.1073/pnas.1232346100 [doi]

Thrupp, L. A. (2000). Linking agricultural biodiversity and food security: The valuable role of agrobiodiversity for sustainable agriculture. *International Affairs, 76*(2), 283-297.

Torné-Noguera, A., Rodrigo, A., Arnan, X., Osorio, S., Barril-Graells, H., da Rocha-Filho, L. C., & Bosch, J. (2014). Determinants of spatial distribution in a bee community: Nesting resources, flower resources, and body size. *PloS One, 9*(5), e97255.

Tscharntke, T., Clough, Y., Wanger, T. C., Jackson, L., Motzke, I., Perfecto, I., Whitbread, A. (2012). Global food security, biodiversity conservation and the future of agricultural intensification. *Biological Conservation, 151*(1), 53-59.

Tscharntke, T., Klein, A. M., Kruess, A., Steffan-Dewenter, I., & Thies, C. (2005). Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters, 8*(8), 857-874.

Vázquez, D. P., & Simberloff, D. (2004). Indirect effects of an introduced ungulate on pollination and plant reproduction. *Ecological Monographs, 74*(2), 281-308.

Veech, J. A. (2013). A probabilistic model for analysing species co-occurrence. *Global Ecology and Biogeography, 22*(2), 252-260.

Venables, B., & Ripley, B. D, (2002). Modern Applied Statistics with S. *Springer*. 4th. Ed.

Vulliamy, B., G Potts, S., & G Willmer, P. (2006). The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. *Oikos, 114*(3), 529-543.

Wcislo, W. T., & Cane, J. H. (1996). Floral resource utilization by solitary bees (hymenoptera: Apoidea) and exploitation of their stored foods by natural enemies. *Annual Review of Entomology, 41*(1), 257-286.

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

Williams, P. H. (1986). Environmental change and the distributions of British bumble bees (bombus latr.). *Bee World, 67*(2), 50-61.

Williams, P. H., Thorp, R. W., Richardson, L. L., & Colla, S. R. (2014). *Bumble bees of North America: An identification guide.* Princeton University Press.

Williams, N., Minckley, R., & Silveira, F. (2001). Variation in native bee faunas and its implications for detecting community changes. *Conservation Ecology, 5*(1), 7.

Willms, W. D. (1991). Cutting frequency and cutting height effects on rough fescue and parry oat grass yields. *Journal of Range Management, 44(1)*, 82-86.

Willms, W. D., Smoliak, S., & Dormaar, J. F. (1985). Effects of stocking rate on a rough fescue grassland vegetation. *Journal of Range Management, 38(3)*, 220-225.

Winfree, R., Aguilar, R., Vázquez, D. P., LeBuhn, G., & Aizen, M. A. (2009). A meta-analysis of bees' responses to anthropogenic disturbance. *Ecology, 90*(8), 2068-2076.

Wright, C. K., & Wimberly, M. C. (2013). Recent land use change in the western corn belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences of the United States of America, 110*(10), 4134-4139. doi:10.1073/pnas.1215404110 [doi]

Xie, Z., Williams, P. H., & Tang, Y. (2008). The effect of grazing on bumblebees in the high rangelands of the eastern Tibetan plateau of Sichuan. *Journal of Insect Conservation, 12*(6), 695-703.

Zeil, J., Kelber, A., & Voss, R. (1996). Structure and function of learning flights in ground-nesting bees and wasps. *The Journal of Experimental Biology, 199*(Pt 1), 245-252.

Zhu, H., Wang, D., Wang, L., Bai, Y., Fang, J., & Liu, J. (2012). The effects of large herbivore grazing on meadow steppe plant and insect diversity. *Journal of Applied Ecology, 49*(5), 1075-1083.

Appendices

Appendix A:

Table A1: Summary of bee species captured and corresponding values organized by year for bees captured in grassland study sites.

