INVESTIGATING THE INFLUENCE OF GRAZING MANAGEMENT PRACTICES ON

POLLINATORS TO INFORM BIODIVERSITY CONSERVATION IN WORKING

GRASSLAND-LANDSCAPES

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Cayla Rose Ruby Bendel

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Investigating the influence of grazing management practices on pollinators
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By

Cayla Rose Ruby Bendel

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SUPERVISORY COMMITTEE:

Torre Hovick

<small>Chair</small>

Ryan Limb

Jason Harmon

Approved:

March 31st, 2017	Francis Casey
Date	Department Chair

ABSTRACT

Declines in pollinator populations worldwide are threatening pollination that supports native plant communities and global food production. Mitigating these impacts will require conservation actions that promote biodiversity and remain practical for private producers. We investigated the influence of grazing management practices on butterfly abundance and community composition in the Sheyenne National Grasslands in the summers of 2015 and 2016. We found that management did not influence floral community composition and thus butterfly communities remained similar between practices. Individual species' abundance varied by management, with no practice optimal for all species.

We also examined relationships between floral resources and native bee-plant interactions. We found floristic resource availability influenced bees' selectivity across the growing season. Furthermore, native bee abundance was driven by availability of native flowers, whereas honey bees were attracted to dense patches of exotic resources. Overall, management which promotes spatial-temporal resource distribution can bolster ecosystem stability and promote pollinator diversity.

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Introduction

Strain on the world's ecosystems is continually intensifying to meet the growing demands

of human consumption (WWF 2014). Continual land use alterations and resource exploitation

drive global biodiversity declines which reduce an ecosystem's provision of ecological functions

and services (Butchart et al. 2010, Cardinale et al. 2013, Duncan et al. 2015). In combination

with stress of climatic changes driven by increased CO_2 emissions (IPCC 2013), ecosystems are

undergoing irrevocable losses (Noss et al. 1995, WWF 2014). Designating protected areas for

biodiversity will not be enough to mitigate these losses while sustaining the demand for natural

resources (Mora and Sale 2011). Responses to global changes will instead require a multi-faceted

approach which preserves remaining intact landscapes while reducing consumption and

increasing efficiency of production in human-dominated ecosystems (WWF 2014). As a result,

conserving biodiversity in order to bolster provision of ecological services and maintain

production in these ecosystems will be essential.

It will be crucial to develop conservation strategies for grassland working landscapes –

ecosystems managed for both biological and economic objectives (Polasky et al. 2005).

Grasslands are among the most endangered ecosystems in the United States (Noss et al. 1995).

The majority of these grasslands are privately owned and critical working landscapes that

contribute to the provision of cereal, meat, and milk production (Noss et al. 1995, Delgado

2005). Historically, grasslands were maintained by large herbivores and frequent fire (Axelrod

1985), and together these disturbances interacted to promote a landscape heterogeneous in both

vegetation composition and structure (Fuhlendorf et al. 2001). Alternatively, current grassland

management practices are aimed at maximizing grazing utility and often distribute disturbance uniformly (Briske et al. 2008, Fuhlendorf et al. 2006). This homogenous management has simplified grassland landscapes by reducing biodiversity and making them more susceptible to invasions (Briggs et al. 2002, Fuhlendorf et al. 2012, Toledo et al. 2014). As a result, declines in many grassland biota, including birds and pollinators, are documented (Allen-Wardell et al. 1998, Kearns and Inouye 1997, Sauer et al. 2014). In addition to their contribution to pollination, these biota and others contribute to ecosystem stability by enhancing overall biodiversity (Kearns and Inouye 1997, Blair 1999). While grazing and fire are essential to maintaining ecosystem function in grasslands, employing these disturbances uniformly across the landscape could be detrimental to the conservation of species like pollinators that rely on a variety of resources throughout the season.

Grassland butterflies provide a multitude of ecosystem services including pollination, biomass conversion and overall contribution to biodiversity (Blair 1999, Guppy and Shepard 2001, Rader et al. 2016). Native pollinators, including butterflies, are responsible for $3.07 billion of food production in the U.S. (Losey and Vaughn 2006), and butterflies are increasingly overlooked as non-bee pollinators (Rader et al. 2016). They also contribute to ecosystems by converting plant biomass to usable energy for higher trophic species (Guppy and Shepard 2001). Moreover, butterflies are sensitive to disturbances (Nelson 2007), and contribute to biodiversity making them useful ecological indicators. Declines in this crucial taxa raise concern both for their role in pollination, and their indication of ecosystem degradation (Blair 1999; Guppy and Shepard 2001, Rader et al. 2016). For these reasons, understanding butterfly responses to grassland management practices will not only be informative for pollinator conservation but more broadly grassland ecosystem conservation.

In grassland working landscapes, it is imperative to understand how fire and grazing disturbances affect butterfly community composition and individual abundances. The limited research that has been done demonstrates large variability in species' responses and exhibits gaps which need further exploration. For instance, restoration of grazing and fire on grasslands has been shown to both promote vegetation quality that increases butterfly abundance (Pöyry et al. 2004, Powell et al. 2007, Vogel et al. 2007), and be detrimental to some butterfly species (Swengel 1996, Swengel 1998, Powell et al. 2007). Often, responses to burning can depend on the spatial and temporal scale the disturbance is applied (Swengel 1996, Swengel 1998). In some cases, the use of disturbances is opposed because of associated larval mortality risks (Swengel and Swengel 2007, Panzer and Schwartz 2000). Population sinks can be created when females are attracted to the floral resources of previously disturbed sites for oviposition and that site is subsequently burned or grazed the following spring (Powell et al. 2007). Under these circumstances, abundance and richness are typically used as indices to assess disturbances that were applied uniformly across entire landscapes (Swengel 1998, Powell et al. 2007, Vogel et al. 2007). However, applying grazing and fire to grasslands by varying the spatial and temporal distribution would be more similar to how these disturbances occurred historically, and may be an effective way of maintaining the disturbances that are necessary for grasslands while mitigating the negative impacts on native butterfly populations.

