EFFECT OF LIVESTOCK SPECIES ON FLORAL RESOURCES AND POLLINATORS IN LOW-DIVERSITY GRASSLANDS

A Thesis
Submitted to the Graduate Faculty
of the
North Dakota State University
of Agriculture and Applied Science

By

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In Partial Fulfillment of the Requirements
for the Degree of
MASTER OF SCIENCE

Major Program:
Range Science

April 2020

Fargo, North Dakota

North Dakota State University
Graduate School

Title

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MASTER OF SCIENCE

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ABSTRACT

Livestock management influences the extent to which grazing lands provide resources for native species. We compared how livestock species – sheep or cattle – affected floral resources and bee and butterfly communities in low-diversity, post-Conservation Reserve Program (CRP) pastures managed with patch-burning. We sampled bees and butterflies three times per season 2017-2019 and counted flowering stems within 1 m of transects. Pastures grazed by sheep had significantly fewer flowers and significantly lower floral richness than cattle pastures. Native bees were three to sixteen times more abundant in cattle pastures compared to sheep. Butterfly communities were similar between grazing treatments, because agricultural-tolerant, habitat generalists comprised the majority of the butterfly community. Grassland-obligate butterflies comprised only 2% of observations. The dearth of grassland-obligate butterfly species and low native bee abundances suggest that post-CRP fields, especially those grazed by sheep, do not provide abundant and diverse floral resources for native bees and imperiled butterfly species.

ACKNOWLEDGEMENTS

This project was funded by U.S. Fish and Wildlife Service and ND Game and Fish Section 6 Funding, the USDA National Institute of Food and Agriculture, Hatch project number ND02394, and North Dakota Agricultural Stations. Thank you to Hettinger Research Extension Center for providing housing, logistical support and for maintaining grassland disturbances necessary for this research. Annie Benson was a delightful and essential data collector, compiler, and all-around fabulous technician during the 2019 season. We would like to thank Jonathan Spiess and his technicians Kelsey Morton, Sam Smith, and Simone Jarvis for collecting vegetation data, and Chyna Pei for help with butterfly surveys. Additionally, we would like to thank Dan Graham, Jonathan Spiess, Alex Rischette, Matt Wagner, Sam Smith, Kelsey Morton for their help with bee sampling and floral counts Many thanks to Chyna Pei for her tolerance for my horrendous pronunciation of Greek and Latin terminology and assistance with bee identification. Innumerable thanks to Carson Butler and Cameron Duquette for assistance with Unmarked and statistics. Megan Dornbusch was an editing, formatting, and moral support hero throughout many steps in this process. Huge thanks to my advisers, Torre Hovick and Ben Geaumont for their guidance and direction. Much obliged to my committee members Devan McGranahan and Jason Harmon for helping to shape the study and this manuscript.

DEDICATION

This thesis is dedicated to all the people who helped get me here today. To Carson Butler, my H.L.&F. for his unwavering support, patience, and willingness to share his wrinkly brain. To my family, especially my grandpa Juan who would've been so stoked to see me get my masters. To the fabulous mentors that have guided me over the last ten years: Nancy Braker, Matt Elbert, Dan Hernández, Ellen Esch, and Chris Helzer.

TABLE OF CONTENTS

ABSTRACT iii

ACKNOWLEDGEMENTS iv

DEDICATION v

LIST OF TABLES vii

LIST OF FIGURES viii

LIST OF APPENDIX TABLES x

LIST OF APPENDIX FIGURES xi

CHAPTER 1: SHEEP GRAZING DIMINISHES FLORAL RESOURCES BUT HAS LITTLE INFLUENCE ON GENERALIST BUTTERFLY COMMUNITY IN LOW-DIVERSITY GRASSLANDS 1

Introduction 1

Methods 6

Results 13

Discussion 22

References 28

CHAPTER 2: SHEEP GRAZING SIMPLIFIES FLORAL RESOURCES AND THE NATIVE BEE COMMUNITY IN LOW-DIVERSITY GRASSLANDS 41

Introduction 41

Methods 45

Results 52

Discussion 59

References 65

APPENDIX A. SUPPLEMENTARY MATERIALS FOR CHAPTER ONE 80

APPENDIX B. SUPPLEMENTARY MATERIALS FOR CHAPTER TWO 83

LIST OF TABLES

Table Page

1.1. Top butterfly density model outputs across 2017 – 2019 at Hettinger Research Extension Center. 21

LIST OF FIGURES

Figure Page

1.1. Precipitation during study period 2017-2019 compared to 30-year average. 6

1.2. Mean floral abundance (A), floral richness (B), and floral diversity (C) by year and grazer in each pasture for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 15

1.3. Effects of grazer species (Cattle vs. Sheep), dry year compared to near-average year (2017 vs. 2018), wet year compared to near-average year (2019 vs. 2018) on floral abundance (A), floral richness (B), and floral diversity (C) in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 16

1.4. Butterfly community NMDS ordination showing minimal variation in groupings by grazer for 2017 – 2019 at Hettinger Research Extension Center..... 18

1.5. Butterfly community NMDS ordination showing species and year (A) and time since fire (B) groupings for 2017 – 2019 at Hettinger Research Extension Center 18

1.6. Butterfly community NMDS ordination showing species and floral characteristic vectors for 2017 – 2019 at Hettinger Research Extension Center 19

1.7. Predicted density estimates for butterfly species based on average floral attributes for 2017 – 2019 at Hettinger Research Extension Center..... 22

2.1. Precipitation during study period 2017-2019 compared to 30-year average. 46

2.2. Mean floral abundance (A), floral richness (B), and floral diversity (C) by year and grazer in each pasture for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 53

2.3. Effects of grazer species (Cattle vs. Sheep), dry year compared to near-average year (2017 vs. 2018), wet year compared to near-average year (2019 vs. 2018) on floral abundance (A), floral richness (B), and floral diversity (C) in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 54

2.4. Average native bee and honeybee abundance per transect by year and grazer for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 55

2.5. Relationship between floral richness and predicted native bee abundance per transect by year and grazer for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 56

2.6. Relationship between floral richness and predicted native bee richness per transect by year and grazer for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 56

2.7. Plant pollinator networks by grazer treatment from 2017-2019 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 58

LIST OF APPENDIX TABLES

Table Page

A.1. Butterfly abundances by year. 80

A.2. Estimated butterfly densities by grazer and year. 81

B.1. Bee species and genera observed from 2017-2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 84

B.2. Native bee abundances across years by grazer treatment in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA 87

B.3. Honeybee abundances across years by grazer treatment in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA 87

B.4. Most competitive model outputs for effects of floral characteristics and year on native bee abundance in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 87

B.5. Most competitive model outputs for effects of floral characteristics and year on native bee richness in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. 88

LIST OF APPENDIX FIGURES

Figure Page

A.1. Butterfly community NMDS ordination showing minimal variation in groupings by time since fire for 2017, 2018, 2019 at Hettinger Research Extension Center..... 82

CHAPTER 1: SHEEP GRAZING DIMINISHES FLORAL RESOURCES BUT HAS LITTLE INFLUENCE ON GENERALIST BUTTERFLY COMMUNITY IN LOW-DIVERSITY GRASSLANDS

Introduction

Biodiversity loss on both global and local scales threatens the stability and resilience of ecosystems (Hooper et al. 2005; Worm et al. 2006; Butchart et al. 2010) and ecosystem services delivery (Hooper et al. 2005; Balvanera et al. 2006; Cardinale et al. 2012). Land-use and land cover change associated with agriculture is one of the main drivers of biodiversity loss (Sala et al. 2000; Tscharntke et al. 2005; Deguines et al. 2014). However, agricultural landscapes exist on a spectrum from simplified landscapes of large, homogenous crop fields with minimal natural areas, to landscapes with a more heterogeneous arrangement of less intensively managed crops and interspersed semi-natural areas (Steffan-Dewenter et al. 2002; Kremen et al. 2002; Duelli & Obrist 2003). In the U.S., perennial cover in agricultural landscapes is often the result of the Conservation Reserve Program (CRP) operated by the U.S. Department of Agriculture, which pays farmers to replant marginal crop lands with perennial grasses and legumes (Farm Service Agency 2019). The amount of biodiversity present on the landscape is greatly affected by how these semi-natural areas are managed (Benayas et al. 2009), the residual effects of previous land-uses (Moranz et al. 2012; Hahn & Orrock 2015), and commodity crop prices and profitability of different land-uses (Wright & Wimberly 2013). There is an urgent need to quantify the influence of management choices and land-use legacies on biodiversity in agricultural landscapes.

Promoting grassland biodiversity within agroecological systems requires recognizing land-uses that are financially viable for landowners and keep lands in perennial cover instead of row crops. When the 10- to 15-year CRP contract expires, landowners can re-enroll in CRP,

transition back to row crops, or can maintain perennial cover and use it as forage for livestock without the strict grazing limitations imposed by the CRP. Using these grasslands for livestock production provides the incentive of livestock income and greater management flexibility while still providing vegetation resources for wildlife. Grazing lands – rangelands and pastures – are a land-use that enables income from livestock production while also being compatible with conservation objectives (Morandin et al. 2007). Such areas are often categorized as "working landscapes" to recognize the cultural, economic, and ecological role that these land-uses fulfill for landowners and native species (Polasky et al. 2005). Understanding how management strategies affect native species in working landscapes is essential for promoting biodiversity in grasslands.

In heavily modified landscapes, grazing lands may be the only areas that can provide essential vegetation and structural resources for native grassland species, but their utility for native species depends on how they are managed (Polasky et al. 2005; Morandin et al. 2007). In these areas, livestock management can promote or diminish biodiversity (Adler et al. 2001; Rook & Tallowin 2003). Grassland organisms can be influenced by many factors associated with grazing management including stocking rate (Herrero-Jáuregui & Oesterheld 2018), grazing duration (Enri et al. 2017), grazing season (Hart et al. 1988), livestock species (Rook et al. 2004; Tóth et al. 2018), and livestock type (Celaya et al. 2010). All of these decisions can influence the structure and composition of the vegetation in grazed landscapes (Rook & Tallowin 2003; Albon et al. 2007; Celaya et al. 2010). Specifically, decisions about timing and stocking rate affect the spatial and temporal distribution, abundance, and availability of vegetation and floral resources within grazing lands (Adler et al. 2001; Kruess & Tscharntke 2002; Cingolani et al. 2005;

Schieltz & Rubenstein 2016). High trophic levels can be positively or negatively affected by these grazing-induced changes in vegetation composition and structure.

Pollinators can be a useful indicator group for how changes in vegetation affect higher trophic levels. Bees and butterflies are dependent on plant communities for forage, host plants, and nesting resources, and thus may be influenced by how grazing shapes vegetation composition and structure (Soderstrom et al. 2001; Di Giulio et al. 2001; Liu et al. 2015; Tadey 2015; Fourcade & Ockinger 2017). In particular, butterflies can act as a useful indicator group because they require a variety of vegetation structure and composition throughout their life cycle, and adults are mobile and can rapidly react to changes in their environment (Fleishman & MacNally 2003; Mac Nally et al. 2003; Kremen et al. 2007; Farhat et al. 2014). Thus, butterfly abundance and community composition can provide useful feedback on how grazing affects other grassland dependent taxa (Debinski et al. 2011; Moranz et al. 2012; Enri et al. 2017).

The influence of livestock species on vegetation and higher trophic levels has often been overlooked when considering grazing management decisions (Rook et al. 2004; Tóth et al. 2018). Grazer species affects plant community characteristics in direct and indirect ways due to differences in animal physiology and associated differences in diet needs and preferences (Rook et al. 2004; Launchbaugh & Walker 2006; Allred et al. 2013). Even species that share the same digestive system type (i.e., ruminants), such as sheep (Ovis aries) and cattle (Bos taurus) can exhibit different selection preferences due to rumen volume and mouth dexterity (Hanley 1982). Sheep have more dexterous lips compared to cattle, which allow them to use their mouth and bottom teeth to bite lower on the plant and to continue grazing as plant height decreases (Rook et al. 2004). Additionally, sheep often selectively graze forbs (Dumont et al. 2011) and are able to discriminate between plants at a fine scale (Ginane et al. 2015). Greater forb consumption by

sheep can result in a different plant community composition when compared to grasslands grazed by cattle exclusively (Dumont et al. 2011; Enri et al. 2017). Furthermore, contrast in forb density may result from cattle indirectly increasing flower abundance by repeatedly keeping grass short in certain areas, giving forbs a competitive advantage (Adler et al. 2001; Dumont et al. 2011). Thus, in working landscapes, grazer species can greatly affect plant communities, especially forb expression, and can influence higher trophic levels that are of conservation concern such as pollinators.

Grassland management that promotes heterogeneity through fire and grazing interaction, such as patch-burn grazing, may be an effective conservation practice for promoting pollinators. Fire can promote forb expression (Moranz et al. 2012; Mola & Williams 2018) by changing the morphology of plants and altering phenology to support longer blooming periods (Wrobleski & Kauffman 2003), and by increasing access to sunlight and nutrients through removal of overstory plants (Jutila & Grace 2002). Combining fire and grazing can create a "magnet effect" (Archibald et al. 2005), which focuses herbivore grazing in recently burned patches, allowing unburned areas to have reduced grazing pressure and potentially greater floral resources. This magnet effect may be able to mitigate the detrimental effects that sheep have on flower abundance; previous research on sheep consistently demonstrates that they decrease floral abundance when compared to areas grazed by cattle (Carvell 2002; Enri et al. 2017; Tóth et al. 2018). Bee and butterfly abundance and diversity likewise have reportedly declined in pastures grazed by sheep (Carvell 2002; Enri et al. 2017). However, these studies did not explore whether the interaction of fire and grazing may overcome the propensity for sheep to overconsume forbs and therefore allow sheep grazing to persist in a way that is less harmful to pollinators. If sheep react similarly to cattle, the recently burned patch will act as an attractant, possibly alleviating

some of the selective pressure for flowers in other portions of the management unit. If sheep grazing patterns are less responsive to the burned patch and forbs continue to be disproportionately consumed, then managers trying to promote pollinators in landscapes grazed by sheep may need to take additional actions to maximize forb abundance and vegetation structure.

This study was designed to investigate the abundance and diversity of butterflies and floral resources in low-diversity, former CRP grasslands. Assessing butterflies and the floral resources on which they depend will develop our understanding of how two different domestic herbivores affect biodiversity in a landscape managed with patch-burn grazing. These data will support the development of management practices for promoting pollinators in working landscapes. Additionally, contributing baseline data on butterfly populations will allow us to monitor changes in abundance and diversity (Allen-Wardell et al. 1998; Potts et al. 2001, 2010; Cardinale et al. 2018) and can inform future policy decisions that consider how management affects threatened and endangered species in the Great Plains. Our specific objectives are: 1) Evaluate the differences between grazer species (sheep or cattle) on floral resource density and richness; 2) Quantify butterfly community composition and individual species' densities in landscapes grazed by sheep or cattle managed within a patch-burn grazing framework. We expect that pastures grazed by sheep will have lower floral density and lower floral richness compared to pastures grazed by cattle, due to sheep's propensity for selective forb consumption (Rook et al. 2004). Consequently, we expect a simplified butterfly community and lower individual species' densities in sheep pastures versus cattle pastures.

Methods

Site Description

We conducted this research in southwest North Dakota at North Dakota State University's Hettinger Research Extension Center (HREC). Cattle and sheep production are major economic enterprises in the Northern Great Plains (Montana, Wyoming, Colorado, North Dakota, South Dakota, and Nebraska), resulting in $21.7 billion in cattle sales, $276 million in sales from sheep meat and an additional $12.7 million from wool production in 2017 (USDA NASS 2019). Thus, questions about sustainable cattle and sheep production are especially relevant for this area. During the study (2017-2019), the average temperatures were 12 ºC in May, 18 ºC in June, 21.9 ºC in July, and 19.3 ºC in August (NDAWN 2019). Thirty-year average precipitation for May – August is 25.1 cm (NDAWN 2018). However, over the course of the three seasons of sampling, May – August precipitation ranged from 11.2 cm in 2017 (NDAWN 2017), to 22.7 cm in 2018, and 33.3 cm in 2019 (Figure 1.1, NDAWN, 2019).

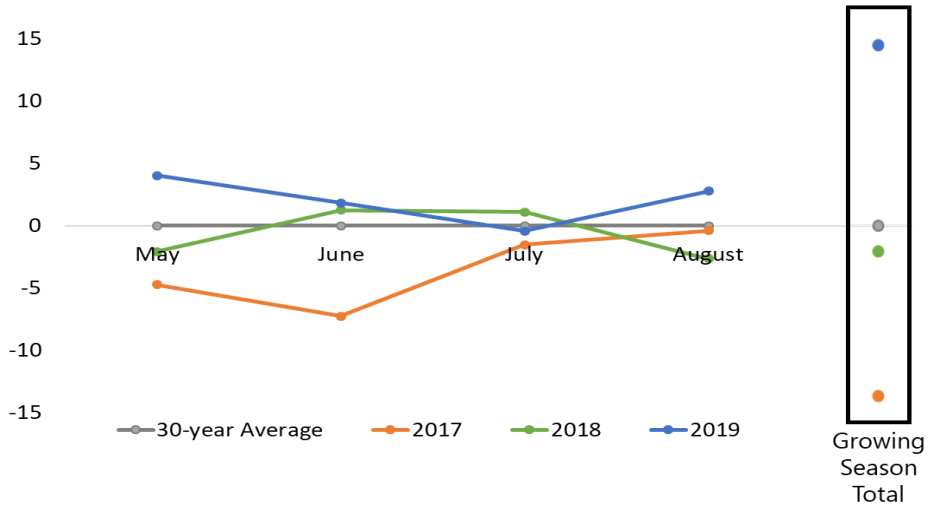

Figure 1.1. Precipitation during study period 2017-2019 compared to 30-year average. In 2017, May – August precipitation was 13.6 cm below average. In 2018, it was 2 cm below average, and in 2019, it was 14.5 cm above average.

Our study sites are former Conservation Reserve Program fields, planted with Natural Resource Conservation Service Conservation Planting 1 (CP1) "introduced grasses" in the late 1980s (Geaumont et al. 2017). Species established under the CP1 planting included intermediate wheatgrass (*Elymus hispidus* [P. Opiz] Melderis), alfalfa (*Medicago sativa* L.), crested wheatgrass (*Agropyron cristatum* [L.]Gaertn), and yellow sweet clover (*Melilotus officinalis* [L.] Lam.) (Geaumont et al. 2017). While alfalfa and sweet clover are still the most dominant forbs, yarrow (*Achillea millefolium* L.), and introduced species common bindweed (*Convolvulus arvensis* L.), field pennycress (*Thlaspi arvense* L.), and herb sophia (*Descurainia sophia* (L.) Webb ex Prantl) were also common. Vegetation composition in the pastures continues to have low-diversity and is cool-season grass dominated.

Experimental Design

We conducted research in six, 65-ha pastures, with three pastures grazed by sheep and three grazed by cattle. Two cattle and two sheep pastures were located 7 km west of Hettinger, ND (site 1, site 2) and the other cattle and sheep pasture were 3 km south of Hettinger (site 3). We targeted a moderate stocking rate of 178 animal unit months in all pastures. We weighed and sorted animals to ensure equal animal units across treatments. Three pastures were moderately-stocked with sheep (168-173/pasture), and three were moderately-stocked with cattle (23-30 cow-calf pairs/pasture). We randomly assigned grazer treatments to each pasture. Cattle and sheep grazed pastures from May until September. Each pasture was divided into quarters, delineated by a 20' fire break disked to mineral soil, however, only the exterior of the pasture was fenced allowing for livestock movement across the entire management unit. We burned one quarter of each pasture annually (i.e., four year fire-return interval) during the dormant season,

similar to other semi-arid patch-burn grazing experiments (Vermeire et al. 2004; Augustine & Derner 2014).

Data Collection

Line Transect Distance Sampling for Butterflies

We sampled for butterflies from late-May to mid-August of 2017-2019 with three sampling periods per season (average of 2.5 weeks per sampling period) to quantify butterfly community composition and individual species' densities in pastures. Three sampling periods enabled us to maximize detections of species with varying flight periods. There were 12, 100 m butterfly transects per pasture, three in each patch, for a total of 72 butterfly transects. To maximize butterfly detections and to minimize variation between surveys, sampling occurred between 0800 h – 1730 h as long as temperatures were between 18.3C – 35.5 °C, sustained winds < 20km/h, and cloud cover was < 50% (Moranz et al. 2012; Harmon-Threatt & Hendrix 2015). We used line transect distance sampling (LTDS) to measure the density of butterflies while accounting for imperfect detection (Brown & Boyce 1998; Buckland et al. 2001). We conducted LTDS surveys by walking 100 m transects at an approximate rate of 10 m · min^{-1} and recorded all butterfly species on either side of the transect, as well as the perpendicular distance from the transect for each observation. For butterflies ≥ 10m away, the observer used a Leupold RX-1000 TBR range finder (± 0.5 m) to determine distance from the transect. For closer distances, the observer visually estimated butterfly distance from the line (Moranz et al. 2012). If an observer could not identify the butterfly through binoculars, the survey was paused while the observer captured the butterfly with a net (Moranz et al. 2012).