Species name	2014	2015	Total
Agapostemon texanus	484	229	713
Agapostemon virescens	84	118	202
Andrena carlini	1	0	1
Andrena cyanophila	3	0	3
Andrena lupinorum	23	68	91
Andrena medionitens	0	30	30
Andrena prunorum	1	0	1
Andrena sp	140	252	392
Andrena trach1	0	2	2
Andrena transnigra	0	4	4
Anthidium clypeodentatum	5	4	9
Anthidium sp	4	0	4
Anthidium tenuiflorae	0	7	7
Anthophora bomboides	1	2	3
Anthophora occidentalis	3	4	7
Anthophora sp	0	1	1
Anthophora terminalis	23	66	89
Bombus appositus	0	1	1
Bombus bifarius	4	12	16
Bombus borealis	50	45	95
Bombus cryptarum	12	8	20
Bombus fervidus	11	2	13
Bombus flavidus	4	0	4
Bombus flavifrons	10	38	48
Bombus frigidus	9	14	23
Bombus huntii	5	1	6
Bombus insularis	6	16	22
Bombus mixtus	3	4	7
Bombus nevadensis	21	3	24
Bombus occidentalis	3	0	3
Bombus rufocinctus	131	187	318
Bombus sandersonii	4	0	4
Bombus sitkensis	0	2	2

Bombus sp	3	1	4
Bombus sylvicola	3	0	3
Bombus ternarius	77	96	173
Bombus terricola	15	10	25
Bombus vagans	51	18	69
Coelioxys rufitarsis	0	1	1
Coelioxys sodalis	0	5	5
Coelioxys sp	1	0	1
Colletes aberrans	4	0	4
Colletes sp	8	25	33
Diadasia diminuta	8	0	8
Diadasia morphA	0	2	2
Diadasia rinconis	2	0	2
Diadasia sp	2	3	5
Dianthidium curvatum	0	7	7
Diantnthidium sp	13	0	13
Dufourea maura	8	5	13
Epeolus minimus	0	10	10
Epeolus sp	0	3	3
Eucera sp	0	4	4
Halictus confusus	195	280	475
Halictus ligatus	2	27	29
Halictus rubicundus	133	454	587
Halictus sp	7	40	47
Holcopasites heliopsis	0	5	5
Hoplitis albifrons	2	3	5
Hoplitis pilosifrons	30	17	47
Hoplitis producta	18	12	30
Hoplitis robusta	1	0	1
Hoplitis sp	2	4	6
Hoplitis spoliata	6	21	27
Hylaeus affinis	13	26	39
Hylaeus annulatus	3	8	11
Hylaeus basalis	1	1	2
Hylaeus mesillae	6	16	22
Hylaeus modestus	1	9	10
Hylaeus sp	8	1	9
Lasioglossum cooleyi	1	0	1
Lasioglossum dialictus perpunctatum	1	0	1
Lasioglossum dialictus red	1	22	23
Lasioglossum dialictus sp	1176	1634	2810
Lasioglossum evylaeus sp	173	55	228
Lasioglossum sensu stricto sp	167	335	502

Lasioglossum sp	19	2	21
Megachile anograe	6	0	6
Megachile brevis	1	1	2
Megachile casadae	1	0	1
Megachile centuncularis	1	1	2
Megachile dentitarsus	1	7	8
Megachile frigida	7	5	12
Megachile gemula	0	1	1
Megachile inermis	13	40	53
Megachile latimanus	1	10	11
Megachile melanophaea	16	35	51
Megachile montivaga	2	0	2
Megachile perihirta	1	8	9
Megachile pugnata	0	1	1
Megachile relativa	5	16	21
Megachile rotundata	0	2	2
Megachile sp	2	1	3
Megachile sublaurita	0	1	1
Melissodes communis	2	0	2
Melissodes sp	42	74	116
Melitta americana	0	1	1
Neolarra sp	1	0	1
Nomada lehighensis	0	1	1
Nomada morph A	0	1	1
Nomada morph E	1	2	3
Nomada morph F	0	1	1
Nomada morph O	0	1	1
Nomada morph Q	0	1	1
Nomada morph R	0	1	1
Nomada morph U	0	1	1
Nomada morph W	0	1	1
Nomada sp	1	2	3
Nomada sp 1	1	2	3
Nomada sp 2	1	0	1
Nomada sp 3	1	3	4
Nomada sp 5	2	6	8
Nomada sp 6	1	0	1
Osmia bucephala	7	0	7
Osmia distincta	15	6	21
Osmia morph D	0	1	1
Osmia morph E	2	0	2
Osmia morph F	1	0	1
Osmia morph G	1	0	1