As contributors to biodiversity and providers of pollination (Blair 1999; Guppy and Shepard 2001), butterflies are an important taxa for guiding ecosystem management. Therefore, we investigated the effects of four grazing management practices (season-long, rotational, rotational with lowland mowing, and patch-burn) on butterfly communities in the tallgrass prairie of the northern Great Plains of the United States. Previous research has contributed to our

understanding of the influence of these practices on vegetation structure, livestock production, and other wildlife (Fuhlendorf et al. 2004, Fuhlendorf et al. 2006, Limb et al. 2011, Hovick et al. 2015). However, we know relatively less about the response of vegetation composition which may be of importance to pollinators. We hypothesized grazing management practices would generate differences in floristic resource availability that would influence grassland butterfly communities. To address this hypothesis, our specific objectives were to quantify the influence of four grazing management practices on butterfly community composition, and individual species' abundances.

Methods

Site Description

We evaluated the influence of grazing management practices on butterfly community composition and species abundance in the Sheyenne National Grasslands (SNG) and Albert Ekre Grassland Preserve (AEGP) located in Richland and Ransom counties, North Dakota, USA (46.3815° N, 97.2760° W) from 2015-2016. These areas are part of the tallgrass prairie ecoregion of eastern North Dakota and are managed for cattle production and wildlife conservation. The region is characterized by sandy soils and is comprised of native grasses including big bluestem (*Andropogon gerardii*), switch grass (*Panicum virgatum)*, and prairie cord grass (*Spartina pectinata)*, but heavily invaded by Kentucky blue grass (*Poa pratensis)* and smooth brome (*Bromus inermis)*. Common native forbs include lead plant (*Amorpha canescens*), common milkweed (*Asclepias syriaca*), pasture rose (*Rosa arkansana)* and meadow anemone (*Anemone Canadensis)*. Additionally, invasive forb species such as leafy spurge (*Euphorbia esula)*, sweet clover (*Melilotus spp.)*, and white clover (*Trifolium repens)* are abundant (USDA 2008). The region has a temperate climate with cold winters and warm, dry summers with an

average annual precipitation of 52.6 cm, and average annual temps of 5.5 °C (NDAWN 2015).

The historical average monthly temperatures for the primary growing season (Jun – Aug) are

19.4, 22.2, and 21.1° C and rainfall totals are 9.8, 8.9, and 5.4 cm, respectively (NDAWN 2015).

Study Design

We selected eight pastures comprising two replicates of four grazing management

practices for use in this study. Five of the eight pastures were located in the SNG and managed

by the United States Forest Service. The remaining three were nearby in the AEGP managed by

North Dakota State University. Pastures ranged in size from 54 to 484 ha (Table A1.). Grazing

management practices included: season-long grazing (SL, *n*=2), rotational grazing (ROT, *n*=2),

rotational grazing with lowland mowing (ROT M, *n*=2), and patch-burn grazing (PBG, *n*=2).

All rotationally grazed pastures used interior fencing to separate the pasture into four

paddocks that were grazed twice throughout the growing season (May-Oct). Pastures with

lowland mowing had sedge dominated regions mowed once each summer at the discretion of the

leasee. Season-long pastures had no internal fencing and cattle were free to select areas

throughout the pasture for the entire growing season. Beginning in the spring 2015, one-third of

each patch-burn grazed pastures was burned in the dormant season. Each year a discrete patch

was burned generating a fire return interval of three years. Throughout the course of this study

however (2015-2016), only two of the three patches in each patch-burned pasture were burned.

There was no internal fencing dividing the patches within the patch-burn treatment so cattle were

free to select areas from the entire pasture throughout the growing season. All pastures were

grazed from May-October with moderate stocking rates, with a mean animal density of 0.2

cow/calf pairs per acre for the SNG pastures and 0.3 cow/calf pairs per acre for the AEGP.

Data collection

We sampled the butterfly community across the eight pastures from June-August of 2015-2016. We visited each pasture three times throughout the growing season to maximize our opportunity of detecting species with varying flight emergence and voltinism. We refer to the three sampling periods as early: June 10-June 30, mid: July 1-July 20, and late: July 21-August 10. Because we were interested in pasture level responses, each pasture had 12 randomly placed 100 m transects allocated for sampling. Twice-over rotationally grazed pastures had four paddocks, each with three transects. Patch-burn graze pastures had three patches, each with four transects, and season-long pastures had 12 transects randomly distributed throughout the pasture.

Sampling occurred between 0900- 1730 h on days with $\geq 17^{\circ}$ C temperatures and sustained winds <15 km/h. We sampled each 100 m transect for ~10 minutes walking at a pace of 10 m/minute while scanning the line in both directions for butterflies (Moranz et al. 2012). Care was taken to ensure all butterflies on the survey line were detected to meet the assumptions of distance sampling (Buckland et al. 2001). For each detection, we recorded the species and perpendicular distance from the survey line at the time it was detected. All observations were made by an individual observer who was trained to accurately estimate distances, and identify butterflies on the wing prior to the field season. We captured any butterflies that could not be identified on the wing, and specimens that were still in question were photographed for later confirmation. We also recorded the number of flowering stems by species that occurred within 2 m of the transect during each butterfly sampling round (Shepherd and Debinski 2005). This information was then used to compare resource availability across management practices and calculate forb richness and abundance.

Data analysis

We calculated butterfly abundance and richness across the study area as well as between management practices and year. We also evaluated differences in floral abundance and richness between management practices. We used these data in more complex analyses to identify relationships between butterflies and floral resources across treatments.