Floral and Vegetation Surveys

We recorded the species of all flowering ramets within 1 m of either side of the transect after each butterfly survey to quantify how different grazers affect floral and vegetation resources (Shepherd & Debinski 2005). We recorded vegetation structure characteristics and vegetation composition along each transect to provide information on which site characteristics affected butterfly abundance and diversity. We collected these data on alternating sides every 10 m along the 100 m transect for 10 sampling points per transect, and we measured vegetation structure (visual obstruction) with a Robel pole marked in both 2 cm and 1 dm increments (Robel *et al*. 1970). The observer scanned from the bottom of the pole upwards and recorded the highest number visible that was > 50% obscured by horizontal vegetation from a distance of 4 m and an elevation of 1 m in all four cardinal directions. We averaged the four visual obstruction readings at each point. The observer also recorded the tallest standing live and standing dead vegetation at each sampling point. Finally, we assessed vegetation composition by species, and percent cover of standing litter, ground litter, and bare ground at each sampling point using a 0.5 m^2 frame and the Daubenmire (1959) cover classification (0-5%, 5-25%, 25-50%, 50-75%, 75-95%, 95-100%) and measured litter depth inside each corner of the 0.5 m^2 frame.

Data Analysis

Effects of Grazer Species and Precipitation on Floral Characteristics

To assess how grazer treatment and year affected floral attributes, we ran general linear mixed-effect models (GLMMs) using the *glmmTMB* package in R (Brooks et al. 2017). Exploratory analysis revealed strong year effects on both floral and butterfly data, likely a result of high variation in annual rainfall. As a result, we summarized data for each transect each year (transect-year) in order to incorporate year as a variable in our analyses. All subsequent floral

variables are based on observations per transect-year. We summarized the floral data for each transect across the three visits per year using maximum annual counts (McGranahan et al. 2013a). We used maximum instead of average to summarize the full flowering potential during the growing season and to avoid any chance of double-counting flowering stems between sampling periods. Floral abundance was the sum of each species' maximum flowering stems for each transect-year. Floral richness was a count of the number of species present for each transect-year. Floral diversity for each transect-year was calculated using the "diversity" function in the *vegan* package to calculate Simpson's Diversity Index (Oksanen et al. 2019).

To determine if grazers influenced floral abundance, floral richness, or floral diversity, we fit GLMMs with grazer plus year as the fixed effects and ran type II ANOVAs to test for evidence of relationships. We used package *glmmTMB* and function "glmmTMB" to develop our GLMM models (Brooks et al. 2017). To account for repeated measures and spatial non-independence, we nested year in transect in site as a random effect. A negative binomial distribution best fit our floral abundance data. A Poisson distribution best fit our richness data, and a beta distribution was the best for floral diversity. Our fixed effects were livestock species plus year. We used the "Anova" function in package *car* to test for significant differences between cattle and sheep (Fox & Weisberg 2019). To get pairwise comparisons between grazers for each year, we used package *emmeans* to compute estimated marginal means for these models (Lenth 2019). Estimated marginal means are the estimated mean at each point in a reference grid created from the combination of all levels of predictor factors (grazer and year) in our glmmTMB model. We obtained pairwise comparisons for the estimated marginal means using the "pairs" functions from *emmeans*, which use a significance level of $\alpha = 0.05$ and the Tukey method for comparing a family of 6 estimates.

In order to compare the relative effects of precipitation versus grazer species, we calculated the effect sizes of sheep vs cattle, our dry year versus our near-average year (2017 vs. 2018), and our wet year versus our near-average year (2019 vs. 2018). We obtained confidence intervals for the pairwise comparisons from the previous GLMMs using the "confint" function. We then extracted the comparisons we were interested in and plotted the resulting effect sizes.

Butterfly Community Analysis

We used the *vegan* package in R to explore relationships between grazer effects, floral resources, and site characteristics on butterfly community composition using non-metric multidimensional scaling (NMDS) ordinations (Oksanen et al. 2019). We used NMDS because it allows us to use the more ecologically-meaningful Bray-Curtis or Canberra dissimilarity distance metrics to describe similarities or differences between sites and species (Kindt & Coe 2005), and we used a type II PERMANOVA to see how much variance is due to grazer-type and floral variables. To assess butterfly community composition using ordination, we summarized butterfly data as the maximum number of observations for each species per transect-year. Species with fewer than 20 total observations were removed so that models could converge. Our final community dataset contained 11 species that ranged from 21 to 5463 detections. We created our ordinations using the "metaMDS" function in *vegan*. Using the Canberra metric in analyses resulted in lower stress values than using Bray-Curtis; therefore, we used the Canberra metric for the butterfly community ordination because it more accurately represents the dissimilarity space (Kindt & Coe 2005).

We assessed the effects of grazer, year, and floral characteristics on the butterfly community via the "envfit" function in *vegan* (Oksanen 2009). To account for effects of inherent spatial heterogeneity, pasture (n = 6) was incorporated as a random effect (strata) within "envfit".

We grouped plant species into the following categories: native forbs, introduced forbs, native grass, introduced grass, and native shrub. Origin of plants (non/native) was verified using the NRCS PLANTS database (USDA 2020). We incorporated site characteristics by taking the average values for plant functional groups, ground cover, bare ground cover, litter cover, litter depth, visual obstruction, tallest live and tallest dead plants. We ran these variables through "envfit" with grazer, year, and floral characteristics. We then assessed how much variance in the ordination was explained by each variable with a type II PERMANOVA using "adonis.II" in package *RVAideMemoire* (Hervé 2020).

Butterfly Density Estimates

We assessed the influence of grazing treatments on individual species' densities by calculating corrected butterfly densities for the five most abundant species (93% of observations) using function "gdistsamp" in package *unmarked* (Fiske & Chandler 2011) in R. This method enables us to incorporate detection probability into our analysis to get a corrected density estimate (Buckland et al. 2001). This robust density estimate can then be compared to those of other studies that calculate density estimates. Of the 27 species we observed during surveys, five species (*Colias philodice, Lycaeides melissa, Vanessa cardui, Pontia protodice, Colias eurytheme*) had sufficient observations each year (50+) to get robust predicted densities (Buckland et al. 2001). We determined which detection function best described the data for each of the five species using the half-normal, hazard rate, exponential, and uniform key functions, and ranked candidate models using Akaike Information Criterion (AIC), models with $\Delta AIC \leq 2$ were considered to have the same explanatory value (Burnham & Anderson 2003). The best key function for *Colias philodice* and *Lycaeides melissa* was exponential, hazard rate was best for *Vanessa cardui* and *Pontia protodice*, for *Colias eurytheme*, we used half-normal. Using the key

function, we then created univariate models to test effects of year, floral abundance, floral richness, and floral diversity on densities for each butterfly species. We standardized floral abundance and richness by subtracting the mean from individual values and dividing by standard deviation ("scale" function in R) before using them in further analyses. Unsurprisingly, Pearson's correlation coefficient showed that floral richness and diversity were correlated. We kept both variables, but assessed them in separate models to examine whether butterflies were influenced by richness or evenness in addition to richness (diversity). We developed univariate models which included a null model, year only, transect-level floral characteristics, and transect-level floral characteristics with year as additive and an interaction. We ranked models using AIC and we considered models with $\Delta AICc \leq 2$ to have the same explanatory power about species density (Burnham & Anderson 2003). We used the "predict" function in *stats* (R Core Team 2018) to compute estimated densities and 95% confidence intervals based on the most competitive model for each species and graphed the resulting relationship.

Results

We counted 196,806 flowering ramets of 95 different species from 2017-2019. Alfalfa was 70.4% of floral counts and native forbs were 8%. Floral abundance and richness increased each year; we counted 35,966 flowering stems of 37 species in 2017, 57,326 ramets of 54 species in 2018, and 103,514 ramets of 66 species in 2019. We observed 13,819 butterflies across the three seasons. Butterfly abundance increased each year with 2,647 observations in 2017, 4,722 in 2018, and 6,450 in 2019. Species richness also increased as the study progressed with 17 species observed in 2017, 20 in 2018, and 26 in 2019. *Colias philodice*, a non-native, disturbance- and agricultural-tolerant species was the most abundant, accounting for 61.1% of observations (8,449 detected), species of conservation concern such as *Speyeria idalia* (regal fritillary) and *Danaus*

plexippus (monarch) represented < 0.5% of observations (Table A1). Fifty-nine percent of butterfly observations occurred in cattle pastures, which encompassed 27 out of 28 observed species. Sheep pastures had lower butterfly richness with 23 species (Table A1).

Effect of Grazer Species and Precipitation on Floral Resources

Pastures grazed by cattle had significantly more flowers than those grazed by sheep (Figure 1.2; χ^2 (1) =184.08, p <0.001) There was a strong year (precipitation) effect on floral abundance in cattle pastures, but floral availability in sheep pastures remained low regardless of year (Figure 1A). Both a wet year compared to a near-average year and cattle grazing compared to sheep grazing had a positive effect on floral abundance, but the positive effect of cattle was much stronger than that of increased precipitation (Figure 1.3 A). Overall, floral richness was also significantly higher in cattle pastures compared to sheep (Figure 1.2 B; χ^2 (1) =45.1, p < 0.001). Floral richness under both grazer treatments responded positively to increased precipitation; pairwise comparisons showed that floral richness significantly increased in cattle pastures and sheep pastures each year (Figure 1.2 B, p < 0.05). Cattle grazing and a wet year both had a positive effect on floral richness, whereas a drought year had a negative effect on number of floral species observed (Figure 1.3 B). Although precipitation did have a significant effect on floral richness, the median floral richness along any transect was only 2.5 to 7 species, highlighting the overall low diversity in floral resources, regardless of grazer treatment. This was further indicated by floral diversity, which was not significantly different between grazers (Figure 1C; χ^2 (1) =0.0013, p = 0.093). However, similar to floral richness, a drought year had a negative effect on floral diversity (Figure 1.3 B).

Figure 1.2. Mean floral abundance (A), floral richness (B), and floral diversity (C) by year and grazer in each pasture for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. Cattle pasture values are displayed in red and sheep in blue, error bars represent standard error. Sites represent our paired pasture replicates.

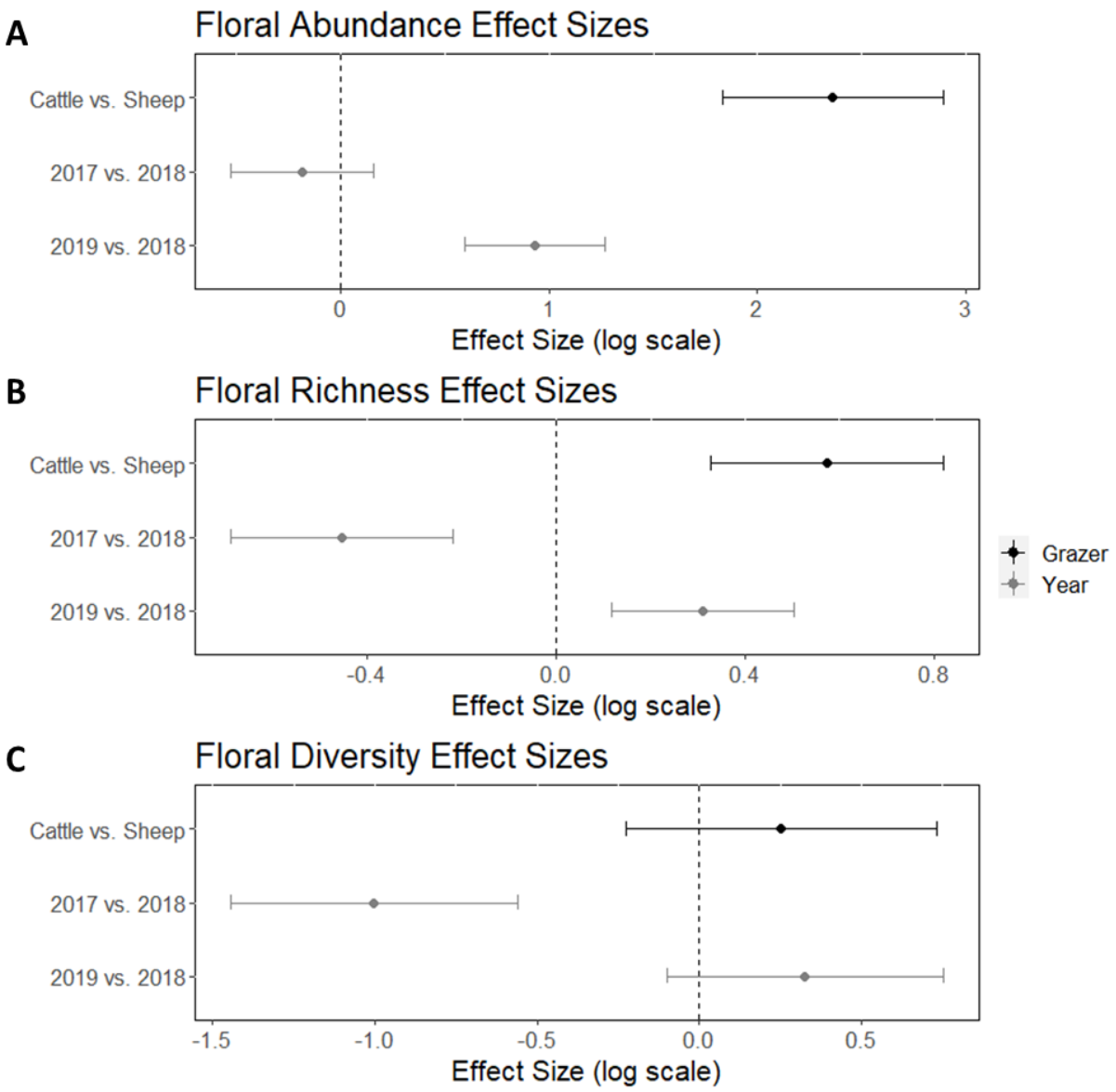

Figure 1.3. Effects of grazer species (Cattle vs. Sheep), dry year compared to near-average year (2017 vs. 2018), wet year compared to near-average year (2019 vs. 2018) on floral abundance (A), floral richness (B), and floral diversity (C) in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. Points are standardized effect sizes ± 95% CI. An effect size is considered significant when its CI does not include zero.

Butterfly community analysis

We found considerable overlap in butterfly communities regardless of grazer treatment using NMDS ordination (Figure 1.4, stress = 0.124, k=4). Grazer species was associated with dissimilarities in butterfly communities, but explained less than 2% of the variance (pseudo-*F* ratios, $p < 0.01$, $R^2 = 0.02$). Year was more strongly associated with distinct patterns in the butterfly community (Figure 1.5 A; pseudo-*F* ratios, $p < 0.01$, $R^2 = 0.19$). Time since fire intervals for unburned, recently burned, and one-year post-fire were clustered around the origin, meaning there was minimal variation between sites based on those time since fire (Figure 1.5 B; pseudo-*F* ratios, $p < 0.01$, $R^2 = 0.04$). Two-years since fire was further from origin, however, 2019 was the only season with 2 years since fire data and those two factors occupy similar ordination space, so that is likely an artifact of year and limited sample size rather than a biological response to two years since fire. To see if year was overshadowing effects of time since fire, we created separate NMDS ordinations for each year, but within each year, time since fire intervals overlapped and were not associated with a distinct pattern in the butterfly community (Figure A1).

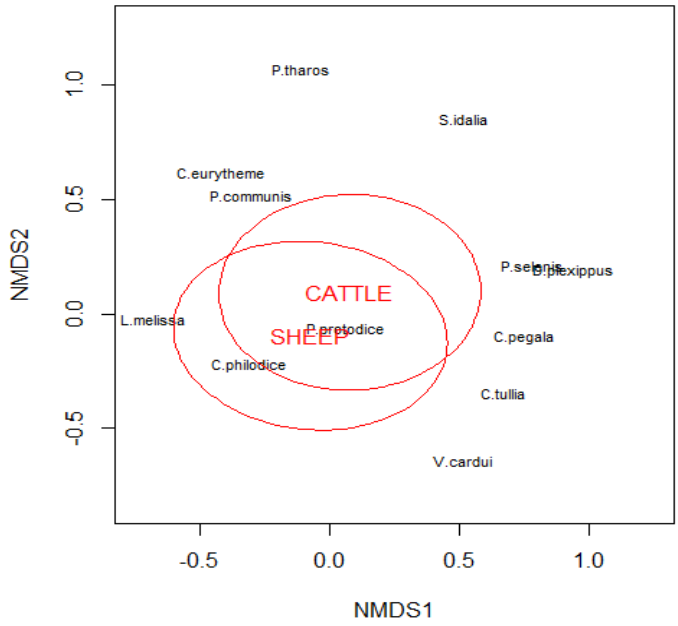

Figure 1.4. Butterfly community NMDS ordination showing minimal variation in groupings by grazer for 2017 – 2019 at Hettinger Research Extension Center (k = 4, stress = 0.124). Grazer had minimal association with variation in the butterfly community (pseudo-*F* ratios, $p < 0.01$, $R^2 = 0.02$).

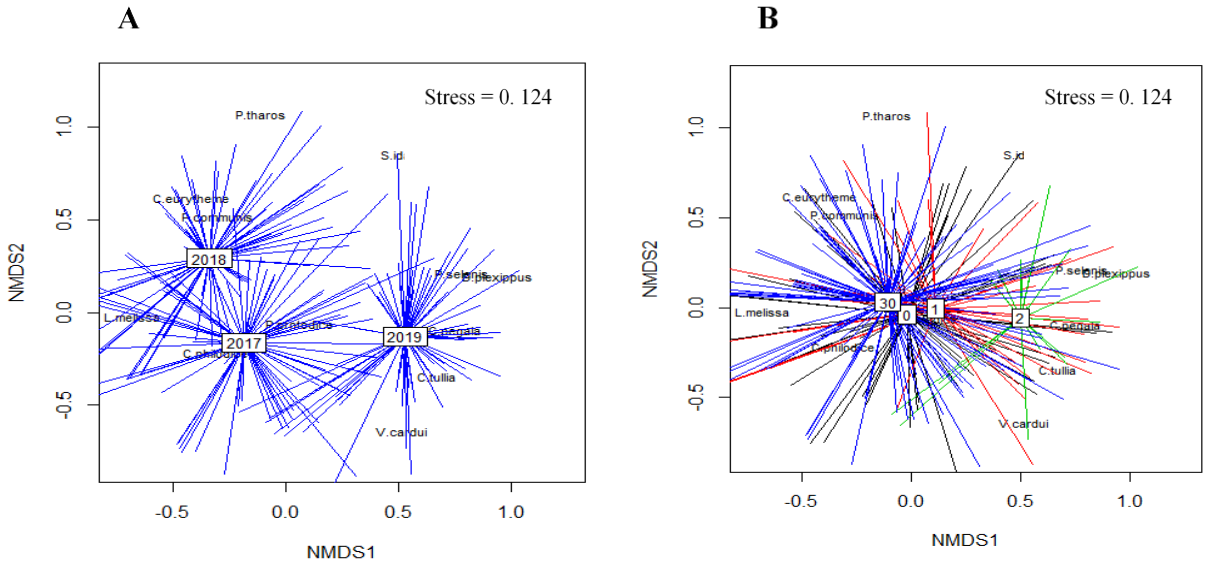

Figure 1.5. Butterfly community NMDS ordination showing species and year (A) and time since fire (B) groupings for 2017 – 2019 at Hettinger Research Extension Center (k = 4, stress = 0.124). Panel A: Year was associated with distinct patterns of variation in butterfly communities (pseudo-*F* ratios, $p < 0.01$, $R^2 = 0.19$). Panel B: Overlap in butterfly communities based on time since fire intervals: never burned (30), recently burned (0), and one year since fire (1). Two years since fire (2) is separate, but likely an artifact of limited sample size and data only from 2019.

In terms of site characteristics, all floral characteristics were significant (pseudo-*F* ratios, $p < 0.001$), but were associated with minimal variation in butterfly communities (Figure 1.6). Based on non-additive R^2 values, floral abundance was associated with only 4% of community variation (pseudo-*F* ratios, $p < 0.01$, $R^2 = 0.04$), floral richness and Simpson's diversity and percent cover of native forbs with only 3% each (pseudo-*F* ratios, $p < 0.01$, $R^2 = 0.03$ for all three). Vegetation structure as measured by visual obstruction was associated with 7% of the variation in the butterfly community (pseudo-*F* ratios, $p < 0.001$, $R^2 = 0.07$), while percent cover of standing litter was associated with 2% (pseudo-*F* ratios, $p < 0.001$, $R^2 = 0.02$). The proximity in ordination space between regal fritillary and floral abundance (Total) suggest that they are positively associated with the amount of floral resources available (Figure 1.6). Similarly, monarchs were positively associated with floral richness (Figure 1.6).

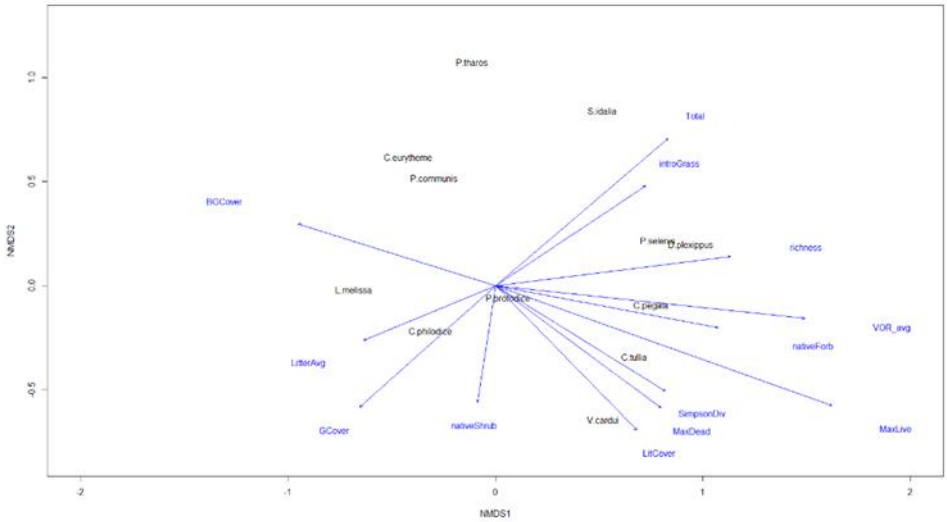

Figure 1.6. Butterfly community NMDS ordination showing species and floral characteristic vectors for 2017 – 2019 at Hettinger Research Extension Center (k = 4, stress = 0.124). A non-metric multi-dimensional scaling (NMDS) showing butterfly communities and vectors of floral characteristics including floral richness (richness), floral abundance (Total), floral diversity (SimpsonDiv), percent cover of: standing litter (LitCover), ground litter (GCover), native forbs (nativeForb), introduced grasses (introGrasses), snowberry (nativeShrub), bare ground (BGCover), structural variables: average visual obstruction per transect (VOR_avg), tallest live plant (MaxLive), tallest dead plant (MaxDead), average litter depth (LitterAvg).