Osmia morph H	3	0	3
Osmia morph I	1	0	1
Osmia simillima	19	6	25
Osmia sp	56	12	68
Osmia sp 1	2	0	2
Osmia tersula	4	1	5
Osmia trevoris	55	17	72
Panurginus ineptus	0	5	5
Panurginus sp	0	1	1
Perdita albipennis	0	15	15
Perdita sp	28	11	39
Pseudopanurgus morph H	0	2	2
Pseudopanurgus sp	19	50	69
Sphecodes solonus	0	1	1
Sphecodes sp	14	19	33
Sphecodes sp 1	3	4	7
Stelis labiata	1	0	1
Stelis lateralis	2	1	3
Stelis nitida	1	0	1
Stelis permaculata	1	0	1
Tetraloniella albata	0	1	1
Trachusa sp	1	0	1
Unknown	7	1	8
Grand Total	3656	4688	8344

Table A2: Summary table for results from generalized mixed effect models testing the effect of rangeland health, natural region and year on the plant community. Significant effects are in bold (<0.05).

		RHS			Natural Region			Year			RHS*NR			RHS*Year			NR*Year			RHS*NR*Year		
Response	Model	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df	F	P	df
Flower abundance	lmer	3.745	**0.057**	1, 66	3.684	**0.017**	3, 59	17.306	**<0.001**	1, 88	3.351	**0.025**	3, 57	14.729	**<0.001**	1, 88	2.254	0.088	3, 89	2.770	**0.046**	3,88
Flower richness	lmer	3.187	0.056	1, 27	1.148	0.348	3, 27	2.884	0.104	1, 21	0.689	0.566	3, 27	1.074	0.312	1, 21	0.602	0.621	3, 21	0.609	0.617	3, 21
Forb cover (%)	lmer	7.062	**0.015**	1, 21	2.374	0.1	3, 21	12.200	**0.002**	1, 21	1.693	0.200	3, 21	7.065	**0.015**	1, 21	2.375	0.1	3, 21	1.694	0.120	3, 21
Plant biomass	lmer	0.043	0.837	1, 36	0.107	0.956	3, 36	3.845	0.063	1, 22	0.137	0.937	3, 36	0.09	0.767	1, 22	0.213	0.887	3, 22	0.034	0.991	3, 22

Table A3: Summary table for results from generalized mixed effect models testing the effect of rangeland health, natural region and year on the bee community. Results organized by trap method. Significant effects are in bold (<0.05).

Bowled bee community

		RHS			Natural Region			Year			RHS*NR			RHS*Year			NR*Year			RHS*NR*Year		
Response	Model	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF
Abundance (log)	lmer	4.298	**0.046**	1,34	2.858	**0.051**	3,34	3.893	0.061	1,22	1.927	0.144	3,34	2.495	0.129	1,22	1.194	0.335	3,22	1.745	0.187	3,22
Richness	lmer	0.364	0.550	1,44	0.716	0.548	3,44	0.269	0.609	1,22	0.358	0.784	3,44	0.441	0.514	1,22	1.946	0.184	3,22	0.098	0.960	3,22
Diversity	lmer	1.631	0.208	1,44	2.051	0.121	3,44	7.929	**0.010**	1,22	2.242	0.097	3,44	8.293	**0.009**	1,22	3.233	**0.042**	3,22	3.327	**0.038**	3,22
Evenness	lmer	5.676	**0.023**	1,35	2.948	**0.046**	3,35	20.352	**<0.001**	1,22	2.388	0.085	3,35	18.280	**<0.001**	1,22	6.835	**0.002**	3,22	6.929	**0.002**	3,22