Community analyses

We used the 'vegan' package in program R to perform metric multidimensional (MDS) ordinations investigating relationships between management practices and both floral and butterfly community composition (R Core Team 2016). Using MDS allowed us to use the more ecologically meaningful Bray-Curtis distance metric while still quantifying the proportion of variance explained by the axes (Kindt and Coe 2005). We calculated species scores using total counts at the transect-level and excluding species with a proportional abundance of less than 5% to increase the amount of variance explained by the ordination (Legendre and Gallagher 2001). Data were pooled between years and round and we used amount of variance explained to assess the explanatory value of the ordinations. To test our hypothesis that management would generate differences in floristic and butterfly community composition, we assessed management as an environmental factor in the community analyses using the function "envfit" in the 'vegan' package with 999 permutations (Oksanen 2009). In the butterfly community analysis we also tested the factor site, and continuous vectors for individual flowering species' pooled abundance using the same methodology as above.

Individual species density estimates

We used package 'unmarked' in the statistical program R (version 3.3.1., R Core Team 2016) to estimate butterfly densities among management practices. We calculated densities for

nine species which met the threshold of 60 detections necessary for acceptable estimates (Buckland et al. 2001). This method provides an estimate of true rather than relative density by incorporating detection probabilities that account for imperfect detection, and is therefore broadly comparable across other studies that follow this methodology. The density estimates reported are generated from an integrated likelihood model and assessed using parametric bootstrapping procedures (Royle et al. 2004).

For each species, we first compared the available key functions half-normal, hazard rate, exponential, and uniform for modeling detection curves. We ranked candidate models using Akaike Information Criterion adjusted for small sample sizes (AIC_c) and we considered models with $\Delta AIC_c \leq 2$ to have the same explanatory value (Burnham and Anderson 2003). The half-normal key function was the best model for all species and was used in all models reported. Next, we generated univariate models to test the effects of management practice, site-level floral richness, transect-level floral richness, and transect-level native floral abundance on individual species' abundance. We tested for correlation between the three numeric covariates using Pearson's correlation coefficient and found no correlations greater than 0.385, thus we included all of these covariates in further analysis. Candidate models were ranked on their relative importance (AIC weight [w_i]) and were compared to a null model. We then built multivariate models for species which had more than one competitive univariate model using combinations of covariates. Models for each species that had greater relative importance than the null model and were within two AIC_c units of the best model for their respective model set were considered explanatory of species abundance (Burnham and Anderson 2003).

Results

We detected 2,578 butterflies representing 34 species from 2015-2016 (Table A2.).

Butterfly abundance increased as sampling rounds (early-middle-late) progressed in both 2015

(98-244-385) and 2016 (421-713-717, Table A2.). However, richness was highest in our middle

sampling round (July 1- July 20) in both years (Figure 1.1.). We detected twice as many

butterflies in 2016 than 2015 and detected an additional seven species in the second year. Non-

native *Colias philodice* was the most abundant species accounting for almost half of our total

detections (1027), followed by *Boloria bellona* with 332 detections and *Boloria selene* with 165
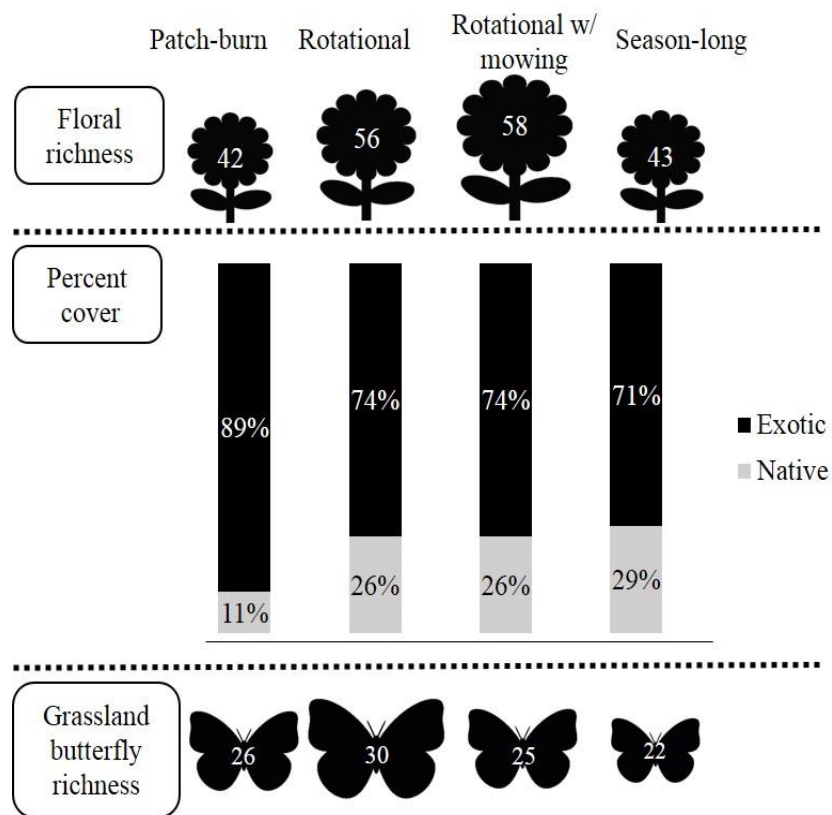
detections (Table A3.).

Figure 1.1. Summary statistics of the floral and butterfly communities. Data was collected in 2015-2016 from four different grassland management practices in the Sheyenne National Grasslands and Albert Ekre Grassland Preserve, ND, USA. Floral richness and percent native cover were not consistently associated with increased butterfly richness.