Individual species density estimates

A model that incorporated floral abundance per transect and an interaction with year was the most competitive model for *V. cardui, P. protodice, C. eurytheme,* and *L. melissa* (Table 1.1). For all four species, higher floral abundance was associated with higher predicted density (Figure 1.7). *V. cardui* is an irruptive species and while abundant in 2017 and 2019, it was nearly absent in 2018, making it difficult for the model to predict *V. cardui* for that year. For *C. philodice*, the most competitive model comprised floral diversity per transect with year as an additive interaction (Table 1.1). Density of *C. philodice* was negatively correlated with Simpson's diversity index (Figure 1.7 E).

Table 1.1. Top butterfly density model outputs across 2017 – 2019 at Hettinger Research Extension Center. Most competitive model outputs for the five grassland butterfly species meeting the minimum detection threshold ford density estimation. A model incorporating floral abundance and year interaction was the most competitive for four of the species. Floral diversity with year as an additive factor best described *C. philodice* abundance.

Model	nPars	AIC	delta AIC	AIC weight	Cumulative weight
Colias eurytheme					
Floral abundance * year	8	1395.59	0	9.20E-01	0.92
Floral abundance + year	6	1401.1	5.51	5.80E-02	0.98
Lycaeides melissa					
Floral abundance * year	8	3245.74	0	1.00E+00	1
Floral abundance + year	6	3257.96	12.22	2.20E-03	1
Pontia protodice					
Floral abundance * year	9	2610.56	0	7.60E-01	0.76
Floral abundance + year	7	2612.85	2.3	2.40E-01	1
Vanessa cardui					
Floral abundance * year	9	2641.56	0	6.40E-01	0.64
Floral abundance + year	7	2642.93	1.37	3.20E-01	0.97
Floral diversity + year	7	2649.68	8.12	1.10E-02	0.98
Colias philodice					
Floral diversity + year	6	-9677.01	0	7.60E-01	0.76
Floral diversity * year	8	-9674.61	2.4	2.30E-01	0.99

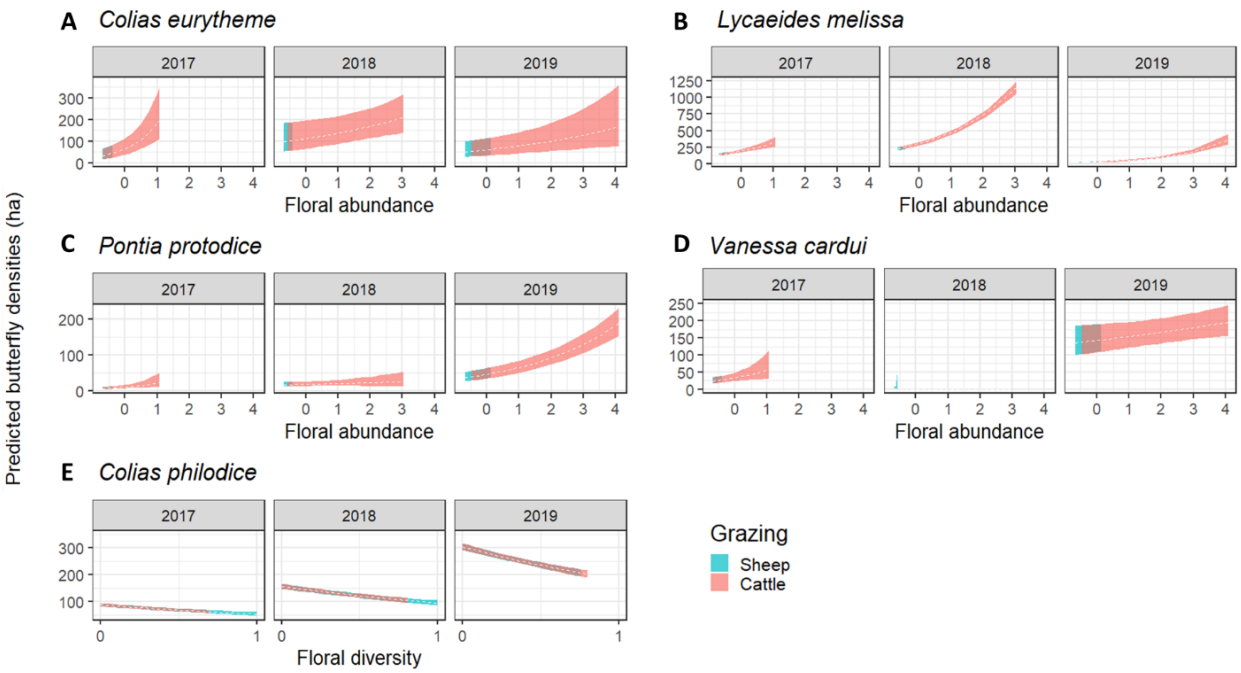

Figure 1.7. Predicted density estimates for butterfly species based on average floral attributes for 2017 – 2019 at Hettinger Research Extension Center. Standardized floral abundance is shown in panels A, B, C, D, floral diversity in shown in panel E. The dotted line shows the estimated butterfly density, the width of the curve represents the upper and lower bounds of the estimate. We shaded predicted density curves to show the relationship between livestock species and depicted floral abundances or diversities. Blue depicts floral attribute ranges that occurred in cattle pastures and pink shows the same for sheep pastures. Panels A, B, C, D show densities for these butterflies increased with increasing floral abundance. Panel E shows *C. philodice* is more abundant in pastures with low floral diversity.

Discussion

Agricultural intensification, specifically the conversion of grasslands to row crops, threatens the ability of native species to persist on the landscape (Sala et al. 2000; Tscharntke et al. 2005; Deguines et al. 2014). Working landscapes offer a compromise between a productive land-use for landowners and a semi-natural resource for native species. Understanding how management choices and precipitation affect floral resources and native pollinators enables producers to make choices that can promote biodiversity and can inform management strategies for threatened and endangered species. Our results indicate that sheep grazing reduces floral resources and may be detrimental to pollinator conservation. Similar to other studies, we found

sheep grazing resulted in lower floral richness and abundance as compared to pastures grazed by cattle (Carvell 2002; Dumont et al. 2011; Jerrentrup et al. 2015; Enri et al. 2017). There was also lower butterfly richness and slightly lower abundance in sheep pastures. However, our community analysis did not show a significant effect of grazer or time-since-fire on butterfly composition, likely due to the homogeneity of the butterfly and plant communities (Bendel et al. 2018). High variability in annual rainfall may have overshadowed some of our expected effects of fire and grazing (Lanta et al. 2014). Our results indicate that higher precipitation and cattle grazing can improve floral and butterfly species richness and abundance in low-diversity grasslands, but in general, these grasslands need proactive measures to restore native forb diversity and abundance to support native pollinator communities.

Sheep grazing reduced floral abundance and richness in our experimental pastures. Similar to other studies, we found lower floral and butterfly abundance and richness (Table A1) in sheep pastures compared to pastures with cattle (Carvell 2002; Ockinger & Smith 2007; Dumont et al. 2011; Jerrentrup et al. 2015; Enri et al. 2017). It is unclear if changing the stocking rate would improve floral conditions. A high stocking rate can reduce sheep selectiveness, but can be more deleterious to flower frequency than a low stocking rate or no sheep (Lanta et al. 2014). Lower stocking rates may reduce overall pressure, but sheep selectivity can still shape grassland community composition (Pittarello et al. 2017). The effect of sheep grazing on floral resources might be different at a site with higher plant-diversity and higher proportion of native plants. However, there are scant examples of how sheep selection changes based on plant diversity in pastures (Ginane et al. 2015; Huang et al. 2018). There is some indication that the effects of sheep grazing vary with precipitation and plant diversity, but effects of sheep grazing

on species richness and functional diversity were not consistent between sites and climatic gradients (De Bello et al. 2006).

Fire may be insufficient to ameliorate sheep's preference for forbs as sheep grazing reduced floral abundance and richness significantly in our experimental patch-burn pastures compared to cattle pastures. We had hoped that patch-burn grazing would focus grazer attention on recently burned areas and lessen pressure on other areas of the pasture (Archibald et al. 2005; Allred et al. 2011). Restricting sheep access to areas of the pasture to allow for floral expression would increase the resources available to pollinators. A rest-rotational sheep grazing system may improve floral abundance and richness compared to continuous sheep grazing (Enri et al. 2017). However the rest-rotational system with sheep still had significantly lower floral richness and diversity than cattle grazing under continuous or rest-rotational (Enri et al. 2017).

Although overall butterfly abundance and richness was higher in cattle pastures, our community analysis did not find a strong association between grazer treatment or site characteristics and patterns of variation in the butterfly community. Contrary to other studies that found site characteristics such as floral abundance, richness, and diversity, percent litter cover, litter depth, and vegetation structure to strongly affect butterfly communities (Pöyry et al. 2006; Davis et al. 2007; Vogel et al. 2007; Sjödin et al. 2008; Debinski et al. 2011), these variables described less than 7% of the variation in the butterfly community at our site. Our results may differ because several of these studies occurred on remnant prairie sites with higher native floral presence and also habitat-specialists comprised a higher proportion of the butterfly community (Davis et al. 2007; Vogel et al. 2007; Debinski et al. 2011). Additionally, the majority of these studies occurred in wetter climates (tallgrass prairie in Iowa, Sweden, Finland), which may influence relationships between site characteristics and butterfly community variation. Our study

sites saw high precipitation variation and showed low diversity in plant and butterfly communities.

The lack of treatment effect may be a result of a homogenous butterfly community at our sites. The dominance of several species suggests there is minimal variation in community composition between pastures. The five dominant species have broad diet breadths that include weedy and/or forage species frequently found in low-diversity grasslands. *C. eurytheme*, *C. philodice*, *L. melissa*, all utilize legumes including alfalfa as host plants, while *P. rapae* and *P. protodiceare* true generalists and can use plants in both the mustard and caper families (Opler 1999). Other studies of grassland butterflies also document a high abundance of these five species (Vogel et al. 2007; Moranz et al. 2012; Farhat et al. 2014; Bendel et al. 2018). However, prairie-associated species with narrower diet breadths such as *Speyeria idalia*, *Cercyonis pegala*, *Boloria bellona* often shared a top-five ranking as well (Vogel et al. 2007; Moranz et al. 2012; Farhat et al. 2014; Bendel et al. 2018). Despite being disturbance-tolerant, generalist species, four of the five dominant butterfly species showed a positive association with increased floral abundance (Table 1.1; Figure 1.6), supporting other studies that highlight the importance of floral abundance for pollinators (Potts et al. 2009; Berg et al. 2013; Curtis et al. 2015).

The lack of grassland-obligate and specialist butterflies at our sites suggests that CRP may not be providing these species of concern with the resources that they need. During our study, less than 3% of observations were butterfly species with host plant diet breadth limited to only one genus, including species of conservation concern *Speyeria Idalia* (violets) and *Danaus plexippus* (milkweeds). Agri-environmental schemes such as the CRP are generally thought to be important refuges for wildlife within agricultural landscapes (Jones-Farrand et al. 2007). Our results challenge this assertion. The dominance of generalist species at our sites suggests either

they are already showing the after-effects of biotic homogenization due to agricultural intensification, or butterfly diversity is still present on the landscape, but CRP sites may not be providing the resources needed for a diverse butterfly community (Ekroos et al. 2010; Börschig et al. 2013; Farhat et al. 2014).

Floral abundance and richness responded positively to a wet year and floral richness and diversity responded negatively to a drought. High annual variability in precipitation is common in grasslands (Lauenroth & Sala 1992), and affects above-ground primary productivity and plant species composition (Lauenroth & Sala 1992; Silvertown et al. 1994; Knapp & Smith 2001; Heisler-White et al. 2009). Precipitation variability can enhance plant community diversity (Silvertown et al. 1994; Knapp et al. 2002). We saw similar trends in our study with increased floral richness with increased precipitation, however, the majority of the increase in forb expression occurred in plants that were already dominant or common at our sites (alfalfa, sweet clover). Our results highlight the important role of precipitation in regulating forb expression, biomass, and community composition in grassland systems.

Due to logistical limitations of pasture and herd availability, our study did not have a paired control, which would have allowed us to parse the extent to which precipitation seems to be the most salient factor influencing floral and butterfly richness and abundance in ungrazed and/or unburned pastures. In keeping with the applied nature of our research, no landowner would leave a pasture idle. Therefore, we accurately documented changes that may occur as grassland previously enrolled in the CRP are transitioned to grazing lands (Claassen 2011). Even without a paired control, the difference in floral availability between cattle and sheep is so stark that if there were to be corresponding effect of grazer type on the butterfly community at our site, we would have observed it.

The effect of time since fire was less pronounced than we expected. Not only were unburned, recently burned and one-year since fire grouped together in ordination space, but they were grouped near the origin, meaning there was minimal variation in butterfly community under each treatment. These results suggest that we have not achieved the patch contrast we sought by using patch-burn grazing (McGranahan et al. 2013b). We burned ¾ of each pasture by the end of this study, but a full application of patch-burn grazing would mean that each unit in the pastures have received fire at least once (Fuhlendorf & Engle 2004; Archibald et al. 2005; Allred et al. 2011). Our sites have not had time to develop the fire and grazing synergy needed for patch contrast and starker differences between livestock species ore years of fire application would also result in greater sample size for each time since fire benchmark (0-, 1-, 2-, 3-years since fire) and more statistical power to determine how time since fire affects specific species and the pollinator community (Potts et al. 2003; Moranz et al. 2012, 2014; McCullough et al. 2019).

Conclusions

Low-diversity grasslands need proactive conservation approaches to restore floral resources that can sustain and improve pollinator populations. As available grassland habitat in the northern Great Plains decreases due to agricultural intensification (Wright & Wimberly 2013), CRP conversion to grazing lands represents possible refuge for pollinators and other species that cannot survive in row crop monocultures. The integrity of grassland resources and grassland-dependent wildlife populations in the region depends on recognizing that low-diversity grasslands require active intervention and restoration in order to provide sufficient native forb diversity and abundance for native pollinators. Without active interventions like seeding native forbs or reconstructing grasslands, low-diversity grasslands show minimal trajectory toward the ecological function and plant-insect interactions present in remnant and/or high diversity

grasslands (Woodcock et al. 2012; Orford et al. 2016). Additionally, supporting pollinators may require adjusting livestock management practices, such as excluding sheep from areas of the pasture, especially during peak bloom, to enhance floral availability and pollinator abundance and richness.

Our results are also salient for landscape-level modeling, which often assumes that perennial cover such as CRP is providing the resources that native pollinators need (Otto et al. 2016). Modeling inherently involves making assumptions and aggregating landcover classes, however the results of our study show that models that do not differentiate between newer pollinator-friendly plantings and older non-native grass plantings may overestimate the amount of pollinator resources available on the landscape.

References

Adler P, Raff D, Lauenroth W. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia **128**:465–479.

Albon SD, Brewer MJ, O'brien S, Nolan AJ, Cope D. 2007. Quantifying the grazing impacts associated with different herbivores on rangelands. Journal of Applied Ecology **44**:1176–1187.

Allen-Wardell G et al. 1998. The Potential Consequences of Pollinator Declines on the Conservation of Biodiversity and Stability of Food Crop Yields. Conservation Biology **12**:8–17.

Allred BW, Fuhlendorf SD, Engle DM, Elmore RD. 2011. Ungulate preference for burned patches reveals strength of fire–grazing interaction. Ecology and Evolution **1**:132–144.

Allred BW, Fuhlendorf SD, Hovick TJ, Dwayne Elmore R, Engle DM, Joern A. 2013. Conservation implications of native and introduced ungulates in a changing climate. Global Change Biology **19**:1875–1883.

Archibald S, Bond WJ, Stock WD, Fairbanks DHK. 2005. Shaping the Landscape: Fire-Grazer Interactions in an African Savanna. Ecological Applications **15**:96–109.

Augustine DJ, Derner JD. 2014. Controls over the strength and timing of fire–grazer interactions in a semi-arid rangeland. Journal of Applied Ecology **51**:242–250.

Balvanera P, Pfisterer AB, Buchmann N, He J-S, Nakashizuka T, Raffaelli D, Schmid B. 2006. Quantifying the evidence for biodiversity effects on ecosystem functioning and services. Ecology Letters **9**:1146–1156.

Benayas JMR, Newton AC, Diaz A, Bullock JM. 2009. Enhancement of Biodiversity and Ecosystem Services by Ecological Restoration: A Meta-Analysis. Science **325**:1121–1124.

Bendel CR, Hovick TJ, Limb RF, Harmon JP. 2018. Variation in grazing management practices supports diverse butterfly communities across grassland working landscapes. Journal of Insect Conservation:1–13.

Berg Å, Ahrné K, Öckinger E, Svensson R, Wissman J. 2013. Butterflies in semi-natural pastures and power-line corridors – effects of flower richness, management, and structural vegetation characteristics. Insect Conservation and Diversity **6**:639–657.

Börschig C, Klein A-M, von Wehrden H, Krauss J. 2013. Traits of butterfly communities change from specialist to generalist characteristics with increasing land-use intensity. Basic and Applied Ecology **14**:547–554.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal **9**:378–400.

Brown JA, Boyce MS. 1998. Line transect sampling of Karner blue butterflies (Lycaeides melissa samuelis). Environmental and Ecological Statistics **5**:81–91.

Buckland S, Anderson D, Burnham K, Laake J, Borchers D, Thomas L. 2001. Introduction to distance sampling estimating abundance of biological populations. Oxford University Press.

Burnham KP, Anderson DR. 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media.

Butchart SHM et al. 2010. Global Biodiversity: Indicators of Recent Declines. Science **328**:1164–1168.

Cardinale BJ et al. 2012. Biodiversity loss and its impact on humanity. Nature **486**:59.

Cardinale BJ, Gonzalez A, Allington GRH, Loreau M. 2018. Is local biodiversity declining or not? A summary of the debate over analysis of species richness time trends. Biological Conservation. Available from https://www.sciencedirect.com/science/article/pii/S000632071732089X (accessed January 17, 2018).

Carvell C. 2002. Habitat use and conservation of bumblebees (Bombus spp.) under different grassland management regimes. Biological Conservation **103**:33–49.

Celaya R, Jáuregui BM, García RR, Benavides R, García U, Osoro K. 2010. Changes in heathland vegetation under goat grazing: effects of breed and stocking rate. Applied Vegetation Science **13**:125–134.

Cingolani AM, Noy-Meir I, Díaz S. 2005. Grazing Effects on Rangeland Diversity: A Synthesis of Contemporary Models. Ecological Applications **15**:757–773.

Claassen RL. 2011. Grassland to Cropland Conversion in the Northern Plains: The Role of Crop Insurance, Commodity, and Disaster Programs. DIANE Publishing.

Curtis RJ, Brereton TM, Dennis RLH, Carbone C, Isaac NJB. 2015. Butterfly abundance is determined by food availability and is mediated by species traits. Journal of Applied Ecology **52**:1676–1684.

Daubenmire R. 1959. Canopy coverage method of vegetation analysis. Northwest Sci **33**:39–64.

Davis JD, Debinski DM, Danielson BJ. 2007. Local and landscape effects on the butterfly community in fragmented Midwest USA prairie habitats. Landscape Ecology **22**:1341–1354.

De Bello F, Lepš J, Sebastià M-T. 2006. Variations in species and functional plant diversity along climatic and grazing gradients. Ecography **29**:801–810. John Wiley & Sons, Ltd.

Debinski DM et al. 2011. A cross- taxonomic comparison of insect responses to grassland management and land-use legacies. Ecosphere **2**:UNSP 131.

Deguines N, Jono C, Baude M, Henry M, Julliard R, Fontaine C. 2014. Large-scale trade-off between agricultural intensification and crop pollination services. Frontiers in Ecology and the Environment **12**:212–217.

Di Giulio M, Edwards PJ, Meister E. 2001. Enhancing insect diversity in agricultural grasslands: the roles of management and landscape structure. Journal of Applied Ecology **38**:310–319.

Duelli P, Obrist MK. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic and Applied Ecology **4**:129–138.

Dumont B, Carrère P, Ginane C, Farruggia A, Lanore L, Tardif A, Decuq F, Darsonville O, Louault F. 2011. Plant–herbivore interactions affect the initial direction of community changes in an ecosystem manipulation experiment. Basic and Applied Ecology **12**:187–194.

Ekroos J, Heliölä J, Kuussaari M. 2010. Homogenization of lepidopteran communities in intensively cultivated agricultural landscapes. Journal of Applied Ecology **47**:459–467.

Enri SR, Probo M, Farruggia A, Lanore L, Blanchetete A, Dumont B. 2017. A biodiversity-friendly rotational grazing system enhancing flower-visiting insect assemblages while maintaining animal and grassland productivity. Agriculture Ecosystems & Environment **241**:1–10.