Netted bee community

		RHS			Natural Region			Year			RHS*NR			RHS*Year			NR*Year			RHS*NR*Year		
Response	Model	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF
Abundance (log)	lmer	0.332	0.568	1,39	0.574	0.636	3,39	13.547	**0.001**	1,22	0.503	0.682	3,39	9.430	**0.006**	1,22	4.378	**0.015**	3,22	2.368	0.098	3,22
Richness	lmer	4.345	**0.043**	1,44	0.950	0.425	3,44	1.630	0.215	1,22	1.507	0.226	3,44	0.765	0.391	1,22	1.946	0.152	3,22	1.552	0.229	3,22
Diversity	lmer	4.558	**0.039**	1,41	1.647	0.193	3,41	1.066	0.312	1,25	1.948	0.137	3,41	0.385	0.541	1,23	0.964	0.428	3,21	0.910	0.453	3,21
Evenness	lmer	3.244	0.080	1,36	2.326	0.091	3,36	0.340	0.566	1,23	1.776	0.169	3,36	0.787	0.385	1,22	2.030	0.142	3,20	2.357	0.103	3,20

Table A4: Summary table for results from generalized mixed effect models testing for the effect of the flowering plant community, natural region and year on the bee community. Results organized by trap method and floral metric. Significant effects are in bold (<0.05).

	Flower Abundance			Natural Region			Year			FA*NR			FA*Year			NR*Year			FA*NR*Year		
Response	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF
Bowled bee abundance	0.010	0.922	1,37	10.55	**<0.01**	3,36	5.111	**0.030**	1,37	0.538	0.660	3,27	8.080	**0.007**	1,35	2.896	**0.056**	3,24	2.662	**0.066**	3,30
Bowled bee richness	0.118	0.733	1,37	3.99	**0.01**	3,37	0.310	0.581	1,37	0.188	0.904	3,37	0.318	0.577	1,35	1.155	0.342	3,31	0.731	0.540	3,36
Bowled bee diversity	1.132	0.294	1,37	0.66	0.58	3,37	4.435	**0.042**	1,37	0.127	0.944	3,37	3.171	0.084	1,35	1.260	0.305	3,31	1.091	0.365	3,36
Bowled bee evenness	2.054	0.162	1,32	1.81	0.16	3,37	11.575	**0.002**	1,37	0.378	0.770	3,33	9.191	**0.005**	1,35	4.651	**0.009**	3,28	3.028	**0.043**	3,34
	Flower richness			Natural region			Year			FR*NR			FR*Year			NR*Year			FR*NR*Year		
Response	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF
Bowled bee abundance	6.597	**0.014**	1,43	10.216	**<0.01**	3,43	7.577	**0.011**	1,25	3.415	**0.026**	3,41	2.30	0.14	1,21	3.837	**0.023**	3,24	2.566	**0.079**	3,23
Bowled bee richness	1.189	0.281	1,44	1.772	0.166	3,44	0.107	0.747	1,25	0.452	0.717	3,44	0.30	0.59	1,24	0.202	0.894	3,30	0.113	0.952	3,31
Bowled bee diversity	0.283	0.598	1,44	0.169	0.917	3,44	1.087	0.307	1,25	0.245	0.865	3,44	2.44	0.13	1,24	0.432	0.732	3,30	0.634	0.599	3,31
Bowled bee evenness	4.853	**0.033**	1,44	2.198	0.102	3,44	7.030	**0.014**	1,24	1.660	0.189	3,44	6.09	**0.02**	1,22	1.377	0.271	3,27	1.624	0.207	3,27
	Forb cover			Natural region			Year			FC*NR			FC*Year			NR*Year			FC*NR*Year		
Response	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF
Bowled bee abundance	0.109	0.743	1,37	0.195	0.899	3,38	0.014	0.908	1,36	0.149	0.930	3,39	0.195	0.661	1,38	0.321	0.810	3,38	0.234	0.873	3,40
Bowled bee richness	0.002	0.968	1,42	0.902	0.448	3,42	0.005	0.947	1,42	1.185	0.327	3,41	0.074	0.788	1,41	1.112	0.355	3,41	1.223	0.314	3,40
Bowled bee diversity	0.986	0.327	1,42	1.803	0.161	3,42	0.964	0.332	1,42	1.736	0.174	3,41	0.651	0.425	1,41	1.901	0.145	3,41	1.855	0.153	3,40
Bowled bee evenness	2.115	0.155	1,36	1.913	0.144	3,38	1.718	0.198	1,35	1.644	0.195	3,39	1.656	0.206	1,38	1.908	0.145	3,38	1.579	0.210	3,39
	Flower abundance			Natural region			Year			FA*NR			FA*Year			NR*Year			FA*NR*Year		
Response	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF
Netted bee abundance	3.680	**0.065**	1,28	3.109	**0.043**	3,27	3.001	**0.092**	1,37	1.057	0.383	3,28	5.282	**0.028**	1,35	2.200	0.113	3,25	1.773	0.173	3,31
Netted bee richness	0.210	0.650	1,32	2.490	**0.076**	3,37	0.047	0.829	1,37	0.469	0.706	3,34	1.297	0.263	1,35	2.406	**0.089**	3,28	1.291	0.293	3,34
Netted bee diversity	0.088	0.768	1,34	1.008	0.401	3,34	0.864	0.359	1,34	0.401	0.753	3,34	0.012	0.915	1,30	1.615	0.207	3,30	1.282	0.297	3,33
Netted bee evenness	0.015	0.903	1,33	0.724	0.545	3,34	1.126	0.297	1,32	0.916	0.444	3,32	0.483	0.492	1,32	0.288	0.834	3,28	1.281	0.298	3,32
	Flower richness			Natural region			Year			FR*NR			FR*Year			NR*Year			FR*NR*Year		
Response	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF
Netted bee abundance	1.14	0.29	1,43	2.72	**0.06**	3,44	4.858	**0.037**	1,24	0.990	0.406	3,44	2.953	**0.100**	1,22	1.731	0.185	3,27	0.156	0.925	3,27