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We detected 81 different flowering plant species on the landscape, five of which were exotic. Invasions by the exotic species leafy spurge, white clover, and sweet clovers formed extensive patches in most pastures, accounting for more than 70% of floral availability in all management practices (Figure 1.1.). Overall, rotationally grazed pastures had the highest floral richness followed by patch-burn graze pastures. Although season-long pastures had the greatest proportion of native floral abundance, they had the least floral richness (Figure 1.1.). Total butterfly richness and abundance were also lowest in the season-long pastures and highest in the rotationally grazed pastures (Figure 1.1.).

Community analyses

Our floral community analysis explained 79% of the variation in three axes and management did not influence floristic community composition ($p = 0.319$, Figure 1.2.). The butterfly community analysis explained 81% of the variance in the grassland butterfly community in three axes. Neither management practice ($p = 0.604$) nor site ($p = 0.999$) were significant factors in explaining butterfly community composition. No management practice accounted for greater than 32% of variation in the butterfly community whereas four of the individual sites accounted for greater than 32% of variation, and three of these accounted for over 50% (Figure 1.3.). Of the 81 available flowering species on the landscape, only abundance of red clover (*Trifolium pratense*) ($r^2 = 0.87$, $p = 0.013$), and total abundance of exotic flowering species ($r^2 = 0.73$, $p = 0.034$) were significantly predictive of butterfly communities (Figure 1.4.). No individual butterfly species accounted for greater than 30% in the grassland butterfly community, but several species including *C. philodice* and *Danaus plexippus* were equally present throughout sites contributing to the lack of variation amongst management practices (Figure 1.3.).
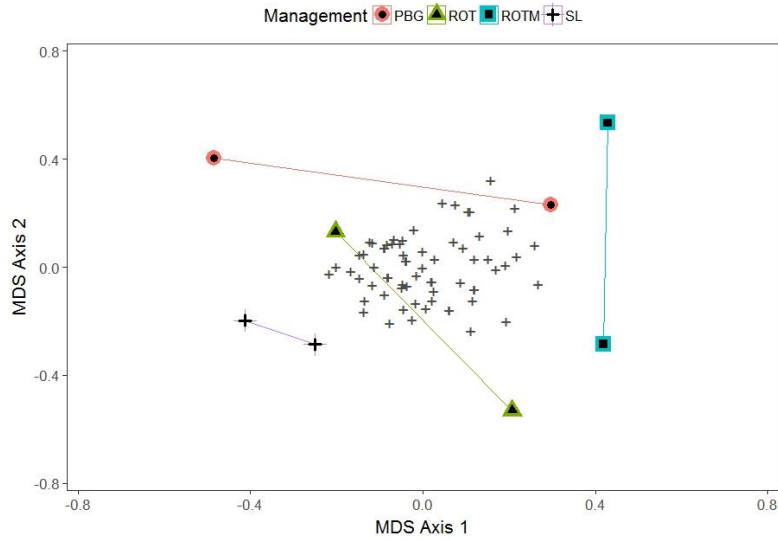
Figure 1.2. Floral community bi-plot. Results from a metric multi-dimensional scaling (MDS) analysis of the floral community between grassland management practices investigated from 2015-2016 in the Sheyenne National Grasslands, ND. Management practices are indicated by shape and color and abbrievated as follows: PBG = patch-burn grazing, ROT = rotational grazing, ROT M = rotational grazing with lowland mowing, SL = season-long grazing. Species are indicated by "+'s." The lack of separation of species by management practice indicates that management was not influencing floristic community composition.
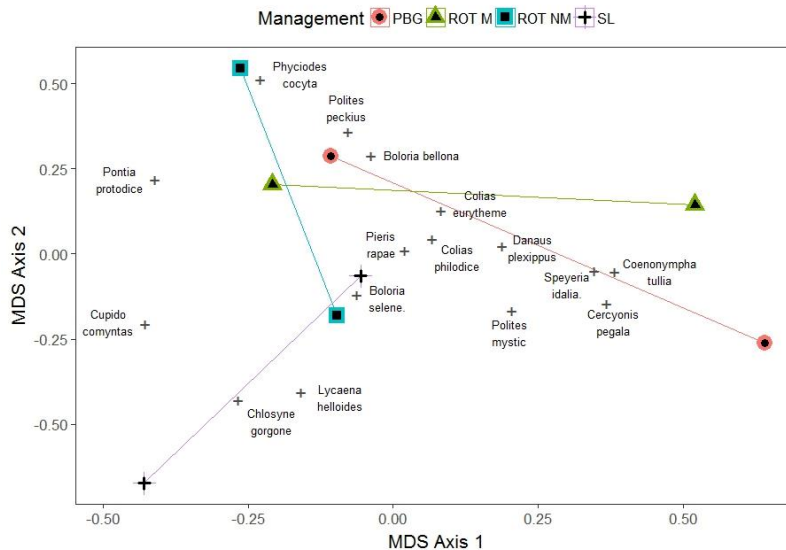
Figure 1.3. Butterfly community bi-plot with species. Results from a metric multi-dimensional scaling (MDS) analysis of the butterfly community between grassland management practices investigated from 2015-2016 in the Sheyenne National Grasslands, ND. Management practices are indicated by shape and color and abbrievated as follows: PBG = patch-burn grazing, ROT = rotational grazing, ROT M = rotational grazing with lowland mowing, SL = season-long grazing. Species are indicated by "+'s" and labelled with their scientific name. Management practice is not driving differences in butterfly community composition, but rather some species are associated with individual sites.
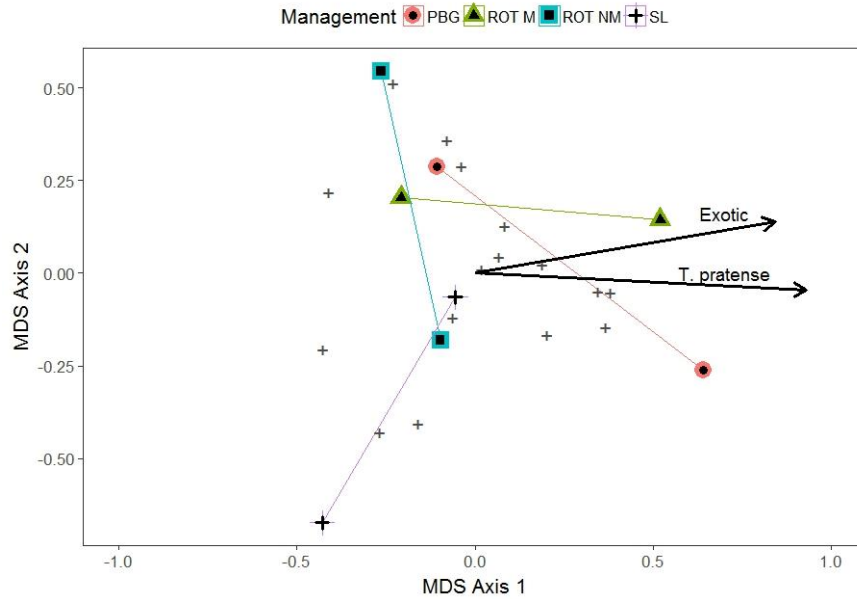
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Figure 1.4. Butterfly community analysis with vectors. Results from the metric multi-dimensional scaling (MDS) analysis of the butterfly community from Figure 3A showing significant floristic abuundance vectors. Species are indicated by "+'s" but not labeled for ease of interpretation. Exotic floral abundance and specifically abundance of red clover (*Trifolium pratense*) were significant vectors mostly assocaited with two individual sites rather than any certain management practice