Farhat YA, Janousek WM, McCarty JP, Rider N, Wolfenbarger LL. 2014. Comparison of butterfly communities and abundances between marginal grasslands and conservation lands in the eastern Great Plains. Journal of Insect Conservation **18**:245–256.

Farm Service Agency. 2019. Conservation Reserve Program. Available from https://www.fsa.usda.gov/programs-and-services/conservation-programs/conservation-reserve-program/ (accessed March 2, 2020).

Fiske I, Chandler R. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. Journal of Statistical Software **43**. Available from http://www.jstatsoft.org/v43/i10/ (accessed November 1, 2019).

Fleishman E, MacNally R. 2003. Distinguishing between signal and noise in faunal responses to environmental change. Global Ecology and Biogeography **12**:395–402.

Fourcade Y, Ockinger E. 2017. Host plant density and patch isolation drive occupancy and abundance at a butterfly's northern range margin. Ecology and Evolution **7**:331–345.

Fox J, Weisberg S. 2019. An R companion to applied regression, 3rd edition. Sage, Thousand Oaks CA. Available from https://socialsciences.mcmaster.ca/jfox/Books/Companion/.

Fuhlendorf SD, Engle DM. 2004. Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology **41**:604–614.

Geaumont BA, Sedivec KK, Schauer CS. 2017. Ring-necked Pheasant Use of Post−Conservation Reserve Program Lands. Rangeland Ecology & Management **70**:569–575.

Ginane C, Manuelian CL, Dumont B. 2015. Sheep herbivory within grassland patches: The potential cost of food item discrimination. Basic and Applied Ecology **16**:347–353.

Hahn PG, Orrock JL. 2015. Land-use legacies and present fire regimes interact to mediate herbivory by altering the neighboring plant community. Oikos **124**:497–506.

Hanley TA. 1982. The Nutritional Basis for Food Selection by Ungulates. Journal of Range Management **35**:146–151.

Harmon-Threatt AN, Hendrix SD. 2015. Prairie restorations and bees: The potential ability of seed mixes to foster native bee communities. Basic and Applied Ecology **16**:64–72.

Hart RH, Samuel MJ, Test PS, Smith MA. 1988. Cattle, Vegetation, and Economic Responses to Grazing Systems and Grazing Pressure. Journal of Range Management **41**:282–286.

Heisler-White JL, Blair JM, Kelly EF, Harmoney K, Knapp AK. 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Global Change Biology **15**:2894–2904.

Herrero-Jáuregui C, Oesterheld M. 2018. Effects of grazing intensity on plant richness and diversity: a meta-analysis. Oikos **0**. Available from https://onlinelibrary-wiley-com.ezproxy.lib.ndsu.nodak.edu/doi/abs/10.1111/oik.04893 (accessed March 24, 2018).

Hervé M. 2020. RVAideMemoire: Testing and plotting procedures for biostatistics. Available from https://CRAN.R-project.org/package=RVAideMemoire.

Hooper DU et al. 2005. Effects of Biodiversity on Ecosystem Functioning: A Consensus of Current Knowledge. Ecological Monographs **75**:3–35.

Huang Y, Wang L, Wang D, Zeng D-H, Li Y, Liu J, Wang Y. 2018. Foraging responses of sheep to plant spatial micro-patterns can cause diverse associational effects of focal plant at individual and population levels. Journal of Animal Ecology **87**:863–873.

Jerrentrup JS, Seither M, Petersen U, Isselstein J. 2015. Little grazer species effect on the vegetation in a rotational grazing system. Agriculture Ecosystems & Environment **202**:243–250.

Jones-Farrand DT, Jr LWB, Johnson DH, Ryan MR. 2007. Grassland Establishment for Wildlife Conservation:20.

Jutila HM, Grace JB. 2002. Effects of disturbance on germination and seedling establishment in a coastal prairie grassland: a test of the competitive release hypothesis. Journal of Ecology **90**:291–302.

Kindt R, Coe R. 2005. Tree diversity analysis: a manual and software for common statistical methods for ecological and biodiversity studies. World Agrofirestry Centre, Nairobi, Kenya.

Knapp AK, Fay PA, Blair JM, Collins SL, Smith MD, Carlisle JD, Harper CW, Danner BT, Lett MS, McCarron JK. 2002. Rainfall Variability, Carbon Cycling, and Plant Species Diversity in a Mesic Grassland. Science **298**:2202–2205.

Knapp AK, Smith MD. 2001. Variation Among Biomes in Temporal Dynamics of Aboveground Primary Production. Science **291**:481–484.

Kremen C et al. 2007. Pollination and other ecosystem services produced by mobile organisms: a conceptual framework for the effects of land-use change. Ecology Letters **10**:299–314.

Kremen C, Williams NM, Thorp RW. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences **99**:16812–16816.

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

Lanta V, Austrheim G, Evju M, Klimesova J, Mysterud A. 2014. Linking sheep density and grazing frequency to persistence of herb species in an alpine environment. Ecological Research **29**:411–420.

Lauenroth WK, Sala OE. 1992. Long-Term Forage Production of North American Shortgrass Steppe. Ecological Applications **2**:397–403.

Launchbaugh KL, Walker JW. 2006. Targeted Grazing -- A New Paradigm for Livestock Managementeted Grazing. Pages 2–9 in K. L. Launchbaugh, J. W. Walker, and R. J. Daines, editors. Targeted Grazing: A Natural Approach to Vegetation Management and Landscape Enhancement. Available from https://targetedgrazing.wordpress.com/other-resources/targeted-grazing/ (accessed November 2, 2017).

Lenth R. 2019. emmeans: Estimated marginal means, aka least-squares means. Available from https://CRAN.R-project.org/package=emmeans.

Liu Y, Duan M, Zhang X, Zhang X, Yu Z, Axmacher JC. 2015. Effects of plant diversity, habitat and agricultural landscape structure on the functional diversity of carabid assemblages in the North China Plain. Insect Conservation and Diversity **8**:163–176.

Mac Nally R, Fleishman E, Fay JP, Murphy DD. 2003. Modelling butterfly species richness using mesoscale environmental variables: model construction and validation for mountain ranges in the Great Basin of western North America. Biological Conservation **110**:21–31.

McCullough K, Albanese G, Haukos DA, Ricketts AM, Stratton S. 2019. Management regime and habitat response influence abundance of regal fritillary (Speyeria idalia) in tallgrass prairie. Ecosphere **10**:e02845.

McGranahan DA, Engle DM, Fuhlendorf SD, Miller JR, Debinski DM. 2013a. Multivariate Analysis of Rangeland Vegetation and Soil Organic Carbon Describes Degradation, Informs Restoration and Conservation. Land **2**:328–350. Multidisciplinary Digital Publishing Institute.

McGranahan DA, Engle DM, Fuhlendorf SD, Winter SL, Miller JR, Debinski DM. 2013b. Inconsistent outcomes of heterogeneity-based management underscore importance of matching evaluation to conservation objectives. Environmental Science & Policy **31**:53–60.

Mola JM, Williams NM. 2018. Fire-induced change in floral abundance, density, and phenology benefits bumble bee foragers. Ecosphere **9**:e02056.

Morandin LA, Winston ML, Abbott VA, Franklin MT. 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? Basic and Applied Ecology **8**:117–124.

Moranz RA, Debinski DM, McGranahan DA, Engle DM, Miller JR. 2012. Untangling the effects of fire, grazing, and land-use legacies on grassland butterfly communities. Biodiversity and Conservation **21**:2719–2746.

Moranz RA, Fuhlendorf SD, Engle DM. 2014. Making sense of a prairie butterfly paradox: The effects of grazing, time since fire, and sampling period on regal fritillary abundance. Biological Conservation **173**:32–41.

NDAWN. 2017. North Dakota Agricultural Weather Network (NDAWN) Station. Available from https://ndawn.ndsu.nodak.edu/station-info.html?station=29 (accessed September 30, 2017).

NDAWN Data Information. 2019. Available from https://ndawn.ndsu.nodak.edu/help-data.html#summ (accessed November 1, 2019).

NDAWN Tables - Monthly Weather Data. 2019. Available from https://ndawn.ndsu.nodak.edu/get-table.html?station=29&variable=mdr&dfn=&year=2019&d5y=&ttype=monthly&quick_pick=&begin_date=2017-05&count=36 (accessed November 1, 2019).

Ockinger E, Smith HG. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of Applied Ecology **44**:50–59.

Oksanen J et al. 2019. vegan: Community Ecology Package. Available from https://CRAN.R-project.org/package=vegan (accessed December 29, 2019).

Opler PA. 1999. A Field Guide to Western Butterflies. Houghton Mifflin Harcourt.

Pittarello M, Gorlier A, Lombardi G, Lonati M. 2017. Plant species selection by sheep in semi-natural dry grasslands extensively grazed in the south-western Italian Alps. Rangeland Journal **39**:123–131.

Polasky S, Nelson E, Lonsdorf E, Fackler P, Starfield A. 2005. Conserving Species in a Working Landscape: Land Use with Biological and Economic Objectives. Ecological Applications **15**:1387–1401.

Potts S, Biesmeijer J, Kremen C, Neumann P, Schweiger O, Kunin W. 2010. Global pollinator declines: Trends, impacts and drivers.

Potts SG, Vulliamy B, Amots D, Ne'eman G, O'Toole C, Roberts S, Willmer P. 2003. Response of plant-pollinator communities to fire: changes in diversity, abundance and floral reward structure. Oikos **101**:103–112.

Potts SG, Willmer P, Dafni A, Ne'eman G. 2001. The Utility of Fundamental Ecological Research of Plant-Pollinator Interactions as The Basis for Landscape Management Practices. Acta Horticulturae:141–144.

Potts SG, Woodcock BA, Roberts SPM, Tscheulin T, Pilgrim ES, Brown VK, Tallowin JR. 2009. Enhancing pollinator biodiversity in intensive grasslands. Journal of Applied Ecology **46**:369–379.

Pöyry J, Luoto M, Paukkunen J, Pykälä J, Raatikainen K, Kuussaari M. 2006. Different Responses of Plants and Herbivore Insects to a Gradient of Vegetation Height: An Indicator of the Vertebrate Grazing Intensity and Successional Age. Oikos **115**:401–412.

R Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Rook AJ, Dumont B, Isselstein J, Osoro K, WallisDeVries MF, Parente G, Mills J. 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. Biological Conservation **119**:137–150.

Rook AJ, Tallowin JRB. 2003. Grazing and pasture management for biodiversity benefit. Animal Research **52**:181–189.

Sala OE et al. 2000. Global Biodiversity Scenarios for the Year 2100. Science **287**:1770–1774.

Schieltz JM, Rubenstein DI. 2016. Evidence based review: positive versus negative effects of livestock grazing on wildlife. What do we really know? Environmental Research Letters **11**:113003.

Shepherd S, Debinski DM. 2005. Evaluation of isolated and integrated prairie reconstructions as habitat for prairie butterflies. Biological Conservation **126**:51–61.

Silvertown J, Dodd ME, McConway K, Potts J, Crawley M. 1994. Rainfall, Biomass Variation, and Community Composition in the Park Grass Experiment. Ecology **75**:2430–2437.

Sjödin NE, 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**:763–772.

Soderstrom B, Svensson B, Vessby K, Glimskar A. 2001. Plants, insects and birds in semi-natural pastures in relation to local habitat and landscape factors. Biodiversity and Conservation **10**:1839–1863.

Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T. 2002. Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds. Ecology **83**:1421–1432.

Tadey M. 2015. Indirect effects of grazing intensity on pollinators and floral visitation. Ecological Entomology **40**:451–460.

Tóth E, Deák B, Valkó O, Kelemen A, Miglécz T, Tóthmérész B, Török P. 2018. Livestock Type is More Crucial Than Grazing Intensity: Traditional Cattle and Sheep Grazing in Short-Grass Steppes. Land Degradation & Development **29**:231–239.

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

USDA N. 2020. PLANTS Database. Available from http://plants.usda.gov (accessed January 23, 2020).

USDA NASS. 2019. 2017 Census of Agriculture. Pages 430–433. vol 1, chapter 2, Table 13. Sheep and Lambs - Inventory, Sales, and Wool Production: 2017 and 2012. U.S. Department of Agriculture.

Vermeire LT, Mitchell RB, Fuhlendorf SD, Gillen RL. 2004. Patch Burning Effects on Grazing Distribution. Journal of Range Management **57**:248–252.

Vogel JA, Debinski DM, Koford RR, Miller JR. 2007. Butterflal, responses to prairie restoration through fire and grazing. Biological Conservation **140**:78–90.

Worm B et al. 2006. Impacts of Biodiversity Loss on Ocean Ecosystem Services. Science **314**:787–790.

Wright CK, Wimberly MC. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proceedings of the National Academy of Sciences **110**:4134–4139.

Wrobleski DW, Kauffman JB. 2003. Initial Effects of Prescribed Fire on Morphology, Abundance, and Phenology of Forbs in Big Sagebrush Communities in Southeastern Oregon. Restoration Ecology **11**:82–90.

CHAPTER 2: SHEEP GRAZING SIMPLIFIES FLORAL RESOURCES AND THE NATIVE BEE COMMUNITY IN LOW-DIVERSITY GRASSLANDS

Introduction

Globally, insect pollinators enable fruit or seed set in 87% of flowering species (Ollerton et al. 2011), including 75% of species grown as crops (Klein et al. 2007). Additionally, insect pollination services contribute nearly $190 billion to world agriculture production (Gallai et al. 2009), emphasizing their importance for global food security. The majority of these pollination services are carried out by bees, both domesticated bees like European honeybees and native, wild bees (Kearns & Inouye 1997). Substantial declines in managed honeybees (Potts et al. 2010b) and native bee richness and abundance have been documented in the United States (Grixti et al. 2009; Burkle et al. 2013) and Europe (Kosior et al. 2007; Goulson et al. 2008). Anthropogenic drivers such as land-use change, intensification of agricultural practices, and habitat fragmentation all contribute to decreases in both native bees and domesticated honeybees, which threaten both global food security and native systems (Foley et al. 2005; Goulson et al. 2008; Potts et al. 2010a; Otto et al. 2016). Decisions about how to manage agricultural lands affect the extent to which bees can persist on the landscape and provide these essential pollination services. Thus, there is an urgent need to understand how management decisions can better support pollinators in landscapes comprised of heavily modified, agricultural land-uses.

Anthropogenic actions primarily impact pollinators and threaten pollination services by decreasing the abundance and diversity of floral and nesting resources (Jauker et al. 2009; Potts et al. 2010a; Scheper et al. 2013, 2014). Although flowering crops provide floral resources for some pollinators, crop fields are often low-diversity, flowering is of short duration, and management practices such as tilling or pesticide application can negatively impact pollinator

populations (Potts et al. 2010a; Williams et al. 2010; Garibaldi et al. 2011). Additionally, agricultural intensification homogenizes the landscape, reducing plant diversity, native plant abundance, and vegetation structural heterogeneity (Tscharntke et al. 2005). As a result, pollinators rely on limited natural and semi-natural lands in an agricultural matrix to provide the majority of the resources that sustain pollinator populations and pollination services for crops and native plants (Ockinger & Smith 2007; Morandin et al. 2007).

Semi-natural areas benefit pollinators by increasing overall floral abundance, augmenting the spatial and temporal continuity of floral resources (Garibaldi et al. 2011), and providing nesting locations (Svensson et al. 2000). Bee communities show a close positive relationship between local flowering plant diversity and local pollinator diversity (Kwaiser & Hendrix 2008; Fründ et al. 2010; Farhat et al. 2014; Orford et al. 2016). Diverse plant communities can benefit pollinators by minimizing seasonal variability in nectar and pollen availability (Garibaldi et al. 2011; Nicolson & Wright 2017). Moreover, vegetation structural and compositional heterogeneity can benefit bee diversity by providing a range of nesting sites and foraging opportunities (Mortimer et al. 1999). Compositionally and structurally diverse plant communities result in diverse bee communities, which are advantageous because they are generally more stable over time (Kremen et al. 2002; Tscharntke et al. 2007) and ultimately provide more consistent pollination services (Klein et al. 2007; Albrecht et al. 2012). Consequently, understanding how management actions affect floral resources will be critical to pollinator conservation.

Semi-natural areas positively influence the abundance of pollinators in agricultural landscapes, however the quantity and quality of remaining semi-natural habitat is decreasing as agricultural operations expand and intensify (Steffan-Dewenter et al. 2002). For example,

Conservation Reserve Program (CRP) re-enrollments are declining in the United States, resulting in lands that were formerly in perennial cover transitioning to crop monocultures (Wright & Wimberly 2013; Morefield et al. 2016). Additionally, older CRP plantings were often seeded with non-native grasses, and persist as simplified grasslands dominated by a few grass and forage species (Jones-Farrand et al. 2007), but lacking the native forb component that is essential for pollinators (Goulson et al. 2015). Older CRP plantings still provide important resources for native bees including less-disturbed nesting conditions, lower pesticide exposure, and are more likely to have (non-native) forb expression persist throughout the growing season as compared to row crops. However, many of the remaining semi-natural areas (pastures, CRP fields, field edges) in agricultural landscapes that have the potential to provide essential floral resources are not being managed in a way that promotes floral richness and abundance (Walker et al. 2004; Plantureux et al. 2005).

Restoring essential disturbance processes such as fire and grazing may be a proactive management approach that could benefit a wide suite of plants and animals by increasing floral resources and promoting structural heterogeneity (Fuhlendorf et al. 2006; Engle et al. 2008; Hovick et al. 2015). Grazing is a dynamic process and species-mediated preferences result in different patterns, which in turn affect how, where, and when vegetation structure and composition change across the landscape (Milchunas et al. 1988; Rook et al. 2004). When grazing is coupled with discrete fire patches, herbivore preference for recently-burned areas causes a shifting mosaic of plant communities and vegetation structure (Fuhlendorf & Engle 2004). These changes to the plant community are frequently associated with more diverse and more stable insect populations (Kral et al. 2017; Welti et al. 2017). Despite the potential for direct mortality, reintroducing fire in a spatially and temporally varied way can also have a

positive influence on pollinator populations by modulating the abundance and temporal stability of floral resources (Wrobleski & Kauffman 2003; Fuhlendorf & Engle 2004; Vulliamy et al. 2006; Wagenius et al. 2020).

The dynamic interaction of fire and grazing promotes heterogeneity in grazing lands (Fuhlendorf et al. 2009). Several studies document this pattern using cattle or bison (Allred et al. 2011b; Kohl et al. 2013), but almost none explore how other domestic livestock, such as sheep, interact with fire. Innate differences in dietary preference or grazing habits of sheep could reduce patch contrast (Illius & Gordon 1987; Morris et al. 1999; Allred et al. 2011b, 2013). Sheep are able to graze more selectively than cattle or bison and tend to preferentially consume forbs to meet their nutritional requirements (Dumont et al. 2011; Ginane et al. 2015). Due to their lip and mouth morphology, sheep can target individual plants and species and can even select for specific parts of plants to consume, including the more nutritious shoots and flowers (Rook et al. 2004). Cattle grazing, in contrast, tends to include a greater proportion of grass consumption and can indirectly increase forb abundance by reducing grass competition (Adler et al. 2001; Dumont et al. 2011). While cattle production is the bigger industry, sheep grazing still has an impact on millions of acres of grassland (Mayne et al. 2015). In 2013, 5.3 million head of sheep and lambs and 29.3 million head of beef cows grazed in the United States (Rimbey et al. 2015). Furthermore, sheep producers rely on public-land allotments twice as much as cattle producers (Rimbey et al. 2015), highlighting the importance of understanding sheep herbivory for grassland management and conservation of pollinators. To understand the influence of sheep versus cattle herbivory on the landscape, it is important to also study how grazer species affects other important taxa in the system, including pollinators (Carvell 2002; Enri et al. 2017). Several studies document that sheep grazing tends to reduce forb abundance and richness and results in a

different plant community composition when compared to grasslands grazed by cattle exclusively (Carvell 2002; Dumont et al. 2011; Enri et al. 2017). If different livestock species have distinct effects on the plant and floral communities (Rook et al. 2004; Scohier & Dumont 2012; Tóth et al. 2018), we anticipate that grazing species will also affect pollinator communities.

We examined the influence of sheep or cattle grazing in a patch-burn grazing management framework on floral resources and the bee community. Additionally, we compared plant-pollinator networks between cattle and sheep pastures to better understand the impacts of grazing species on these relationships. Our specific objectives were to 1) Examine how different grazers (sheep or cattle) affect floral resource abundance, richness, and diversity in a patch-burn grazing framework; 2) Examine how floral abundance, richness, and Simpson's diversity influence native bee abundance in a patch burn-grazing framework; and 3) Examine plant-pollinator networks across grazer treatments. We expect that sheep pastures will have lower floral density and richness as compared to cattle pastures, which will result in lower bee richness and simpler plant-pollinator networks in sheep pastures.

Methods

Site Description

We conducted research from 2017 – 2019 on private lands leased by North Dakota State University's Hettinger Research Extension Center (HREC) in Adams county in southwest North Dakota. Understanding how cattle and sheep production can more sustainably coexist with pollinators is a highly relevant question for this area as cattle, sheep, and honey production are all major industries in the Northern Great Plains. In the Northern Great Plains states of Montana, Wyoming, Colorado, North Dakota, South Dakota, and Nebraska, cattle sales accounted for

$21.7 billion dollars, sheep meat provided $276 million, and an additional $12.7 million came from wool in 2017 (USDA NASS 2019).

During the study, the average temperature in May was 12 ºC, 18 ºC in June, 21.9 ºC in July, and 19.3 ºC in August (NDAWN 2019). Thirty-year average precipitation for May – August is 25 cm (NDAWN 2018). However, over the course of the three seasons of sampling, precipitation during May – August ranged from 11.2 cm in 2017 (NDAWN 2017), to 22.7 cm in 2018, and 33.3 cm in 2019 (Figure 2.1, NDAWN, 2019).