Netted bee richness	3.67	**0.06**	1,44	1.91	0.14	3,44	0.233	0.634	1,24	1.832	0.155	3,44	0.016	0.900	1,23	0.758	0.527	3,28	1.552	0.223	3,29
Netted bee diversity	1.11	0.30	1,41	0.71	0.55	3,41	0.240	0.629	1,24	0.567	0.640	3,41	0.043	0.838	1,21	0.564	0.644	3,27	1.123	0.358	3,26
Netted bee evenness	0.09	0.77	1,40	0.25	0.86	3,38	0.014	0.906	1,23	0.057	0.982	3,37	0.952	0.342	1,19	0.195	0.899	3,22	0.405	0.751	3,22

	Forb cover			Natural region			Year			FC*NR			FC*Year			NR*Year			FC*NR*Year		
Response	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF
Netted bee abundance	0.184	0.671	1,42	0.515	0.674	3,43	0.032	0.859	1,42	0.437	0.728	3,43	0.040	0.842	1,44	0.75	0.53	3,43	0.563	0.643	3,44
Netted bee richness	0.004	0.950	1,44	0.411	0.746	3,44	0.108	0.744	1,44	0.369	0.776	3,44	0.100	0.754	1,44	0.80	0.50	3,43	0.691	0.563	3,43
Netted bee diversity	0.123	0.727	1,41	0.229	0.875	3,40	0.438	0.512	1,40	0.157	0.925	3,40	0.324	0.572	1,41	0.55	0.65	3,40	0.378	0.769	3,40
Netted bee evenness	0.070	0.793	1,37	1.005	0.402	3,34	0.081	0.777	1,37	0.934	0.435	3,33	0.006	0.941	1,38	0.57	0.64	3,34	0.506	0.681	3,35

Appendix B:

Table B1: Site characteristics including mean annual precipitation, mean annual temperature and elevation summarized by natural region. The mean temperature and mean precipitation were generated from ClimateAB v3.21.

Natural Region	n	MAP (mm)	MAT °C	Elevation (m)
Boreal	8	479	2.49	952
Grassland	10	364	4.08	980
Fescue	7	470	3.90	1169
Parkland	10	440	2.49	805

Table B2: Bees captured in canola (*Brassica napus*) identified to genus separated by survey year. Values are total captured.