Table 1.1. Grassland butterfly densities. Estimates from line-transect distance sampling conducted from 2015-2016 in the Sheyenne National Grasslands. Density estimates are presented for the nine species which met the 60 detection threshold. We investigated four different grassland management practices: rotational grazing (ROT), rotational grazing with lowland mowing (ROT M), season long grazing (SL), and patch-burn grazing (PBG). Six of nine species showed at least one significant difference in density estimates between management practices, but no single management practice resulted in the greatest densities of all species.

Scientific Name	Common Name	Detections	ROT	ROT M	SL	PBG
Boloria bellona	Meadow Fritillary	332	106.24	96.66	21.8	36.56
Boloria selene	Silver-bordered Fritillary	165	2.95	2.42	5.89	1.48
Coenonympha tullia	Common Ringlet	66	77.22	59.05	103.23	40.88
Danaus plexippus	Monarch	88	5.98	6.76	6.08	4.02
Lycaena helloides	Purplish Copper	78	41.46	37.7	10.7	150.6
Phyciodes tharos	Pearl Crescent	163	42.07	21.84	12.65	22.92
Polites mystic	Long Dash	65	92.27	285.32	122.35	101.72
Polites peckius	Peck's Skipper	121	13.84	14.1	12.18	10.89
Speyeria idalia	Regal Fritillary	69	0.23	3.91	2.54	0

Individual species density estimates

Butterfly density estimates across management practices were variable with no single management practice being optimal for all species (Table 1.1.). The highest density species included *B. Bellona, Coenonympha tullia,* and *Polites mystic*, reaching densities over 100 individuals per hectare in some management practices (Table 1.1.). The species of conservation concern *D. plexippus* and *Speyeria idalia* as well as *B. selene* occurred at the lowest densities consistently less than seven individuals per hectare (Table 1.1.). For a full list of common names see Table A3.

When comparing the effects of covariates, management was a competitive model for six of the nine species (Table 1.2.) and for all six of those species it was also the only competitive model (Table 1.2.). *B. selene* was the only species which had a competitive multivariate model that included management and site-level floral richness. For the species *Polites peckius* and *D. plexippus* floral diversity at multiple scales were explanatory models (Table 1.2.). The only species in which abundance was influenced by native floral availability was *Coenonympha tullia* (Table 1.2.).

Discussion

With demands for ecological resources increasing, global biodiversity conservation cannot be limited to isolated preserves (Mora and Sale 2011, Miller et al. 2012, WWF 2014). Working landscapes present an opportunity to sustain resource production while managing for ecosystem function and provision of services. In our investigation of how different grazing practices influenced grassland butterfly populations, we found no difference among management practices at the community level but did find differences across individual sites, suggesting that other landscape factors may be contributing to butterfly community dynamics (Debinski et al.

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2011, Moranz et al. 2012, Aguirre-Gutiérrez et al. 2015). Furthermore, we found that floristic composition did not differ between management practices and could therefore contribute to the lack of differences seen in the butterfly communities. At the specie level, management practice was a predictor of abundance for six of nine species, but no individual management practice resulted in the highest density of a majority of species. Based on the richness of butterfly species detected and comparisons to other grassland butterfly density estimates (Vogel et al. 2007, Pocewicz et al. 2009, Moranz et al. 2012), our study area is supporting a diverse suite of butterfly species. Therefore, we speculate that the diverse number of grassland management practices being used in this landscape create a rich and diverse butterfly community at larger, landscape levels.