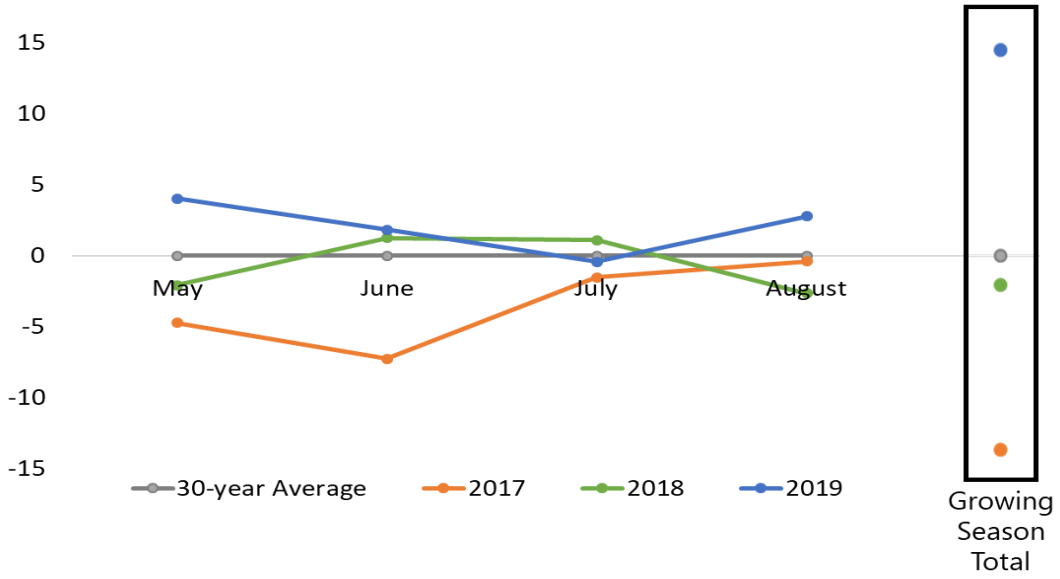

Figure 2.1. Precipitation during study period 2017-2019 compared to 30-year average. In 2017, May – August precipitation was 13.6 cm below average. In 2018, it was 2 cm below average, and in 2019, it was 14.5 cm above average.

The study sites were planted with Natural Resource Conservation Service Conservation Planting 1 (CP1) "introduced grasses" under the Conservation Reserve Program in the late 1980s (Geaumont et al. 2017). Species established under the CP1 planting included intermediate wheatgrass (*Elymus hispidus* [P. Opiz] Melderis), crested wheatgrass (*Agropyron cristatum* [L.]Gaertn), alfalfa (*Medicago sativa* L.), and yellow sweet clover (*Melilotus officinalis* [L.]

Lam.) (Geaumont et al. 2017). Although they are no longer enrolled in the CRP, the pastures are managed to promote vegetation structure for wildlife cover, and the vegetation composition continues to have low-diversity and is cool-season grass dominated.

Experimental Design

We conducted research in six, 65-ha pastures, with three pastures grazed by sheep and three grazed by cattle. Two cattle and two sheep pastures were located 7 km west of Hettinger, ND (site 1, site 2) and the other cattle and sheep pasture were 3 km south of Hettinger (site 3). We targeted a moderate stocking rate of 178 animal unit months in all pastures. We weighed and sorted animals to ensure equal animal units across treatments. Three pastures were moderately-stocked with sheep (168-173 dry ewes/pasture), and three were moderately-stocked with cattle (23-30 cow-calf pairs/pasture). We randomly assigned grazer treatments to each pasture. Cattle and sheep grazed pastures from May until September. Each pasture was divided into quarters, delineated by a 20’ fire break disked to mineral soil, however, only the exterior of the pasture was fenced allowing for livestock movement across the entire management unit. We burned one quarter of each pasture annually (i.e., four year fire-return-interval) during the dormant season, similar to other semi-arid patch-burn grazing experiments (Augustine & Derner 2014).

Data Collection

Floral Visitor and Floral Resource Sampling

We sampled bees and flowers from late-May to mid-August of 2017-2019 with three sampling periods per season to quantify bee abundance, community composition, and floral interactions. Three sampling periods enabled us to maximize detections of species with varying voltinism and phenology. There were 24, 25 m transects per pasture with six in each burn unit, for a total of 144 bee transects. To maximize bee detections and to minimize variation between

surveys, sampling occurred between 0800 h – 1730 h as long as temperatures were between 18.3C – 35.5 °C, sustained winds < 20 km/h, and cloud cover was < 50% (Royer et al. 1998; Davis et al. 2008; Harmon-Threatt & Hendrix 2015). We recorded the number and species of all flowering stems within 1 m of the transect. If a transect had no flowers within 1 m, it was recorded as "no flowers" and the observer moved on. We collected all native bees and honeybees touching the reproductive parts of flowers within 1 m of the transect (Bendel et al. 2019). We sampled transects for 10 minutes, not including handling time for each specimen.

Bee identification

We stored each bee specimen with a label that included data on when and where it was captured, including pasture, transect, date, time, and flower. In the lab, we determined lowest practical taxonomic class using a 10x microscope and taxonomic reviews, revisions, and books (LaBerge 1961; Michener 2007; Rightmyer 2008; Gibbs 2010, 2011; Dumesh & Sheffield 2012). Some *Lasiolgossum* specimens are considered nearly indistinguishable and were grouped accordingly in the *Lasioglossum viridatum* group or *Lasioglossum trigeminum-versatum* complex (Gibbs 2010, 2011)

Data Analyses

Effects of Grazer Type on Floral Abundance, Richness, and Diversity

We used a generalized linear mixed-effect model (GLMM) with a zero-inflated Poisson distribution to assess the influence of grazer species and year on floral abundance and richness, and a GLMM with a beta distribution to assess the influence of grazer species and year on Simpson's diversity index. We used the "glmmTMB" function in the *glmmTMB* package in R to execute the GLMMs (Brooks et al. 2017). We summarized floral data for each transect each year (transect-year) to account for year effects due to high variation in annual precipitation. We

summarized the floral data for each transect across the three visits per year using maximum annual counts (McGranahan et al. 2013a). We used maximum instead of average to summarize the full flowering potential during the growing season and to avoid any chance of double-counting flowering stems between sampling periods. Using these maximum counts, we calculated the following floral characteristics for each transect-year. Floral abundance was the sum of maximum flowering stems for each transect-year. Floral richness was a count of the number of species present for each transect-year. Floral diversity for each transect-year was calculated using Simpson's Diversity Index via the "diversity" function in *vegan* (Oksanen et al. 2018). Transect-years with zero flowers were assigned a diversity value of zero. To account for repeated measures and spatial non-independence, we nested year in transect in site as random effects in all models.

Floral abundance and richness data were best described by a zero-inflated Poisson distribution. Even after summarizing data to transect-year level, 20 transects never had a flower present throughout a year. Therefore, a zero-inflated Poisson distribution better accounted for the abundance of zeroes in our dataset. We used a beta distribution for Simpson's diversity which is on a scale from zero to one. To meet the assumptions of a beta distribution ($0 < y < 1$), we added 0.001 to all Simpson's diversity values. We calculated mean floral abundance, floral richness, and floral diversity and standard errors for each pasture each year.

We used R package *emmeans* to compute estimated marginal means and pairwise comparisons for our floral models (Lenth 2019). Estimated marginal means are the estimated mean at each point in a reference grid created from the combination of all levels of predictor factors (grazer and year) in our glmmTMB model. We obtained pairwise comparisons for the

estimated marginal means using the "pairs" functions from *emmeans*, which use a significance level of $\alpha = 0.05$ and the Tukey method for comparing a family of 6 estimates.

In order to compare the relative effects of precipitation versus grazer species, we compared the effect sizes of sheep vs cattle, our dry year (2017) vs our near-average year (2018), and our wet year (2019) vs our near-average year (2018). We created models with floral abundance, floral richness, and floral diversity as the response variables, grazer species plus year as the predictors, and nested year in transect in site as our random effects. We calculated the estimated marginal means and pairwise comparisons for these models using *emmeans* and confidence intervals for the pairwise comparisons using the "confint" function. We then extracted the comparisons we were interested in and plotted the resulting effect sizes.

Effects of Floral Characteristics on Native Bee Abundance and Richness

To quantify the relationship between floral characteristics such as floral abundance, floral richness, and floral diversity and native bee abundance and richness we used a GLMM and the *glmmTMB* package in R (Brooks et al. 2017). We excluded honeybees because we were most interested in assessing native bee responses to management and site characteristics. For native bee models, we excluded surveys without flowers (n = 272), as we could not observe bees on transects with no flowers. We then calculated the maximum values for floral abundance, richness, and Simpson's diversity for the remaining transect-years (412 transect-years observations). We pooled bee observations within years so that we had native bee abundance and native bee richness for transect-year as the response variables. Floral characteristics included total floral abundance, floral richness, and floral diversity (Simpson's), and we tested those alone and with year as an additive and interactive term. To account for repeated measures and spatial non-independence, we nested year in transect in site as a random effect in all models. A negative

binomial distribution best described native bee abundance and native bee richness. We ranked models using Akaike Information Criterion adjusted for small sample sizes (AIC_c). We considered models with $\Delta AIC_c \leq 2$ to be competitive (Burnham & Anderson 2003).

Plant-pollinator Interactions

We quantified plant-pollinator interactions in sheep and cattle pastures with the *bipartite* package in R (Dormann et al. 2017). Ecological network properties such as nestedness, network size and connectance influence the stability of mutualistic networks (Tylianakis et al. 2010; Popic et al. 2013). Quantifying plant-pollinator interactions gives insight into the stability of these interactions and how they varied with changes in floral richness and grazer-type. We calculated the network-level index H2', which measures specialization. H2' quantifies the frequency of interactions between bee species and a plant as the proportion of total interactions (Blüthgen et al. 2006). A higher H2' value indicates a more specialized network. We also examined the nestedness of the networks using weighted NODF ("nestedness metric based on overlap and decreasing fill"), which quantifies how many times a set of interactions is a true subset of more generalized interactions (Almeida-Neto et al. 2008; Almeida-Neto & Ulrich 2011). Nestedness means that specialist species' interactions are nested within interactions of generalist species. Generally, bee networks are more nested than would be expected randomly (Bascompte et al. 2003; Joppa et al. 2010). Lower values indicate less-nested while a value of 100 would be completely nested (Dormann et al. 2017). More nested networks are thought to be more resilient to extinctions because they contain a "central core" of interactions between generalist species, which supports the persistence of those resources for more specialized species (Bascompte et al. 2003). To better compare differences between cattle and sheep pastures, observed nestedness values were compared to null models that were randomized based on the

structure of the observed networks. Displaying interaction networks helps illustrate the relative abundance of plant and floral visitors and the frequency of those interaction under different grazing regimes.

Results

We counted 129,158 flowering stems of 68 different species from 2017-2019. Native plants comprised 50 of the 68 species, but only 12% of flowering stems. The most abundant species were alfalfa (*Medicago sativa*) 67.4% of flowering stems, sweet clover (*Melilotus alba and M. officinalis*) 12.3%, and yarrow (*Achillea millefolium*) 8.5%. Abundance and richness increased annually (Figure 2.2). We counted 21,553 flowering stems of 24 species in 2017, 52,010 flowering stems of 47 species in 2018, and 55,595 flowering stems of 51 species in 2019. Of the 1296 transect visits over the three years, we documented zero flowers 272 times (21%). We captured 574 native bees and 357 honeybees with 170.1 hours of survey time (Table B2; Table B3). Native bees represented 18 genera and 53 species plus two species complexes (Table B1). *Lasioglossum* sweat bees were the most abundant native genera with 340 specimens. Across all years, native bees were more abundant in cattle pastures than sheep pastures.

Pastures grazed by cattle had significantly more flowers than those grazed by sheep (χ^2 (1) =253.65, $p < 0.001$; Figure 2.2). Floral abundance and richness increased significantly each year in cattle pastures, paralleling the trend of increased precipitation each year (Figure 2.2 A, 2.2 B). However, floral abundance remained low in sheep pastures all years, regardless of rainfall (Figure 2.2 A). To illustrate, alfalfa was the dominant floral resource across all pastures, however, cattle pastures had 62 times more flowering stems of alfalfa than sheep pastures. In addition to abundance, floral richness was also significantly higher in cattle pastures compared to sheep (Figure 2.2 B, χ^2 (1) =106.41, $p < 0.001$). Overall, Simpson's diversity index was

significantly higher in cattle pastures than sheep pastures sheep (Figure 2.2 C, χ^2 (1) = 19.345, $p < 0.001$). There were pairwise differences in cattle and sheep 2018 and 2019, but not in the drought year of 2017.

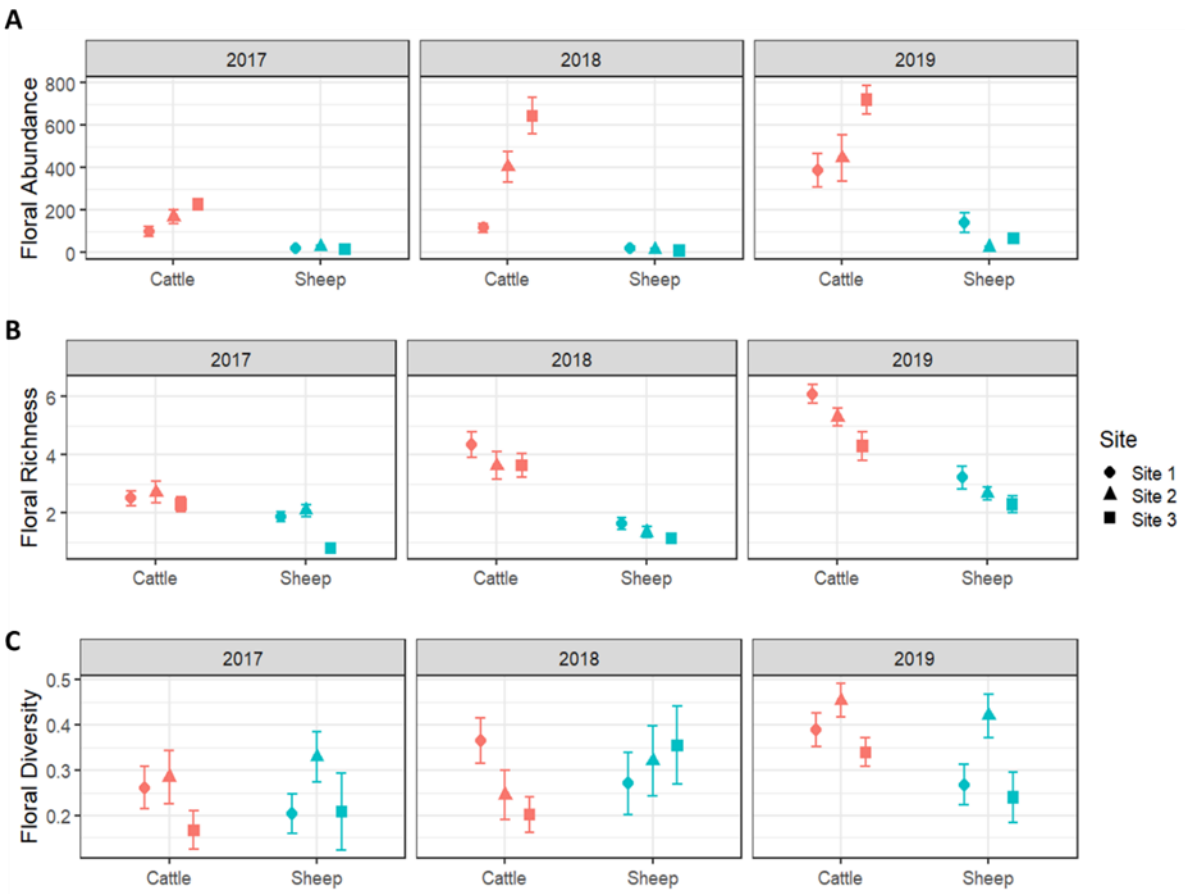

Figure 2.2. Mean floral abundance (A), floral richness (B), and floral diversity (C) by year and grazer in each pasture for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. Cattle pasture values are displayed in red and sheep in blue, error bars represent standard error. Sites represent our paired pasture replicates.

Comparing the relative effects of grazer species and precipitation showed that cattle grazing and a wetter year had a positive effect on floral abundance, floral richness and floral diversity (Figure 2.3). Cattle grazing compared to sheep grazing had a larger positive effect on floral abundance than a wet year compared to a near-average year (2019 vs. 2018) (Figure 2.3 A). Cattle grazing and a wetter year had similar positive effects on floral richness and floral

diversity (Figure 2.3 B, Figure 2.3 C). There was not a significant effect of drier year versus a near-average year (2017 vs. 2018) on floral abundance or diversity. Though a drier year did have a negative impact on floral richness (Figure 2.3 B).

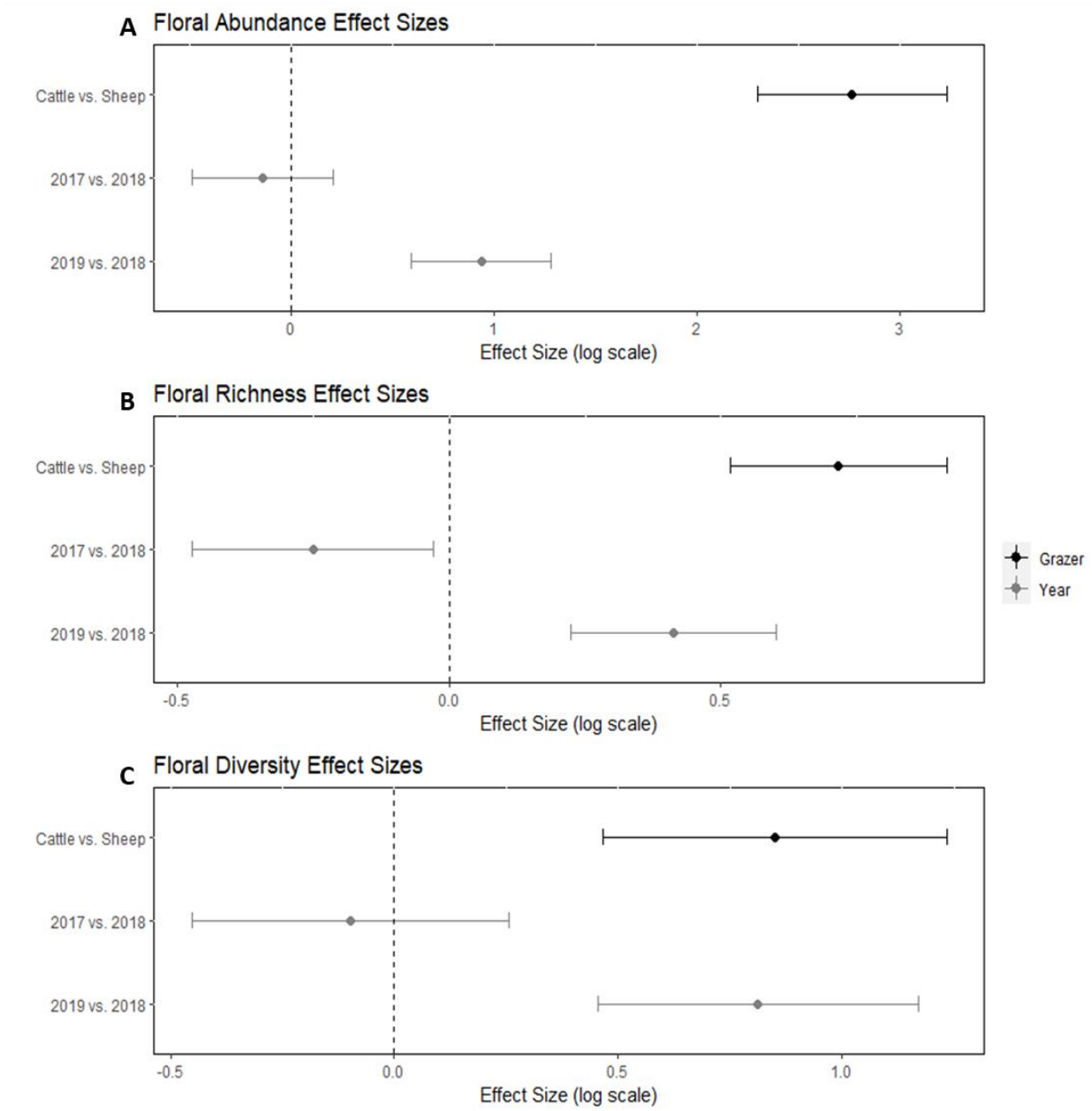

Figure 2.3. Effects of grazer species (Cattle vs. Sheep), dry year compared to near-average year (2017 vs. 2018), wet year compared to near-average year (2019 vs. 2018) on floral abundance (A), floral richness (B), and floral diversity (C) in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. Points are standardized effect sizes ± 95% CI. An effect size is considered significant when its CI does not include zero.