	2014	2015	Total
AGAPOSTEMON	79	383	462
ANDRENA	300	1793	2093
ANTHIDIUM	1	2	3
ANTHOPHORA	52	59	111
BOMBUS	385	420	805
CERATINA	2	0	2
COELIOXYS	2	6	8
COLLETES	1	16	17
DIADASIA	10	5	15
DIANTHIDIUM	0	9	9
DUFOUREA	1	6	7
EPEOLUS	0	2	2
EUCERA	0	1	1
HALICTUS	147	570	717
HOLCOPASITES	0	5	5
HOPLITIS	14	39	53
HYLAEUS	47	59	106
LASIOGLOSSUM	737	2628	3365
MEGACHILE	36	141	177
MELISSODES	6	391	397
NOMADA	36	182	218
OSMIA	6	8	14
PANURGINUS	0	114	114
PERDITA	3	2	5
PSEUDOPANURGUS	66	394	460
SPHECODES	16	39	55
STELIS	1	4	5
TRIEPEOLUS	0	2	2
UNKNOWN	7	0	7
TOTAL	11013	2022	8763

Table B3: Bees captured in rangelands identified to genus separated by survey year. Values are total captured.

	2014	2015	Total
AGAPOSTEMON	568	347	915
ANDRENA	168	356	524
ANTHIDIUM	9	11	20
ANTHOPHORA	27	73	100
BOMBUS	422	458	880
COELIOXYS	1	6	7
COLLETES	12	25	37
DIADASIA	12	5	17
DIANTHIDIUM	13	7	20
DUFOUREA	8	5	13
EPEOLUS	0	13	13
EUCERA	0	4	4
HALICTUS	337	801	1138
HOLCOPASITES	0	5	5
HOPLITIS	59	57	116
HYLAEUS	32	61	93
LASIOGLOSSUM	1538	2048	3586
MEGACHILE	57	129	186
MELISSODES	44	74	118
MELITTA	0	1	1
NEOLARRA	1	0	1
NOMADA	8	23	31
OSMIA	166	43	209
PANURGINUS	0	6	6
PERDITA	28	26	54
PSEUDOPANURGUS	19	52	71
SPHECODES	17	24	41
STELIS	5	1	6
TETRALONIELLA	0	1	1
TRACHUSA	1	0	1
UNKNOWN	7	1	8
TOTAL	3656	4688	8344

Table B4: Summary values for total bees captured separated by lifestyle, land-use type and year.

2014	Canola	Grassland
Cleptoparasite community	60	42
Host bee community	1564	3194
Non-parasitized community	324	316
Total	1948	3552
2015	Canola	Grassland
Cleptoparasite community	247	88
Host bee community	6215	4201
Non-parasitized community	769	371
Total	7231	4660

Table B5: Summary values of co-occurrence analysis for the bumble bee community only (*Bombus*). No observations exceeded the expected rate of co-occurrence, hence lack of relationship between Bombus Psithyrus sp. and host bumble bees. Results are separated by year and every possible taxa pairing.

2014										
sp1	sp2	sp1_inc	sp2_inc	obs_cooccur	prob_cooccur	exp_cooccur	p_lt	p_gt	sp1_name	sp2_name
1	2	9	17	1	0.04	2.30	0.26	0.94	Bombus_fervidus	Bombus_nevadensis
1	4	9	55	9	0.11	7.50	1.00	0.17	Bombus_fervidus	Bombus_rufocinctus
1	5	9	11	3	0.02	1.50	0.96	0.16	Bombus_fervidus	Bombus_terricola
2	4	17	55	14	0.22	14.20	0.58	0.70	Bombus_nevadensis	Bombus_rufocinctus
2	5	17	11	2	0.04	2.80	0.42	0.84	Bombus_nevadensis	Bombus_terricola
2	6	17	4	1	0.02	1.00	0.73	0.71	Bombus_nevadensis	Bombus_flavidus
2	7	17	7	1	0.03	1.80	0.42	0.89	Bombus_nevadensis	Bombus_insularis
3	4	2	55	2	0.03	1.70	1.00	0.69	Bombus_occidentalis	Bombus_rufocinctus
4	5	55	11	11	0.14	9.20	1.00	0.11	Bombus_rufocinctus	Bombus_terricola
4	6	55	4	4	0.05	3.30	1.00	0.47	Bombus_rufocinctus	Bombus_flavidus
4	7	55	7	7	0.09	5.80	1.00	0.26	Bombus_rufocinctus	Bombus_insularis
5	7	11	7	0	0.02	1.20	0.26	1.00	Bombus_terricola	Bombus_insularis
2015										
sp1	sp2	sp1_inc	sp2_inc	obs_cooccur	prob_cooccur	exp_cooccur	p_lt	p_gt	sp1_name	sp2_name
2	4	2	52	2	0.03	1.60	1.00	0.66	Bombus_fervidus	Bombus_rufocinctus
3	4	5	52	4	0.06	4.10	0.66	0.77	Bombus_nevadensis	Bombus_rufocinctus
4	5	52	10	8	0.13	8.10	0.60	0.72	Bombus_rufocinctus	Bombus_terricola
4	6	52	12	10	0.15	9.80	0.72	0.60	Bombus_rufocinctus	Bombus_insularis
5	6	10	12	2	0.03	1.90	0.72	0.60	Bombus_terricola	Bombus_insularis