Our community analyses did not discern clear patterns in floral or butterfly species composition between management practices. This finding is contradictory to other community studies which found that combinations of fire and grazing can generate unique butterfly community compositions (Vogel et al. 2007, Moranz et al. 2012). However, other factors can influence butterfly communities including edge to area ratio and historical land use (Davis et al. 2008, Moranz et al. 2012). There a several cases where land-use legacies were more predictive of butterfly abundance and community composition than current management practices (Debinski et al. 2011, Aguirre-Gutiérrez et al. 2015). It is also plausible that specific sites are acting as outliers (Vogel et al. 2007), and the greater amount of variation explained by several sites in our analyses supports this explanation. Differences in management practices may have been diluted by species which occurred in equal abundance in all sites, including two commonly occurring generalist species *C. philodice* and *Pieris rapae* and two rarer species of conservation concern *D. plexippus* and *S. idalia* (New et al. 1995, Swengel and Swengel 1999, Farhat et al. 2014). These

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species were not strongly associated with any one site or management practice. Largely, we

found management practices in our study did not generate unique butterfly communities but

analyses at the specie level better described responses to disturbance.

Table 1.2. Density model outputs. Model outputs for the nine grassland butterfly species meeting the minimum detection threshold for density estimation. The scores represent the models which include the covariates: management, site-level floral richness, transect-level floral richness, and native floral availability compared to a null model. Management was the most explanatory model for six of nine species. Floral richness was the best model for two species, and native floral availability was the best model for only one species.

Model	AIC_c	ΔAIC_c	*w*	K
Boloria bellona				
Management	1186.72	0	1	2
Null	1269.75	83.03	0	1
Boloria selene				
Management + Site- level floral richness	759.37	0	0.98	3
Null	784.71	25.34	0	1
Coenonympha tullia				
Native floral availability	470.32	0	0.82	2
Null	475.62	5.3	0.053	1
Danaus plexippus				
Null	695.42	0	0.498	1
Site-level floral richness	697.26	1.84	0.22	2
Transect-level floral richness	697.56	2.14	0.19	2
Management	699.38	3.96	0.097	2
Lycaena helloides				
Management	442.04	0	1	2
Null	480.72	38.68	0	1
Phyciodes tharos				
Management	692.79	0	1	2
Null	708.15	15.36	0.00033	1
Polites mystic				
Management	378.18	0	0.96	2
Null	385.42	7.24	0.98	1
Polites peckius				
Null	525.4	0	0.43	1
Transect-level floral richness	526.75	1.35	0.24	2
Site-level floral richness	527.58	2.18	0.16	2
Native floral availability	527.85	2.45	0.14	2
Speyeria idalia				
Management	426.61	0	1	2
Null	486.42	59.81	0	1

We found that management and floristic availability were the most included parameters in models explaining individual species' abundance. Because of previous correlations between floral resources and pollinator richness and abundance (Potts et al. 2003, Reeder et al. 2005, Vogel et al. 2007, Moranz et al. 2014), we had hypothesized that the grazing management practices would generate differences in floristic resource availability that would influence grassland butterfly abundance and richness. However, based on our assessment of floral resources across treatments, this was not the case. While management was a competitive model for six of nine species, it was the only competitive model for these species indicating the floral availability factors we examined were not explanatory of these differences. Therefore, some other outcome of management is driving this relationship, or a site specific land-use legacy could be responsible for differences in abundance. This lack of correlation with floral availability for most species could be because specific host-plant abundance (Curtis et al. 2015), percent litter (Davis et al. 2007, Moranz et al. 2012), or broader landscape factors such as connectivity (Davis et al. 2007) that often override finer-scale factors. For conservation purposes, it should be noted that both site and transect-level floral richness were predictive of *D. plexippus* abundance, but overall these findings merit further investigation of our understanding of both grassland butterfly resource needs and the influence of management practices on floral composition.

Exploration of species' density estimates form some associations that are supported by species' resource needs. Butterflies which had the highest densities in rotational pastures, *Phyciodes tharos, P. peckius*, and *P. mystic,* are generalist species whose larva feed on grasses and common flowers such *Asters* (Brock and Kaufman, 2003). We would expect that rotationally grazed pastures would have an abundance of grasses and reduced forb community composition (Brikse et al. 2008). Similarly, *C. tullia* prefers moist meadows and larva feed primarily on

grasses. This species was most abundant in season-long pastures which had the lowest floral

abundance and richness. Moreover, *Lycaena helloides* had the highest densities in patch-burn

grazed pastures (Table 1, Figure 3), and are known to prefer disturbed habitats (Brock and

Kaufman 2003). The fritillaries *B. bellona,* and petitioned endangered species *S. idalia*, were

highest in rotational pastures consistent with studies which show their sensitivity to fire (Powell

et al. 2007, Moranz et al. 2014). However, these studies also acknowledge the ability of fire to

increase abundance of nectar sources and facilitate recolonization of burned pastures. Similar

relationships between butterfly abundance and food or host plant availability have been observed

other studies as well (Curtis et al. 2015, Fischer et al. 2015). For individual species

conservation, as well as maintaining a diverse butterfly community at the landscape level, these

associations should be taken into account.

In comparison to other studies which report grassland butterfly densities, our study of the

SNG and AEGP show some stark contrasts. Our second most abundant butterfly was *B. bellona*

at 332 total observations and densities up to 100 ind./ha. This is much greater than the 25

detections from grassland landscapes in Iowa (Moranz et al. 2012), and only one detection

equaling 0.2 ind./ha from remnant prairies in Iowa (Vogel et al. 2007). Similarly, we detected

121 total *P. peckius* which averaged 12 ind./ha in our study but were only observed 5 times in

grassland landscapes (Moranz et al. 2012), and averaged 13 ind./ha in remnant prairies (Vogel et

al. 2007). This suggests our study area is currently providing the resources to support abundant

populations of these species. Our *D. plexippus*, density estimates are comparable to the studies

mentioned but it is notable that we detected much fewer in 2016 than 2015. However, for the

other species of conservation concern *S. idalia*, our detections and density estimates are much

lower, with density confidence intervals overlapping 0 ind./ha in some management practices in

contrast to 20 ind./ha (Moranz et al. 2012), and up to 50 ind./ha (Vogel et al. 2007). This could

be a reflection of the declining trend of this species, but it is also possible that grazing depleted

the resources *S. idalia* depends on (Moranz et al. 2014). If this were the case, The SNG and

AEGP could be better managed for *S. idalia* by incorporating areas which are burned and not

grazed (Moranz et al. 2014). Regardless, research which contributes to our understanding of

relationships between management practices and these valuable species, followed by

implementation of said practices, is imperative for effective conservation.