Paralleling floral trends, bees were much more abundant in cattle pastures than sheep pastures (Figure 2.4). Native bee abundance and species richness were both driven by floral richness. An interaction between floral richness and year best described native bee abundance (Figure 2.5, Table B4). Across all years, more flower species per transect had a positive effect on number of bees per transect, but the slope of the relationship differed between years. The slopes in 2017 and 2018 were similar ($\beta_{abundance2017}$ = 0.64, lower CI 0.34, upper CI 0.93; $\beta_{abundance2018}$ = 0.67, lower CI 0.46, upper CI 0.88), however in 2019, the slope was less steep ($\beta_{abundance2019}$ = 0.28 lower CI 0.13, upper CI 0.43). A model with floral richness and an interaction with year best described native bee richness (Figure 2.6, Table B5). Similar to native bee abundance, there was a positive relationship between floral richness and bee richness, but the slope of the relationship differed between years. Again, the slopes in 2017 and 2018 were similar ($\beta_{richness2017}$ = 0.61, lower CI 0.37, upper CI 0.85; $\beta_{richness2018}$ = 0.59, lower CI 0.43, upper CI 0.76), however in 2019, the slope was shallower ($\beta_{richness2019}$ = 0.22, lower CI 0.09, upper CI 0.34).

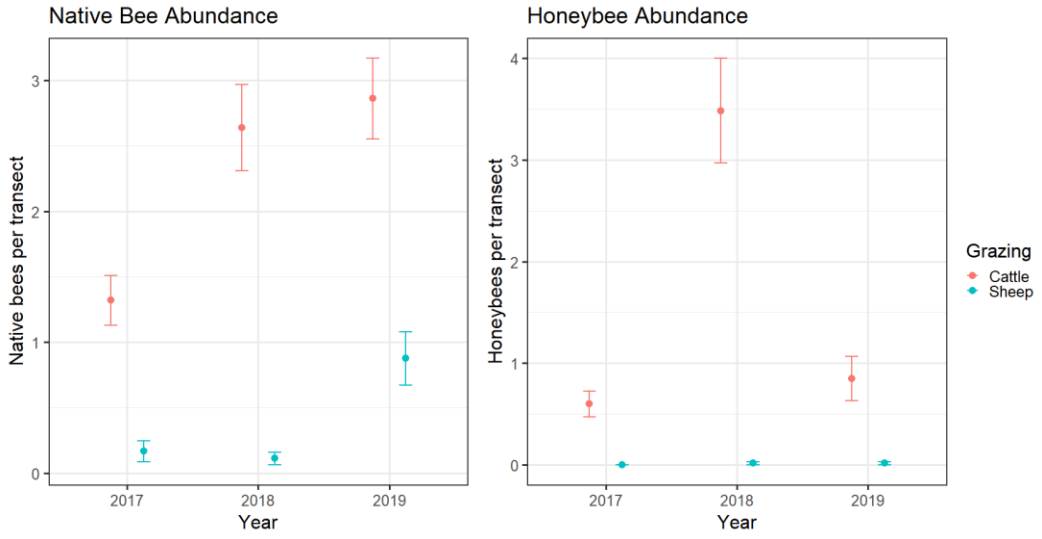

Figure 2.4. Average native bee and honeybee abundance per transect by year and grazer for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. Cattle pasture values are displayed in red and sheep in blue, error bars represent standard error. Overall, cattle pastures had 419 native bees compared to 83 in sheep pastures. There were 355 honeybees caught in cattle pastures and only 2 caught in sheep pastures.

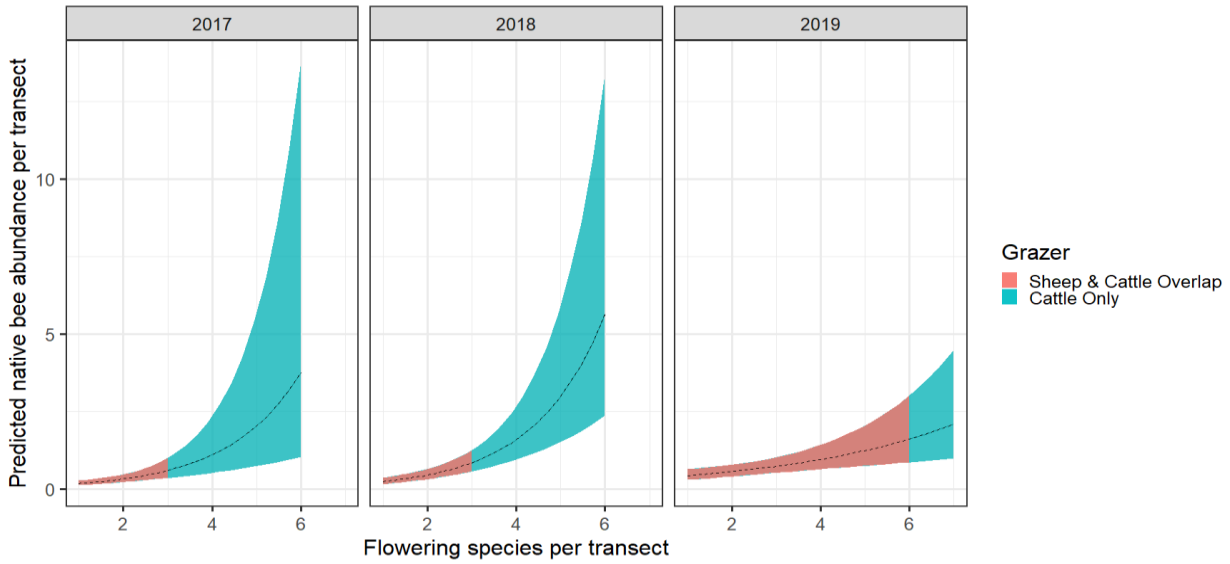

Figure 2.5. Relationship between floral richness and predicted native bee abundance per transect by year and grazer for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. The dotted line represents the predicted native bee abundance and the width of the ribbon represents the confidence intervals. Pink areas of the curve represent floral richness values that occurred in sheep and cattle pastures and blue areas only occurred in cattle pastures.

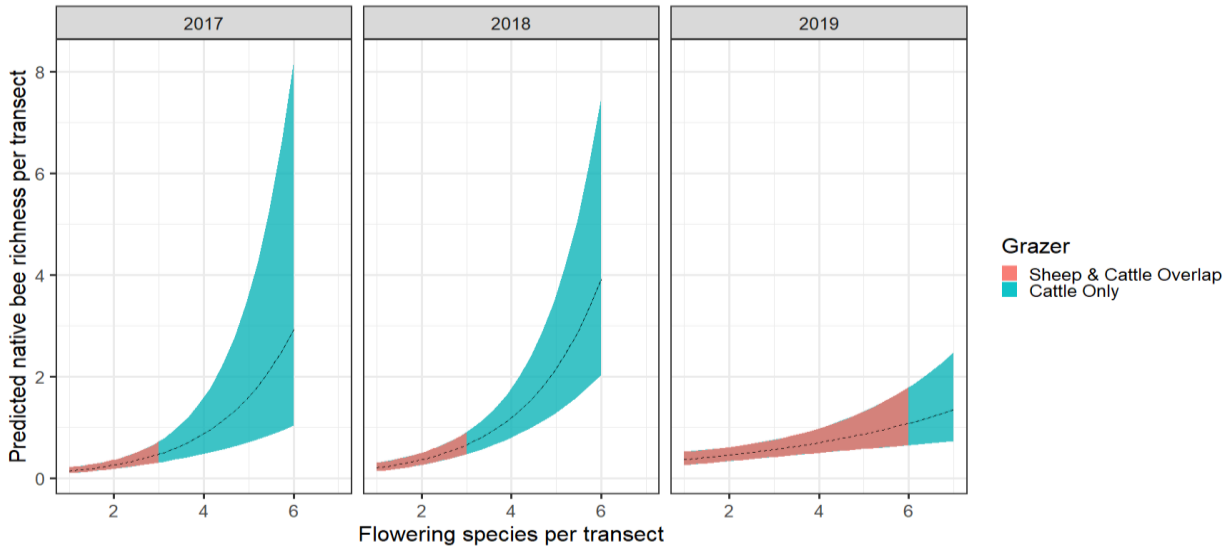

Figure 2.6. Relationship between floral richness and predicted native bee richness per transect by year and grazer for 2017 – 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. The dotted line represents the predicted native bee richness and the width of the ribbon represents the confidence intervals. Pink areas of the curve represent floral richness values that occurred in sheep and cattle pastures and blue areas only occurred in cattle pastures.

Bee-flower interaction networks showed 55 native bee species and honeybees in cattle pastures interacted with 25 of 68 available flowering species (Figure 2.7). Five plant species in cattle pastures – Canada thistle (*Cirsium arvense* (L.) Scop.), curlycup gumweed (*Grindelia squarrosa* (Pursh) Dunal), annual sunflower (*Helianthus annuus* L.), Maximilian sunflower (*Helianthus maximiliani* Schrad.), and prairie fleabane (*Erigeron strigosus* Muhl. ex Willd.) – harbored 27 out of 55 bee species indicating their importance for supporting a variety of bee species. In sheep pastures, we documented 14 native bee species and honeybees interacting with 10 of 34 available flowering plants (Figure 2.7). In cattle pastures, honeybees were the most abundant bee and interacted with nine plant species, predominantly alfalfa and sweet clover.

Network specialization was slightly higher in cattle pastures (H2' = 0.396) compared to sheep (H2' =0.383), suggesting that there is slightly more niche partitioning across plant and bee species in cattle pastures. Cattle pastures were less nested than predicted by the null model (weighted NODF = 17.84). The interactions in sheep pastures were more nested (weighted NODF 27.33) and within the range of values produced by the null model. Less nested suggests that rather than most bee species visiting most flower species in the network, there were discrete subsets of interactions between certain bee species and certain flowers. This difference between cattle and sheep networks is visually apparent in the interaction webs. The majority of the lines representing interactions in the sheep network have thicker lines, showing that most flowers were visited by more than one bee species and many bee species visited more than one flower species (Figure 2.7). Only three flowers in the sheep network were visited by only one bee species and eight bee species only interacted with one flower species. In the cattle pasture, there are many more thin lines, which shows that there were fewer redundancies in visitors and flowers visited (Figure 2.7). Cattle networks included 10 flowers that were only visited by one bee species and

22 bees that only visited one flower species. Nestedness values can decrease as floral richness and floral visitor richness increase and cattle pastures had greater richness of flowers and bees relative to sheep pastures (Welti & Joern 2018). Comparing the metrics between the cattle and sheep networks suggests that the sheep network should be more resilient to extinctions and perturbations as its interactions were less specialized (H2') and there were more redundancies in interactions (nestedness).

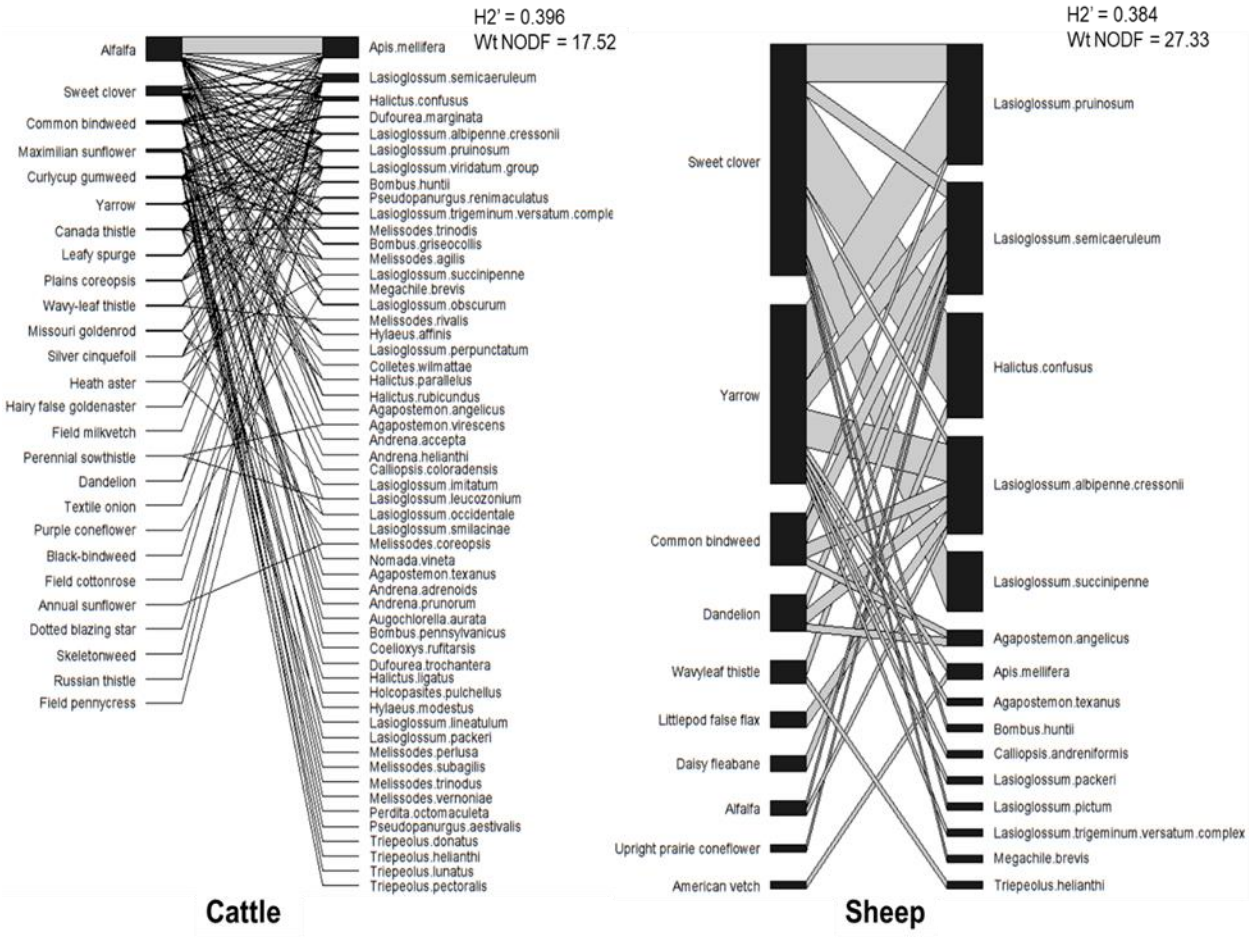

Figure 2.7. Plant pollinator networks by grazer treatment from 2017-2019 2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. Networks were combined across pastures and years and plotted to show differences by grazer species. Bars on the right represent native bee genera and honeybees, left bars are flowering species. Lines show which bee genera were captured on which flowers; the width of the line represents the frequency of that interaction. The H2' for each network is listed to indicate the level of specialization in network interactions. A higher H2' represents a more specialized network.

Discussion

In an increasingly intensified agricultural landscape, grasslands used for livestock grazing are an important semi-natural resource for wildlife species (Morandin et al. 2007). Understanding how grazing management decisions affect the quality and quantity of floral resources will help us conserve native bees in agroecosystems (Duelli & Obrist 2003; Morandin et al. 2007; Garibaldi et al. 2011). In examining the influence of sheep or cattle grazing on floral resources and bees, we found that sheep grazing significantly reduced floral resources and resulted in lower bee abundances and richness compared to cattle herbivory. Our findings align with other studies that found similar importance of floral abundance and diversity for abundance and diversity of bees, and similar detrimental effects of sheep on floral resources (Carvell 2002; Enri et al. 2017; Tóth et al. 2018). The flower-bee network of sheep pastures suggests that only generalist bees were able to persist the low-richness and low-abundance of flowers found in sheep pastures. The network for cattle pastures included many more native bee and flower species, but still lower overall abundance and richness of native bees than other grassland pollinator studies (Welti & Joern 2018), even those that look at degraded (native) grasslands (Bendel et al. 2019). Our results suggest that native bees do use former-CRP pastures, but in general, these pastures consisted of a simplified floral and bee community.

Sheep grazing significantly reduced forb abundance and richness under a patch-burn grazing management framework compared to pastures grazed by cattle. Given sheep's predilection for consuming forbs (Dumont et al. 2011; Jerrentrup et al. 2015; Tóth et al. 2018), these results were predicted, although the magnitude of difference exceeded expectations. Other studies examining the effects of sheep grazing also found much lower floral abundance and richness in pastures grazed by sheep compared to those grazed by cattle (Carvell 2002; Enri et al.

2017; Tóth et al. 2018). Sheep are able to graze more precisely than cattle due to their mouth dexterity and can target which plants and which parts of the plant they want to consume. The smaller stomach volume of sheep forces them to maximizing their nutrition per bite, which is often easier to access in forbs (Grant et al. 1985; Rook et al. 2004). Additionally, their nutritional imperative not only affects which plants they consume, but also leads them to select the most nutritious parts of those plants, which include flowers, pods, and shoots (Rook et al. 2004). Thus, sheep are not only consuming more forbs, but they are also specifically consuming more flowers than cattle. The reduction in forb abundance and richness, especially in a system already limited in floral diversity, suggests that season-long grazing by sheep is not compatible with pollinator conservation objectives even in a framework that is designed to focus grazing on recently burned areas.

Limiting sheep's access to portions of the pasture or rotationally grazing sheep may increase floral resources for pollinators (Enri et al. 2017). However, even if sheep are grazed rotationally, cattle grazing will still result in higher floral cover and pollinator richness and abundance, regardless of grazing system (Enri et al. 2017). A site with a higher plant-diversity and a higher abundance of native plants may also result in a different relationship between sheep and forbs, but there is minimal research on how plant community composition in pastures affects sheep grazing behaviors. There is some indication that the effects of sheep grazing on pastures vary with precipitation and plant diversity (De Bello et al. 2006), but most studies examine sheep foraging preferences using troughs or limited plant species (Ginane et al. 2015; Huang et al. 2018).

We had the expectation that patch-burn grazing might lessen some of the impacts of sheep on flowers by focusing grazer attention on recently burned areas and reducing pressure on

other areas of the pasture (Archibald et al. 2005; Allred et al. 2011a). However, because we saw such large differences in floral and bee abundances based on grazer species it seems that patch-burning with continuous grazing did not modulate forb consumption by sheep. Our observation may result from weaker fire-induced patch-attraction with sheep than with cattle or our study may need more years of fire to develop stronger patch contrast and thus a greater magnet effect (McGranahan et al. 2013b).

Bee abundances and native bee richness closely followed floral trends with significantly more bees in cattle pastures than sheep. Native bee abundance and native bee richness were best described by models comprised of an interaction between floral richness and year. Our results align with other studies that found bee richness positively associated with floral richness (Steffan-Dewenter & Tscharntke 2001; Potts et al. 2003; Hopwood 2008). However, our results diverge slightly from these other studies in that we found that floral richness was also the most explanatory for native bee abundance, whereas the other studies found floral abundance to be the strongest predictor of native bee abundance (Steffan-Dewenter & Tscharntke 2001; Hopwood 2008). The importance of floral richness for native bee abundance and native bee richness highlights the extent to which native bees depend on diverse nectar resources. At our sites, three species accounted for 88.2% of flowering stems, suggesting that there is ample opportunity to increase the diversity of species present on former-CRP fields.

Although we encountered 68 different flowering species during our study, richness per transect was low with sheep pastures averaging 1.9 and cattle 3.9 flowering species per transect. Thus, the majority of the bees we encountered needed to be able to feed their larvae on pollen collected from alfalfa, sweet clover, yarrow, or bindweed, or be able to forage outside the pastures. Alfalfa is a useful nectar plant, but is less attractive as a pollen source for many bees,

including honeybees (Jevtić et al. 2012). Thus, a flower community comprised of 67% alfalfa provides thousands of flowering stems, but may only be useful for a subset of bees (Rollin et al. 2013). The near-absence of honeybees in sheep pastures may be another reflection the poor resource availability in these pastures. Honeybees are able to survey resources within several kilometers of their hive and direct foragers to focus on high-quality patches (Visscher & Seeley 1982). While honeybee abundance is influenced by proximity to hives (Woodcock et al. 2013), their foraging range is large enough that all of our sites were within 2 km of a honeybee hive (Visscher & Seeley 1982). Thus, their near-absence suggests they did not view sheep pastures as worth visiting.

Floral richness and abundance showed strong annual variation, likely in response to changes in precipitation. Our effect sizes show that a wet year compared to a year with near-average precipitation had the greatest positive effect on floral abundance, but was consistently positive for all floral metrics. A drought year was only definitively worse than a near-average year in terms of effect on floral richness. Grasslands plant communities are frequently influenced by high annual variability in precipitation (Lauenroth & Sala 1992; Silvertown et al. 1994; Knapp & Smith 2001; Heisler-White et al. 2009). Precipitation can account for 39-45% of the variability in biomass production (Lauenroth & Sala 1992). One interesting example from our study is the biennial sweet clover. Sweet clover received ample rainfall in 2018 and 2019, likely benefited from reduced competition due to the drought in 2017, and then and had a boom year in 2019. In 2019, sweet clover was 27.6% of flowering stem counts, but was 0.80% of flowering stems in 2018 and 0.31 % in 2017. This trend is especially striking in sheep pastures where we captured 31 bees of eight species on sweet clover in 2019, but encountered no bees using sweet clover in 2017 or 2018.

Our flower-pollinator interaction networks suggest that the sheep network is slightly more resilient than our cattle network due to its increased nestedness, which is a measure of the extent to which specialist species' interactions are nested within interactions of generalist species. Interactions in cattle pastures were less nested, indicating that more of the interactions could be described as modular, i.e., grouped into discrete subgroups of interactions rather than specialized interactions nested in generalized ones (Bascompte et al. 2003). However, there were also significantly more flowering species available in the cattle pastures and other studies have shown a correlation between higher species richness and lower nestedness (Bascompte et al. 2003; Welti & Joern 2018). For example, we observed no sunflowers (*Helianthus spp.*) or curlycup gumweed (*Grindelia squarrosa*) blooming in sheep pastures. In our cattle pastures, these were species on which we more frequently encountered bees with specialized pollen preferences (Sheffield et al. 2014). Therefore, greater species richness of native plants in cattle pastures likely provided more opportunity to observe specialist interactions, which is reflected in the higher specialization (H2'). Although less nested is generally disadvantageous for network resilience (Thébault & Fontaine 2010), lower nestedness in our cattle sites may be more a reflection that their network involved ~2.6 times more flowers and bees than sheep pastures.