Table B6: Summary table for results from generalized mixed effect models testing for the effect of cleptoparasite abundance, natural region and land-use type on the bee community. Results organized by survey year and lifestyle grouping. Significant effects are in bold (<0.05).

2014 Bee community responses and abundance

	Clepto abundance			Region			Type			Clepto X Region			Clepto X Type		
Response	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P
host and non-host abundance	1, 58	16.42	**<0.01**	3, 55	4.31	0.23	1, 54	1.02	0.31	3, 51	8.21	**0.04**	1, 50	0.08	0.78
host abundance	1, 58	21.3	**<0.01**	3, 55	8.04	**0.05**	1, 54	2.1	0.15	3, 51	10.32	**0.02**	1, 50	0.00	0.95
non-host abundance	1, 56	0.32	0.57	3, 53	22.00	**<0.01**	1, 52	1.07	0.3	3, 49	4.03	0.26	1, 48	0.03	0.87
Cleptoparasite abundance				3,60	1.62	0.65	1,59	0.12	0.73						

2015 Bee community responses and abundance

	Clepto abundance			Region			Type			Clepto X Region			Clepto X Type		
Response	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P
host and non-host abundance	1, 52	25.44	**<0.01**	3, 49	29.93	**<0.01**	1, 48	0.04	0.85	3, 45	2.75	0.43	1, 44	0.06	0.81
host abundance	1, 52	27.69	**<0.01**	3, 49	49.14	**<0.01**	1, 48	3.28	0.07	3, 45	1.16	0.76	1, 44	1.32	0.25
non-host abundance	1, 56	1.44	0.23	3, 53	113.43	**<0.01**	1, 52	5.92	**0.02**	3, 49	19.39	**<0.01**	1, 48	2.67	0.10
Cleptoparasite abundance				3,55	19.57	**<0.01**	1,54	15.73	**<0.01**						

Table B7: Summary table for results from generalized mixed effect models testing for the effect of the cleptoparasite richness, natural region and land-use type on the bee community. Results organized by survey year and lifestyle grouping. Significant effects are in bold (<0.05).

2014 Bee community responses and richness

	Clepto richness			Region			Type			Clepto X Region			Clepto X Type		
Response	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P
overall bee richness	1,50	4.97	**0.03**	3,50	4.75	**0.01**	1,50	7.35	**0.01**	3,50	1.8	0.16	1, 50	3.72	0.06
host richness	1,50	0.85	0.36	3,50	0.57	0.64	1,50	0.18	0.67	3,50	1.07	0.37	1, 50	0.96	0.33
non-parasitized richness	1,50	3.09	0.09	3,50	1.51	0.22	1,50	0.47	0.5	3,50	2.13	0.11	1, 50	3.08	0.09
Cleptoparasite richness				3,58	0.92	0.44	1,58	1.07	0.31						

2015 Bee community responses and richness

	Clepto richness			Region			Type			Clepto X Region			Clepto X Type		
Response	DF	F	P	DF	F	P	DF	F	P	DF	F	P	DF	F	P
overall bee richness	1,48	0.54	0.47	3,48	2.24	0.1	1,48	0.02	0.88	3,48	1.46	0.24	1,48	0.15	0.7
host richness	1,48	0.3	0.59	3,48	1.35	0.27	1,48	0	0.99	3,48	0.98	0.41	1,48	0.02	0.89
non-parasitized richness	1,48	0.27	0.61	3,48	1.55	0.21	1,48	0	0.97	3,48	0.79	0.5	1,48	0.33	0.57
cleptoparasite richness				3,56	0.07	0.98	1,56	4.03	**0.05**						