We further speculate that historic management on our sites may have superseded the

current management practices. We were unable to obtain knowledge of private leasee's long-

term practices on sites but this may have been a good metric to better delineate butterfly

communities. Our patch-burn grazed pastures were located in the AEGP and were historically

heavily sprayed for *E. esula* with broad-leaf herbicide. This herbicide application could have

negative effects on non-target forbs if intervals were too frequent or the herbicide persists in the

soil (Crone et al. 2009). Nevertheless, invasions by *E. esula* and *Melilotus spp.* continue to

dominate pastures located in the AEGP and SNG. These exotic invasions could be contributing

to the butterfly responses we observed by thwarting the influence of current management and

instead emphasizing individual pastures with diverse floristic patches void of extensive

invasions.

We acknowledge there are aspects of the study design that may have contributed to our

findings. Patch-burn grazed pastures included in this study only had two years of burns

conducted, whereas the desired contrast between patches in these pastures will most likely take

several years to develop (Moranz et al. 2012, Moranz et al. 2014). Positive pollinator responses

to burning, including increased *S. idalia* density, are often found two years post-fire and beyond

(Swengel 1996, Potts et al. 2003, Moranz et al. 2014). Further development of these pastures may influence butterfly community composition differently as the treatment persists. Statistical differences could also have been made more powerful by increasing management replication but logistic barriers limited our study. Finally, it is possible that the similarity seen in butterfly community composition was a result of butterflies making use of the larger landscape to key in on patches of available resources. This pattern of smaller pastures containing subsets of species of the richer surrounding landscape was found in Sweden with butterfly communities in semi-natural grasslands (Öckinger and Smith 2006). Nevertheless, this supports our recommendation for promoting diverse management regimes at the landscape scale.

In order to guide practical butterfly conservation, we investigated the influence of grassland management practices on butterfly communities and species' abundance in grassland working landscapes. We had hypothesized that management practices would generate differences in floristic resources that would be predictive of butterfly community composition and species' abundance. However, we found that management practices did not support unique floristic communities, and therefore were not driving differences in grassland butterflies at the community level. Instead, our individual density estimates showed that management was predictive of species abundance, but no single management practice resulted in the highest densities of all grassland butterfly species. Thus, despite concerns of butterflies' sensitivity to fire and grazing (Swengel 1996, Swengel 1998), these disturbances could be necessary to maintaining a diverse butterfly community at the landscape scale. We therefore contend that by employing a mosaic of management practices at the landscape level, working landscapes can promote butterfly diversity by generating shifts in species' abundance within communities. While a diversity of management practices has been previously recommended for pollinator

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conservation (Vogel et al. 2007, Fahrig et al. 2011), our study provides quantitative evidence of the influence of management practices in a working landscape that is also managed for cattle production. Further investigation of management which can enhance butterfly conservation is inarguably needed, but it is evident that conservation and production are simultaneously being achieved in grasslands managed with both fire and grazing. In order to be practical and effective, solutions for conserving biodiversity will need to comprise the use of ecological resources while upholding the biological integrity of the landscape.

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DENSITY VS. DIVERSITY: HONEY BEES RESPOND TO RESOURCE DENSITY

WHEREAS AVAILABILITY OF NATIVE FLOWERS PROMOTES BEE DIVERSITY

Introduction

Human-induced global change has evoked irreversible effects on the world's ecosystems

(Cardinale et al. 2012, Solomon et al. 2009). Dramatic declines in biodiversity may be the most

prominent of these effects (WWF 2014). Biodiversity, includes variation of not only species, but

also genes, functional traits, and interactions (Cardinale et al. 2012), which are fundamental to

maintaining the stability of ecosystems and production of ecosystem services (Hammond 1995).

Declines in biodiversity decreases the ability of an ecosystem to provide services such as clean

water, soil retention, and pollination (Cardinale et al. 2012, De Groot et al. 2002). Biodiversity

conservation will thus be critical to restoring the state of these systems and the services society

relies on.

Pollination is one of the most economically valuable ecosystem services, but the

pollinators sustaining ecosystem stability and agricultural production are endangered (Kearns et

al. 1998). Pollination has significant economic value as bees are responsible for pollinating two-

thirds of the world's crops (Williams et al. 2010). While much of the pollination can be

attributed to European honey bees (*Apis mellifera*) (Morse and Calderone 2000), native

pollinators, mostly native bees, are responsible for an estimated $3.07 billion of food production

in the United States (Losey and Vaughn 2006). Pollinators also play a key role in maintaining

biotic communities by providing pollination services to plant populations and facilitating gene

flow (Potts et al. 2010). With dramatic declines in pollinators being recognized globally (Kearns

and Inouye 1997, Kearns et al. 1998), understanding how to maintain plant-pollinator

interactions is becoming increasingly important for both crop production and native plant management (Allen-Wardell et al. 1998).