The majority of the bees caught in sheep pastures were small-bodied and diet generalists (Sheffield et al. 2014), and thus able to persist in sheep pastures despite the low floral abundance and diversity. Some small bees can provision a single larvae with the pollen from only 7-10 flowers (Müller et al. 2006). Studies that compare higher quality (remnant prairie or high-diversity restorations) to lower quality floral patches frequently find more homogenous pollinator communities in the lower quality patches (Potts et al. 2003; Kwaiser & Hendrix 2008; Sutter Louis et al. 2017).

Overall bee abundance and richness at our sites were lower compared to other studies of grassland plant-pollinator networks. After roughly 48 hours of sampling time, a one-year study at Konza Prairie in Kansas, USA observed 7,070 bee specimens of 369 different morphospecies interacting with 44 different plant species (Welti & Joern 2018). A two-year study in central North Dakota on degraded native grasslands captured 1,111 bee specimens of 68 species on 39 flowering plants with 153 hours of sampling (Bendel et al. 2019). Whereas our study encompassed ~ 170 sampling hours and resulted in 931 specimens, but only 55 species interacting with 31 flowering plants. These disparities in network size highlight the importance of implementing strategies that can bolster forb availability and diversity so that more bee species are able to find the nectar and pollen resources that they need. More diverse bee communities provide greater pollination services and are also better able to maintain these services despite temporal, spatial, or climatic perturbations (Fontaine et al. 2006; Questad & Foster 2008; Burkle & Alarcón 2011).

Conclusion

In landscapes with few semi-natural areas, such as agricultural areas, the quality of floral resource patches has an outsized influence on bee richness and abundance across the landscape (Kleijn & van Langevelde 2006). Our results suggest that former-CRP fields, especially those grazed by sheep, are not providing sufficient floral resources to support a diverse bee community. In addition to guiding land managers, our results should be considered by researchers modeling pollinator habitat in the Great Plains (Otto et al. 2016). Classifying all perennial cover, including older CRP plantings as useful habitat for pollinators may overestimate the amount of floral resources on the landscape.

If livestock producers decide to graze sheep, limiting sheep's access to portions of the

pasture should benefit floral availability and pollinator abundance (Enri et al. 2017). However, cattle grazing is more compatible with pollinator conservation objectives as cattle consume fewer forbs and may actually benefit forb expression by reducing grass competition (Adler et al. 2001; Dumont et al. 2011). Given the importance of pollinators to natural and agricultural systems, it is imperative that we select management strategies that are compatible with maintaining or bolstering the diversity and abundance of flowering plants in agricultural landscapes. Ensuring there are sufficient resources may necessitate not only carefully selecting livestock species, but also taking proactive action such as overseeding native forbs or more actively restoring former agricultural lands in order to maintain a bee community that can support these services. Several studies show that without active restoration efforts like seeding native forbs, low-diversity grasslands such as former-CRP show minimal trajectory towards the plant and insect communities present in remnant or high diversity restorations (Woodcock et al. 2012; Orford et al. 2016). Policies and programs that incentivize land owners and land managers to restore low-diversity grasslands and to plant high-diversity seed mixes will be essential to conserve native bees and the systems which depend on their services.

References

Adler P, Raff D, Lauenroth W. 2001. The effect of grazing on the spatial heterogeneity of vegetation. Oecologia **128**:465–479.

Albrecht M, Schmid B, Hautier Y, Muller CB. 2012. Diverse pollinator communities enhance plant reproductive success. Proceedings of the Royal Society B: Biological Sciences **279**:4845–4852.

Allred BW, Fuhlendorf SD, Engle DM, Elmore RD. 2011a. Ungulate preference for burned patches reveals strength of fire–grazing interaction. Ecology and Evolution **1**:132–144.

Allred BW, Fuhlendorf SD, Hamilton RG. 2011b. The role of herbivores in Great Plains conservation: comparative ecology of bison and cattle. Ecosphere **2**:1–17.

Allred BW, Fuhlendorf SD, Hovick TJ, Dwayne Elmore R, Engle DM, Joern A. 2013. Conservation implications of native and introduced ungulates in a changing climate. Global Change Biology **19**:1875–1883.

Almeida-Neto M, Guimarães P, Guimarães PR, Loyola RD, Ulrich W. 2008. A consistent metric for nestedness analysis in ecological systems: reconciling concept and measurement. Oikos **117**:1227–1239.

Almeida-Neto M, Ulrich W. 2011. A straightforward computational approach for measuring nestedness using quantitative matrices. Environmental Modelling & Software **26**:173–178.

Archibald S, Bond WJ, Stock WD, Fairbanks DHK. 2005. Shaping the Landscape: Fire-Grazer Interactions in an African Savanna. Ecological Applications **15**:96–109.

Augustine DJ, Derner JD. 2014. Controls over the strength and timing of fire–grazer interactions in a semi-arid rangeland. Journal of Applied Ecology **51**:242–250.

Bascompte J, Jordano P, Melián CJ, Olesen JM. 2003. The nested assembly of plant–animal mutualistic networks. Proceedings of the National Academy of Sciences **100**:9383–9387.

Bendel CR, Kral-O'Brien KC, Hovick TJ, Limb RF, Harmon JP. 2019. Plant–pollinator networks in grassland working landscapes reveal seasonal shifts in network structure and composition. Ecosphere **10**:e02569.

Blüthgen N, Menzel F, Blüthgen N. 2006. Measuring specialization in species interaction networks. BMC ecology **6**:9.

Brooks ME, Kristensen K, van Benthem KJ, Magnusson A, Berg CW, Nielsen A, Skaug HJ, Maechler M, Bolker BM. 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal **9**:378–400.

Burkle LA, Alarcón R. 2011. The future of plant–pollinator diversity: Understanding interaction networks across time, space, and global change. American Journal of Botany **98**:528–538.

Burkle LA, Marlin JC, Knight TM. 2013. Plant-Pollinator Interactions over 120 Years: Loss of Species, Co-Occurrence, and Function. Science **339**:1611–1615.

Burnham KP, Anderson DR. 2003. Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer Science & Business Media.

Carvell C. 2002. Habitat use and conservation of bumblebees (Bombus spp.) under different grassland management regimes. Biological Conservation **103**:33–49.

Davis JD, Hendrix SD, Debinski DM, Hemsley CJ. 2008. Butterfly, bee and forb community composition and cross-taxon incongruence in tallgrass prairie fragments. Journal of Insect Conservation **12**:69–79.

De Bello F, Lepš J, Sebastià M-T. 2006. Variations in species and functional plant diversity along climatic and grazing gradients. Ecography **29**:801–810. John Wiley & Sons, Ltd.

Dormann CF, Fruend J, Gruber B, Dormann MCF, LazyData T. 2017. Package ‘bipartite.’

Duelli P, Obrist MK. 2003. Regional biodiversity in an agricultural landscape: the contribution of seminatural habitat islands. Basic and Applied Ecology **4**:129–138.

Dumesh S, Sheffield CS. 2012. Bees of the Genus Dufourea Lepeletier (Hymenoptera: Halictidae: Rophitinae) of Canada. Canadian Journal of Arthropod Identification **20**.

Dumont B, Carrère P, Ginane C, Farruggia A, Lanore L, Tardif A, Decuq F, Darsonville O, Louault F. 2011. Plant–herbivore interactions affect the initial direction of community changes in an ecosystem manipulation experiment. Basic and Applied Ecology **12**:187–194.

Engle DM, Fuhlendorf SD, Roper A, Leslie DM. 2008. Invertebrate Community Response to a Shifting Mosaic of Habitat. Rangeland Ecology & Management **61**:55–62.

Enri SR, Probo M, Farruggia A, Lanore L, Blanchetete A, Dumont B. 2017. A biodiversity-friendly rotational grazing system enhancing flower-visiting insect assemblages while maintaining animal and grassland productivity. Agriculture Ecosystems & Environment **241**:1–10.

Farhat YA, Janousek WM, McCarty JP, Rider N, Wolfenbarger LL. 2014. Comparison of butterfly communities and abundances between marginal grasslands and conservation lands in the eastern Great Plains. Journal of Insect Conservation **18**:245–256.

Foley JA, DeFries R, Asner GP, Barford C, al et. 2005. Global Consequences of Land Use. Science; Washington **309**:570–4.

Fontaine C, Dajoz I, Meriguet J, Loreau M. 2006. Functional Diversity of Plant–Pollinator Interaction Webs Enhances the Persistence of Plant Communities. PLoS Biology **4**. Available from https://www.ncbi.nlm.nih.gov/pmc/articles/PMC1310649/ (accessed October 15, 2017).

Fründ J, Linsenmair KE, Blüthgen N. 2010. Pollinator diversity and specialization in relation to flower diversity. Oikos **119**:1581–1590.

Fuhlendorf SD, Engle DM. 2004. Application of the fire–grazing interaction to restore a shifting mosaic on tallgrass prairie. Journal of Applied Ecology **41**:604–614.

Fuhlendorf SD, Engle DM, Kerby J, Hamilton R. 2009. Pyric Herbivory: Rewilding Landscapes through the Recoupling of Fire and Grazing. Conservation Biology **23**:588–598.

Fuhlendorf SD, Harrell WC, Engle DM, Hamilton RG, Davis CA, Leslie DM. 2006. Should Heterogeneity Be the Basis for Conservation? Grassland Bird Response to Fire and Grazing. Ecological Applications **16**:1706–1716.

Gallai N, Salles J-M, Settele J, Vaissière BE. 2009. Economic valuation of the vulnerability of world agriculture confronted with pollinator decline. Ecological Economics **68**:810–821.

Garibaldi LA et al. 2011. Stability of pollination services decreases with isolation from natural areas despite honey bee visits. Ecology Letters **14**:1062–1072.

Geaumont BA, Sedivec KK, Schauer CS. 2017. Ring-necked Pheasant Use of Post−Conservation Reserve Program Lands. Rangeland Ecology & Management **70**:569–575.

Gibbs J. 2010. Revision of the metallic species of Lasioglossum (Dialictus) in Canada (Hymenoptera, Halictidae, Halictini). Zootaxa **2591**:1–382.

Gibbs J. 2011. Revision of the metallic species of Lasioglossum (Dialictus) in of eastern North America (Hymenoptera: Halictidae: Halictini). Zootaxa **3073**:1–216.

Ginane C, Manuelian CL, Dumont B. 2015. Sheep herbivory within grassland patches: The potential cost of food item discrimination. Basic and Applied Ecology **16**:347–353.

Goulson D, Lye GC, Darvill B. 2008. Decline and Conservation of Bumble Bees. Annual Review of Entomology **53**:191–208.

Goulson D, Nicholls E, Botías C, Rotheray EL. 2015. Bee declines driven by combined stress from parasites, pesticides, and lack of flowers. Science **347**:1255957.

Grant SA, Suckling DE, Smith HK, Torvell L, Forbes TDA, Hodgson J. 1985. Comparative Studies of Diet Selection by Sheep and Cattle: The Hill Grasslands. Journal of Ecology **73**:987–1004. [Wiley, British Ecological Society].

Grixti JC, Wong LT, Cameron SA, Favret C. 2009. Decline of bumble bees (Bombus) in the North American Midwest. Biological Conservation **142**:75–84.

Harmon-Threatt AN, Hendrix SD. 2015. Prairie restorations and bees: The potential ability of seed mixes to foster native bee communities. Basic and Applied Ecology **16**:64–72.

Heisler-White JL, Blair JM, Kelly EF, Harmoney K, Knapp AK. 2009. Contingent productivity responses to more extreme rainfall regimes across a grassland biome. Global Change Biology **15**:2894–2904.

Hopwood JL. 2008. The contribution of roadside grassland restorations to native bee conservation. Biological Conservation **141**:2632–2640.

Hovick TJ, Elmore RD, Fuhlendorf SD, Engle DM, Hamilton RG. 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. Ecological Applications **25**:662–672.

Huang Y, Wang L, Wang D, Zeng D-H, Li Y, Liu J, Wang Y. 2018. Foraging responses of sheep to plant spatial micro-patterns can cause diverse associational effects of focal plant at individual and population levels. Journal of Animal Ecology **87**:863–873.

Illius AW, Gordon IJ. 1987. The Allometry of Food Intake in Grazing Ruminants. Journal of Animal Ecology **56**:989–999.

Jauker F, Diekötter T, Schwarzbach F, Wolters V. 2009. Pollinator dispersal in an agricultural matrix: opposing responses of wild bees and hoverflies to landscape structure and distance from main habitat. Landscape Ecology **24**:547–555.

Jerrentrup JS, Seither M, Petersen U, Isselstein J. 2015. Little grazer species effect on the vegetation in a rotational grazing system. Agriculture Ecosystems & Environment **202**:243–250.

Jevtić G, Radović J, Hristov N. 2012. The importance of honey bee (Apis mellifera carnica Poll.) in pollination and seed yield of alfalfa (Medicago sativa L.).

Jones-Farrand DT, Jr LWB, Johnson DH, Ryan MR. 2007. Grassland Establishment for Wildlife Conservation:20.

Joppa LN, Montoya JM, Solé Vicente R, Sanderson J, Pimm SL. 2010. On nestedness in ecological networks. Evolutionary Ecology. Available from http://repositori.upf.edu/handle/10230/25584 (accessed February 27, 2020).

Kearns CA, Inouye DW. 1997. Pollinators, Flowering Plants, and Conservation Biology. BioScience **47**:297–307.

Kleijn D, van Langevelde F. 2006. Interacting effects of landscape context and habitat quality on flower visiting insects in agricultural landscapes. Basic and Applied Ecology **7**:201–214.

Klein A-M, Vaissière BE, Cane JH, Steffan-Dewenter I, Cunningham SA, Kremen C, Tscharntke T. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B: Biological Sciences **274**:303–313.

Knapp AK, Smith MD. 2001. Variation Among Biomes in Temporal Dynamics of Aboveground Primary Production. Science **291**:481–484.

Kohl MT, Krausman PR, Kunkel K, Williams DM. 2013. Bison Versus Cattle: Are They Ecologically Synonymous? Rangeland Ecology & Management **66**:721–731.

Kosior A, Celary W, Olejniczak P, Fijał J, Król W, Solarz W, Płonka P. 2007. The decline of the bumble bees and cuckoo bees (Hymenoptera: Apidae: Bombini) of Western and Central Europe. Oryx **41**:79–88. Cambridge University Press.

Kral KC, Limb RF, Harmon JP, Hovick TJ. 2017. Arthropods and Fire: Previous Research Shaping Future Conservation. Rangeland Ecology & Management **70**:589–598.

Kremen C, Williams NM, Thorp RW. 2002. Crop pollination from native bees at risk from agricultural intensification. Proceedings of the National Academy of Sciences **99**:16812–16816.

Kwaiser KS, Hendrix SD. 2008. Diversity and abundance of bees (Hymenoptera: Apiformes) in native and ruderal grasslands of agriculturally dominated landscapes. Agriculture, Ecosystems & Environment **124**:200–204.

LaBerge W. 1961. A Revision of the Bees of the Genus Melissodes in North and Central America. Part III (Hymenoptera, Apidae). University of Kansas Science Bulletin:283–663.

Lauenroth WK, Sala OE. 1992. Long-Term Forage Production of North American Shortgrass Steppe. Ecological Applications **2**:397–403.

Lenth R. 2019. emmeans: Estimated marginal means, aka least-squares means. Available from https://CRAN.R-project.org/package=emmeans.

Mayne K, Titolo A, Glazer S, Quamen F. 2015, February 4. West-Wide Bighorn Sheep Occupied Habitat and Domestic Sheep Grazing Allotments 2014. Bureau of Land Management, Wildlife Habitat Spatial Analysis Lab. Available from https://www.wafwa.org/Documents%20and%20Settings/37/Site%20Documents/Working%20Groups/Wild%20Sheep/Maps/Western%20Bighorn%20Allotments/BLM-BighornSheep_Westwide_26x34_v10.pdf.

McGranahan DA, Engle DM, Fuhlendorf SD, Miller JR, Debinski DM. 2013a. Multivariate Analysis of Rangeland Vegetation and Soil Organic Carbon Describes Degradation, Informs Restoration and Conservation. Land **2**:328–350. Multidisciplinary Digital Publishing Institute.

McGranahan DA, Engle DM, Fuhlendorf SD, Winter SL, Miller JR, Debinski DM. 2013b. Inconsistent outcomes of heterogeneity-based management underscore importance of matching evaluation to conservation objectives. Environmental Science & Policy **31**:53–60.

Michener CD. 2007. The bees of the world2nd ed. Johns Hopkins University Press, Baltimore.

Milchunas DG, Sala OE, Lauenroth WK. 1988. A Generalized Model of the Effects of Grazing by Large Herbivores on Grassland Community Structure. The American Naturalist **132**:87–106.

Morandin LA, Winston ML, Abbott VA, Franklin MT. 2007. Can pastureland increase wild bee abundance in agriculturally intense areas? Basic and Applied Ecology **8**:117–124.

Morefield PE, LeDuc SD, Clark CM, Iovanna R. 2016. Grasslands, wetlands, and agriculture: the fate of land expiring from the Conservation Reserve Program in the Midwestern United States. Environmental Research Letters **11**:094005.

Morris C, Derry J, Hardy MB. 1999. Effect of cattle and sheep grazing on the structure of Highland Sourveld swards in South Africa. Tropical Grasslands **33**:111–121.

Mortimer SR, van der Putten WH, Brown VK, Olff, H., Brown, V.K., Drent, R.H., Multitrofe Interacties (CTE / MTI). 1999. Insect and nematode herbivory below ground: interaction and role in vegetation succesion. Pages 205–238 Herbivores Between Plants and Predators. Blackwell. Available from https://pure.knaw.nl/portal/en/publications/insect-and-nematode-herbivory-below-ground-interaction-and-role-in-vegetation-succesion(ca4015cc-4c34-4812-9580-6d513ca4ad19).html (accessed April 14, 2018).

Müller A, Diener S, Schnyder S, Stutz K, Sedivy C, Dorn S. 2006. Quantitative pollen requirements of solitary bees: Implications for bee conservation and the evolution of bee–flower relationships. Biological Conservation **130**:604–615.

NDAWN. 2017. North Dakota Agricultural Weather Network (NDAWN) Station. Available from https://ndawn.ndsu.nodak.edu/station-info.html?station=29 (accessed September 30, 2017).

NDAWN Data Information. 2019. Available from https://ndawn.ndsu.nodak.edu/help-data.html#summ (accessed November 1, 2019).

NDAWN Tables - Monthly Weather Data. 2019. Available from https://ndawn.ndsu.nodak.edu/get-table.html?station=29&variable=mdr&dfn=&year=2019&d5y=&ttype=monthly&quick_pick=&begin_date=2017-05&count=36 (accessed November 1, 2019).

Nicolson SW, Wright GA. 2017. Plant–pollinator interactions and threats to pollination: perspectives from the flower to the landscape. Functional Ecology **31**:22–25.

Ockinger E, Smith HG. 2007. Semi-natural grasslands as population sources for pollinating insects in agricultural landscapes. Journal of Applied Ecology **44**:50–59.

Oksanen J et al. 2018. vegan: Community Ecology Package. Available from https://CRAN.R-project.org/package=vegan.

Ollerton J, Winfree R, Tarrant S. 2011. How many flowering plants are pollinated by animals? Oikos **120**:321–326.

Orford KA, Murray PJ, Vaughan IP, Memmott J. 2016. Modest enhancements to conventional grassland diversity improve the provision of pollination services. Journal of Applied Ecology **53**:906–915.

Otto CRV, Roth CL, Carlson BL, Smart MD. 2016. Land-use change reduces habitat suitability for supporting managed honey bee colonies in the Northern Great Plains. Proceedings of the National Academy of Sciences of the United States of America **113**:10430–10435.

Plantureux S, Peeters A, McCracken D. 2005. Biodiversity in intensive grasslands: Effect of management, improvement and challenges. Agronomy Research **3**:153–164.

Popic TJ, Wardle GM, Davila YC. 2013. Flower-visitor networks only partially predict the function of pollen transport by bees. Austral Ecology **38**:76–86.

Potts S, Biesmeijer J, Kremen C, Neumann P, Schweiger O, Kunin W. 2010a. Global pollinator declines: Trends, impacts and drivers.

Potts SG, Roberts SPM, Dean R, Marris G, Brown MA, Jones R, Neumann P, Settele J. 2010b. Declines of managed honey bees and beekeepers in Europe. Journal of Apicultural Research **49**:15–22. Taylor & Francis.

Potts SG, Vulliamy B, Dafni A, Ne'eman G, Willmer P. 2003. Linking bees and flowers: How do floral communities structure pollinator communities? Ecology **84**:2628–2642.

Questad EJ, Foster BL. 2008. Coexistence through spatio-temporal heterogeneity and species sorting in grassland plant communities. Ecology Letters **11**:717–726.

Rightmyer MG. 2008. A review of the cleptoparasitic bee genus Triepeolus (Hymenoptera: Apidae).-Part I. Zootaxa **1710**:1.

Rimbey NR, Tanaka JA, Torell LA. 2015. Economic considerations of livestock grazing on public lands in the United States of America. Animal Frontiers **5**:4.

Rollin O, Bretagnolle V, Decourtye A, Aptel J, Michel N, Vaissière BE, Henry M. 2013. Differences of floral resource use between honey bees and wild bees in an intensive farming system. Agriculture, Ecosystems & Environment **179**:78–86.

Rook AJ, Dumont B, Isselstein J, Osoro K, WallisDeVries MF, Parente G, Mills J. 2004. Matching type of livestock to desired biodiversity outcomes in pastures – a review. Biological Conservation **119**:137–150.

Royer RA, Austin JE, Newton WE. 1998. Checklist and "Pollard Walk" Butterfly Survey Methods on Public Lands. The American Midland Naturalist **140**:358–371.

Scheper J, Holzschuh A, Kuussaari M, Potts SG, Rundlöf M, Smith HG, Kleijn D. 2013. Environmental factors driving the effectiveness of European agri-environmental measures in mitigating pollinator loss – a meta-analysis. Ecology Letters **16**:912–920.

Scheper J, Reemer M, Kats R van, Ozinga WA, Linden GTJ van der, Schaminée JHJ, Siepel H, Kleijn D. 2014. Museum specimens reveal loss of pollen host plants as key factor driving wild bee decline in The Netherlands. Proceedings of the National Academy of Sciences **111**:17552–17557.

Scohier A, Dumont B. 2012. How do sheep affect plant communities and arthropod populations in temperate grasslands? Animal **6**:1129–1138.

Sheffield C, Frier D, Dumesh S. 2014. The Bees (Hymenoptera: Apoidea, Apiformes) of the Prairies Ecozone with Comparisons to other Grasslands of Canada. Pages 426–467.

Silvertown J, Dodd ME, McConway K, Potts J, Crawley M. 1994. Rainfall, Biomass Variation, and Community Composition in the Park Grass Experiment. Ecology **75**:2430–2437.

Steffan-Dewenter I, Münzenberg U, Bürger C, Thies C, Tscharntke T. 2002. Scale-Dependent Effects of Landscape Context on Three Pollinator Guilds. Ecology **83**:1421–1432.

Steffan-Dewenter I, Tscharntke T. 2001. Succession of bee communities on fallows. Ecography **24**:83–93.

Sutter Louis, Jeanneret Philippe, Bartual Agustín M., Bocci Gionata, Albrecht Matthias, MacIvor Scott. 2017. Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. Journal of Applied Ecology **54**:1856–1864.

Svensson B, Lagerlöf J, G. Svensson B. 2000. Habitat preferences of nest-seeking bumble bees (Hymenoptera: Apidae) in an agricultural landscape. Agriculture, Ecosystems & Environment **77**:247–255.

Thébault E, Fontaine C. 2010. Stability of Ecological Communities and the Architecture of Mutualistic and Trophic Networks. Science **329**:853–856. American Association for the Advancement of Science.

Tóth E, Deák B, Valkó O, Kelemen A, Miglécz T, Tóthmérész B, Török P. 2018. Livestock Type is More Crucial Than Grazing Intensity: Traditional Cattle and Sheep Grazing in Short-Grass Steppes. Land Degradation & Development **29**:231–239.

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

Tscharntke T, Tylianakis J, Wade MR, Wratten SD, Bengtsson J, Kleijn D. 2007. Insect conservation in agricultural landscapes. Insect Conservation Biology: Proceedings of the Royal Entomological Society's 23rd Symposium:383–404.

Tylianakis JM, Laliberté E, Nielsen A, Bascompte J. 2010. Conservation of species interaction networks. Biological Conservation **143**:2270–2279.

USDA NASS. 2019. 2017 Census of Agriculture. Pages 430–433. vol 1, chapter 2, Table 13. Sheep and Lambs - Inventory, Sales, and Wool Production: 2017 and 2012. U.S. Department of Agriculture.

Visscher PK, Seeley TD. 1982. Foraging Strategy of Honeybee Colonies in a Temperate Deciduous Forest. Ecology **63**:1790–1801.

Vulliamy B, Potts SG, Willmer PG. 2006. The effects of cattle grazing on plant-pollinator communities in a fragmented Mediterranean landscape. Oikos **114**:529–543.

Wagenius S, Beck J, Kiefer G. 2020. Fire synchronizes flowering and boosts reproduction in a widespread but declining prairie species. Proceedings of the National Academy of Sciences. Available from http://www.pnas.org/content/early/2020/01/21/1907320117 (accessed January 29, 2020).

Walker KJ, Stevens PA, Stevens DP, Mountford JO, Manchester SJ, Pywell RF. 2004. The restoration and re-creation of species-rich lowland grassland on land formerly managed for intensive agriculture in the UK. Biological Conservation **119**:1–18.

Welti E, Helzer C, Joern A. 2017. Impacts of plant diversity on arthropod communities and plant-herbivore network architecture. Ecosphere **8**:e01983.

Welti EAR, Joern A. 2018. Fire and grazing modulate the structure and resistance of plant–floral visitor networks in a tallgrass prairie. Oecologia **186**:517–528.

Williams NM, Crone EE, Roulston TH, Minckley RL, Packer L, Potts SG. 2010. Ecological and life-history traits predict bee species responses to environmental disturbances. Biological Conservation **143**:2280–2291.

Woodcock BA, Bullock JM, Mortimer SR, Pywell RF. 2012. Limiting factors in the restoration of UK grassland beetle assemblages. Biological Conservation **146**:136–143.

Woodcock BA, Edwards M, Redhead J, Meek WR, Nuttall P, Falk S, Nowakowski M, Pywell RF. 2013. Crop flower visitation by honeybees, bumblebees and solitary bees: Behavioural differences and diversity responses to landscape. Agriculture, Ecosystems & Environment **171**:1–8.

Wright CK, Wimberly MC. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. Proceedings of the National Academy of Sciences **110**:4134–4139.

Wrobleski DW, Kauffman JB. 2003. Initial Effects of Prescribed Fire on Morphology, Abundance, and Phenology of Forbs in Big Sagebrush Communities in Southeastern Oregon. Restoration Ecology **11**:82–90.

APPENDIX A. SUPPLEMENTARY MATERIALS FOR CHAPTER ONE

Table A.1. Butterfly abundances by year. List of butterfly abundances by year and percent of observations in cattle pastures during line-transect distance sampling conducted from 2017-2019 in southwest North Dakota.

Butterfly Species	2017	2018	2019	Total	% in Cattle Pastures
Colias philodice	1406	2429	4614	8449	52.7
Lycaeides melissa	894	1759	286	2939	74.7
Vanessa cardui	104	1	491	596	51.0
Pontia protodice	51	108	349	508	65.4
Colias eurytheme	53	114	71	238	62.2
Cercyonis pegala	21	22	151	194	51.0
Phyciodes selenis	2	44	129	175	64.0
Phyciodes tharos	0	99	44	143	88.1
Coenonympha tullia	37	14	66	117	73.5
Pyrgus communis	24	49	35	108	71.3
Glaucopsyche lygdamus	13	21	38	72	77.8
Pieris rapae	15	25	7	47	57.4
Vanessa atalanta	4	0	34	38	36.8
Danaus plexippus	0	9	20	29	48.3
Speyeria aphrodite or *Speyeria cybele*	4	1	22	27	55.6
Phyciodes batesii	4	1	18	23	87.0
Euptoieta claudia	0	15	6	21	47.6
Speyeria idalia	7	5	9	21	47.6
Polites themistocles	5	0	5	10	100
Vanessa virginiensis	2	2	6	10	80.0
Pholisora catullus	0	0	6	6	50.0
Polites mystic	0	0	5	5	100
Lycaena helloides	0	3	0	3	100
Boloria selene	0	0	1	1	100
Chlosyne gorgone	0	0	1	1	100
Erynnis persius	0	0	1	1	100
Speyeria aphrodite	0	1	0	1	0
richness	17	20	25	27	
#/ year	2647	4722	6450	13819	59.0

Table A.2. Estimated butterfly densities by grazer and year. We input average floral abundance and diversity for each grazer treatment and year into the most competitive model for each species to calculate a butterfly density estimate under those flower conditions. Floral variables are presented as standardized and unstandardized to allow comparison with density graphs. Density estimates are butterflies per hectare.

Butterfly	Year	Grazer	Avg. floral abundance per transect (equivalent standardized value)	Estimated butterfly density/ha (lower and upper)
COLEUR	2017	Cattle	562.64 (-0.13)	43 (21 – 89)
		Sheep	84.56 (-0.6)	42 (20 - 85)
	2018	Cattle	1140.81 (0.44)	129 (72 – 233)
		Sheep	62.14 (-0.62)	91 (48 – 171)
	2019	Cattle	2131 (1.41)	104 (56 – 195)
		Sheep	201.22 (-0.49)	38 (18 – 78)
LYCMEL	2017	Cattle	562.64 (-0.13)	208 (183 – 236)
		Sheep	84.56 (-0.6)	142 (123 – 164)
	2018	Cattle	1140.81 (0.44)	554 (510 – 602)
		Sheep	62.14 (-0.62)	126 (109 – 146)
	2019	Cattle	2131 (1.41)	75 (62 – 91)
		Sheep	201.22 (-0.49)	22 (16 – 30)
PONPRO	2017	Cattle	562.64 (-0.13)	10 (6 -17)
		Sheep	84.56 (-0.6)	5 (3 – 9)
	2018	Cattle	1140.81 (0.44)	19 (13 – 28)
		Sheep	62.14 (-0.62)	16 (10 – 24)
	2019	Cattle	2131 (1.41)	73 (54 – 99)
		Sheep	201.22 (-0.49)	39 (28 – 54)
VANCAR	2017	Cattle	562.64 (-0.13)	28 (19 – 42)
		Sheep	84.56 (-0.6)	23 (15 – 35)
	2018	Cattle	1140.81 (0.44)	0 (0 – 0)
		Sheep	62.14 (-0.62)	0 (0 – 10)
	2019	Cattle	2131 (1.41)	137 (103 – 182)
		Sheep	201.22 (-0.49)	139 (101 – 190)
Butterfly	Year	Grazer	Avg. floral diversity per transect	Estimated butterfly density/ha (lower and upper)
COLPHI	2017	Cattle	0.27	75 (69 – 80)
		Sheep	0.22	77 (72 – 83)
	2018	Cattle	0.38	129 (121 – 138)
		Sheep	0.41	127 (119 – 135)
	2019	Cattle	0.48	253 (244 – 263)
		Sheep	0.44	249 (239 – 258)

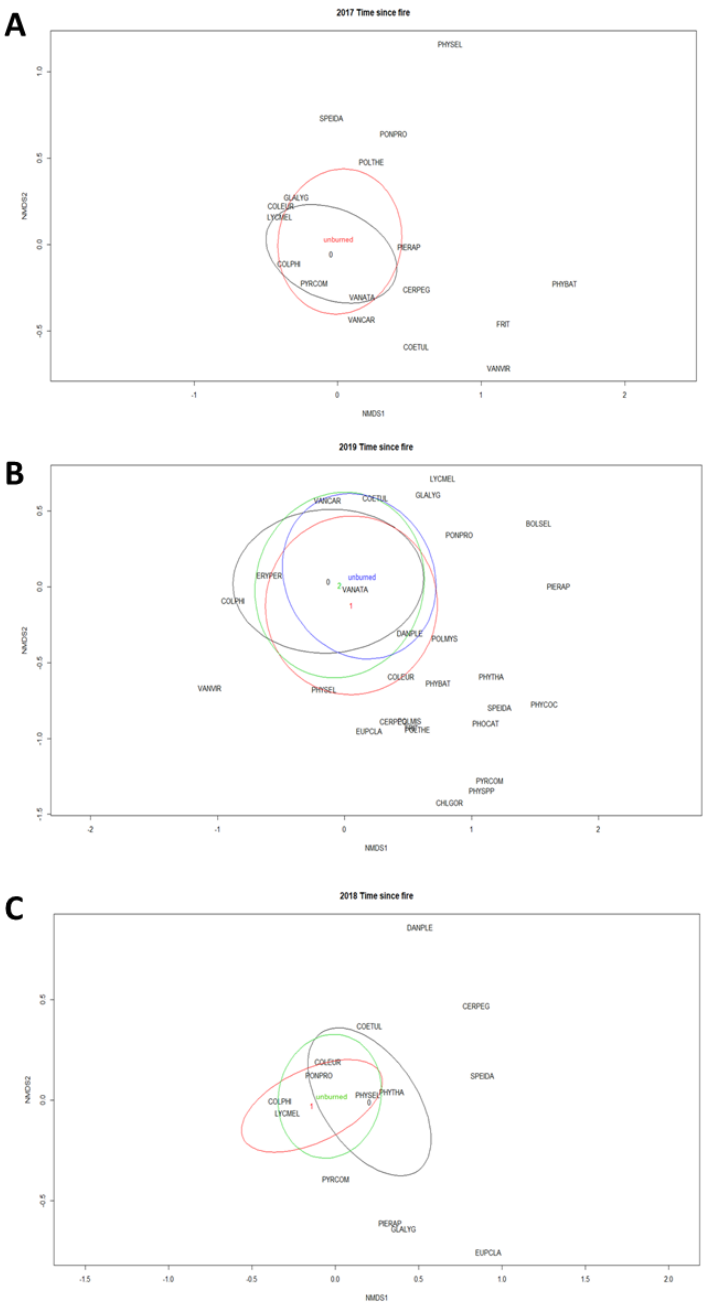

Figure A.1. Butterfly community NMDS ordination showing minimal variation in groupings by time since fire for 2017, 2018, 2019 at Hettinger Research Extension Center. Panel A shows a NMDS ordination using Bray-Curtis dissimilarity metric for the butterfly community (17 species) in 2017 (k = 4, stress = 0.14) and overlap between unburned, recently burned (0). Panel B shows a NMDS ordination using Bray-Curtis dissimilarity metric for the butterfly community (17 species) in 2018 (k = 4, stress = 0.13) and overlap between unburned, recently burned (0), and 1 year since fire (1). Panel C shows a NMDS ordination using Canberra dissimilarity metric for the butterfly community (25 species) in 2019 (k = 4, stress = 0.12) and overlap between unburned, recently burned (0), 1 year since fire (1), and 2 years since fire (2).

APPENDIX B. SUPPLEMENTARY MATERIALS FOR CHAPTER TWO

Table B.1. Bee species and genera observed from 2017-2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. Abundances categorized by grazer and survey year.

		2017			2018			2019			
Genus	Bee Species	Cattle	Sheep	Total	Cattle	Sheep	Total	Cattle	Sheep	Total	Grand Total
Agapostemon	*Agapostemon angelicus*	1	-	1	-	-	-	1	2	3	4
	Agapostemon texanus	1	1	2	-	-	-	-	-	-	2
	Agapostemon virescens	-	-	-	1	-	1	1	-	1	2
Andrena	*Andrena accepta*	-	-	-	2	-	2	-	-	-	2
	Andrena adrenoids	-	-	-	1	-	1	-	-	-	1
	Andrena helianthin	-	-	-	1	-	1	1	-	1	2
	Andrena prunorum	-	-	-	-	-	-	1	-	1	1
Apis	*Apis mellifera*	43	-	43	251	1	252	61	1	62	357
Augochlorella	*Augochlorella aurata*	-	-	-	1	-	1	-	-	-	1
Bombus	*Bombus griseocollis*	-	-	-	5	-	5	2	1	3	8
	Bombus huntii	3	-	3	-	-	-	7	1	8	11
	Bombus pennsylvanicus	-	-	-	-	-	-	1	-	1	1
Calliopsis	*Calliopsis andreniformis*	-	1	1	-	-	-	-	-	-	1
	Calliopsis coloradensis	-	-	-	1	-	1	1	-	1	2
Coelioxys	*Coelioxys rufitarsis*	-	-	-	1	-	1	-	-	-	1
Colletes	*Colletes wilmattae*	-	-	-	3	-	3	-	-	-	3
Dufourea	*Dufourea marginata*	-	-	-	9	-	9	25	-	25	34
	Dufourea trochantera	-	-	-	-	-	-	1	-	1	1
Halictus	*Halictus confuses*	3	-	3	22	-	22	49	14	63	88
	Halictus ligatus	-	-	-	-	-	-	1	-	1	1
	Halictus parallelus	-	-	-	-	-	-	3	-	3	3
	Halictus rubicundus	-	-	-	2	-	2	1	-	1	3

Table B.1. Bee species and genera observed from 2017-2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA (continued). Abundances categorized by grazer and survey year.

		2017			2018			2019			
Genus	Bee Species	Cattle	Sheep	Total	Cattle	Sheep	Total	Cattle	Sheep	Total	Grand Total
Holcopasites	*Holcopasites pulchellus*	-	-	-	-	-	-	1	-	1	1
Hylaeus	*Hylaeus affinis*	2	-	2	-	-	-	2	-	2	4
	Hylaeus modestus	-	-	-	-	-	-	1	-	1	1
Lasioglossum	*Lasioglossum albipenne/cressonii*	11	3	14	10	4	14	12	7	19	47
	Lasioglossum imitatum	-	-	-	2	-	2	-	-	-	2
	Lasioglossum leucozonium	-	-	-	1	-	1	1	-	1	2
	Lasioglossum lineatulum	-	-	-	1	-	1	-	-	-	1
	Lasioglossum obscurum	4	-	4	1	-	1	-	-	-	5
	Lasioglossum occidentale	-	-	-	2	-	2	-	-	-	2
	Lasioglossum packeri	-	-	-	1	-	1	-	2	2	3
	Lasioglossum perpunctatum	-	-	-	1	-	1	3	-	3	4
	Lasioglossum pictum	-	-	-	-	-	-	-	1	1	1
	Lasioglossum pruinosum	4	-	4	6	1	7	23	17	40	51
	Lasioglossum semicaeruleum	52	6	58	71	3	74	34	6	40	172
	Lasioglossum smilacinae	-	-	-	2	-	2	-	-	-	2
	Lasioglossum succinipenne	-	-	-	4	-	4	2	8	10	14
	Lasioglossum trigeminum-versatum complex	2	-	2	1	-	1	6	1	7	10
	Lasioglossum viridatum group	2	-	2	7	-	7	13	-	13	22
	Lassioglossum spp.	-	-	-	-	-	-	-	2	2	2

Table B.1. Bee species and genera observed from 2017-2019 in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA (continued). Abundances categorized by grazer and survey year.

		2017			2018			2019			
Genus	Bee Species	Cattle	Sheep	Total	Cattle	Sheep	Total	Cattle	Sheep	Total	Grand Total
Megachile	*Megachile brevis*	1	-	1	2	-	2	3	1	4	7
	Megachile spp.	-	-	-	-	-	-	2	-	2	2
Melissodes	*Melissodes agilis*	-	-	-	6	-	6	1	-	1	7
	Melissodes coreopsis	-	-	-	2	-	2	-	-	-	2
	Melissodes perlusa	-	-	-	1	-	1	-	-	-	1
	Melissodes rivalis	4	-	4	1	-	1	-	-	-	5
	Melissodes subagilis	1	-	1	-	-	-	-	-	-	1
	Melissodes trinodis	1	-	1	8	-	8	1	-	1	10
	Melissodes vernoniae	-	-	-	-	-	-	1	-	1	1
	Melissodes spp.	-	-	-	1	-	1	-	-	-	1
Nomada	*Nomada vineta*	-	-	-	1	-	1	1	-	1	2
Perdita	*Perdita octomaculeta*	-	-	-	1	-	1	-	-	-	1
Pseudopanurgus	*Pseudopanurgus aestivalis*	-	-	-	-	-	-	1	-	1	1
	Pseudopanurgus renimaculatus	3	-	3	5	-	5	2	-	2	10
Triepeolus	*Triepeolus donatus*	-	-	-	1	-	1	-	-	-	1
	Triepeolus helianthin	-	1	1	1	-	1	-	-	-	2
	Triepeolus lunatus	-	-	-	-	-	-	1	-	1	1
	Triepeolus pectoralis	-	-	-	1	-	1	-	-	-	1
Surveys with flower(s) but no bees		2	133	135	26	102	128	105	130	235	498
Grand Total		138	12	150	441	9	450	267	64	331	931

Table B.2. Native bee abundances across years by grazer treatment in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA

Grazer	2017	2018	2019	Native bee Total
Cattle	95	190	206	491
Sheep	12	8	63	83
Total	107	198	269	574

Table B.3. Honeybee abundances across years by grazer treatment in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA

Grazer	2017	2018	2019	Honeybee Total
Cattle	43	251	61	355
Sheep	0	1	1	2
Total	43	252	62	357

Table B.4. Most competitive model outputs for effects of floral characteristics and year on native bee abundance in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. The top model had the lowest AICc score of 1903.12 and the next best model had a score of greater than 2 Δ AICc.

Native bee abundance models	K	Δ AICc	AICcWt	Cum.Wt
floral richness * year	9	0	0.94	0.94
floral richness + year	7	6.17	0.04	0.99
flower abundance * year	9	9.32	0.01	1
floral richness	5	11.43	0	1
flower abundance + year	7	25.93	0	1
floral abundance	5	41.11	0	1
Simpson diversity * year	9	46.43	0	1
Simpson diversity + year	7	47.01	0	1
year	6	51.38	0	1
Simpson diversity	5	64.59	0	1
null	4	74.55	0	1

Table B.5. Most competitive model outputs for effects of floral characteristics and year on native bee richness in Post-Conservation Reserve Program grasslands in southwest North Dakota, USA. The top model had the lowest AICc score of 1018.68 and the next best model had a score of greater than 2 Δ AICc..

Native bee richness models	K	Δ AICc	AICcWt	Cum.Wt
floral richness * year	9	0	0.92	0.92
floral richness + year	7	5.89	0.05	0.97
floral richness	5	6.64	0.03	1
flower abundance * year	9	17.63	0	1
flower abundance + year	7	24.81	0	1
floral abundance	5	37	0	1
year	6	48.47	0	1
Simpson diversity + year	7	48.78	0	1
Simpson diversity * year	9	48.93	0	1
Simpson diversity	5	73.1	0	1
null	4	81.04	0	1