One goal of ecosystem conservation should be promoting pollinator diversity. Increased bee diversity has been positively correlated with pollination services to plants and can bolster ecosystem stability (Potts et al. 2010, Orford et al. 2016). Conserving native bees will be an important part of promoting pollinator diversity. Native bees have evolved interacting with native plants in the biomes in which they occur (Kearns and Inouye 1997, Kearns et al. 1998), whereas honey bees are commonly used for agricultural purposes in foreign landscapes and therefore lack an evolutionary history with the native flora in these systems (Huryn 1997). Thus, honey bees have not developed the same mutualistic relationships with these plants. While honey bees can be effective pollinators of some plants (Huryn 1997), a diverse community of bees is required to maximize productivity within a landscape (Kearns and Inouye 1997, Kearns et al. 1998). However, it is also important to expand considerations for diversity beyond species richness. Functional trait diversity has been positively correlated with fruit sets of worldwide crops (Garibaldi et al. 2015), and plant-pollinator interactions play a key role in maintaining the stability of ecosystems (Kearns et al. 1998, Ashman et al. 2004). Whether due to competition, phenological changes, or other factors, these species interactions can become eliminated before the individual species involved become extinct (Santamaría et al. 2015). Therefore, the diversity of pollinators and their interactions with plants should be a primary goal of pollinator conservation efforts (Carman and Jenkins 2016).

Much of recent pollinator research focused only on managed honey bees (*Apis mellifera*) (Aizen et al. 2009, Pettis et al. 2010, Mogren et al. 2016, Smart et al. 2016), which then drives policy initiatives that can have indirect negative consequences on other bee species (Colla and

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MacIvor 2016). Recently, evidence of honey bees impacting native bees includes reduced bumblebee density when honey bee hives are added (Herbertsson et al. 2016), and negative correlations between honey bee and bumblebee populations (Thomson et al. 2016). Therefore, management strategies that are beneficial to the non-native honey bee may not necessarily promote native bee populations. While it is inarguable that honey bees are effective pollinators of certain monoculture crops, maintaining diverse native bee communities has been shown to benefit agriculture (Klein et al. 2003, Garibaldi et al. 2015, Orford et al. 2016) while simultaneously promoting biodiversity that sustains ecosystem stability, and native plant communities (Kearns 1998, Ashman et al. 2004). Conservation initiatives should therefore focus on bolstering diverse bee communities rather than any one species.

Vegetation diversity may be an important element in the conservation of pollinator diversity (Fahrig et al. 2011). Multiple plant communities within a landscape have been found to enhance pollination services (Potts et al. 2006), and the number of land cover types in an area can be a significant predictor of butterfly richness (Kerr 2001). Restoring natural processes such as fire and grazing are effective ways to achieve plant community heterogeneity and potentially pollinator diversity (Moranz et al. 2012, McGranahan et al. 2016). However, responses to disturbances can vary greatly by species and taxon. For example, a global review of fire effects on bees found that traits such as nesting strategies elicited variable response by species (Williams et al. 2010). Moreover, butterflies and bees, both valuable native pollinators, had little similarity in their responses to management practices across tallgrass prairie remnants in Iowa (Davis et al. 2008). Collectively, this suggests that meeting the needs of a diverse assemblage of pollinators requires a need for a diversity of management regimes that promote heterogeneity across the landscape.

Our study examined plant-pollinator interactions in working grassland-landscapes managed with a combination of disturbances including grazing, mowing and prescribed fire. These are common practices applied by private ranchers and grassland managers in the region. Specifically our objectives were to determine the influence of resource availability on plant-pollinator interaction networks in working grassland-landscapes, and quantify the relationship between floral availability and native bee abundance. We hypothesized that resource availability would promote increased specialization of plant-pollinator interactions and an increase in native bee abundance. This information will be important for land managers and scientists to achieve native bee conservation in working landscapes.

Methods

Site Description

From 2015-2016 we evaluated the influence of floral availability on pollinator communities and resource use in the Sheyenne National Grasslands (SNG) and Albert Ekre Grassland Preserve (AEGP) located in Richland and Ransom counties, North Dakota, USA (general GPS coordinates). The grasslands are in the tallgrass prairie region which is characterized by sandy soils and is comprised of native grasses such as big bluestem (*Andropogon gerardii*), switch grass (*Panicum virgatum)*, and prairie cord grass (*Spartina pectinata)*, but heavily invaded by Kentucky blue grass (*Poa pratensis)* and smooth brome (*Bromus inermis)*. Common native forbs include lead plant (*Amorpha canescens*), common milkweed (*Asclepias syriaca*), pasture rose (*Rosa arkansana)* and meadow anemone (*Anemone Canadensis)*. Additionally, invasive species such as leafy spurge (*Euphorbia esula)*, sweet clover (*Melilotus spp.)*, and white clover (*Trifolium repens)* are abundant (USDA 2008). The region has

a temperate climate with cold winters and warm, dry summers. The average annual precipitation

is 52.6 cm, and average annual temps are 5.5 $^\circ$ C (NDAWN 2015). The historical average

temperatures for the growing season (Jun-Aug) are 19.4, 22.2, and 21.1 $^\circ$ C and rainfall totals are

9.8, 8.9, and 5.4 cm respectively (NDAWN 2015). SNG is managed with a combination of fire,

mowing, and grazing leases (USDA 2008).

We selected eight pastures comprising a variety of grazing management practices for use

in this study. Five of the eight pastures were located in the Sheyenne National Grasslands and

managed by the United States Forest Service. The remaining three (EPSW, EPNE, ER) were

nearby in the AEGP managed by North Dakota State University. Pastures ranged in size from 54

to 484 ha. Grazing management practices included season-long grazing, rotational grazing,

lowland mowing, prescribed fire, and some herbicide use. Knowledge of precise stocking rates

and historical land use is limited because of private lessee management of these lands.

Data collection

Floral visitor surveys

We sampled the bee community from June to August of 2015-2016 across three sampling

rounds per year (June 10-June 30, July 1-July 20, July 21-August 10). We used 24, 25 m

transects that were randomly distributed within each pasture for a total of 192 floral-visitor

transects. Sampling occurred between 900 h- 1730 h on calm, sunny days with temperatures $\geq$

17° C and sustained winds < 15 km/h (Popic et al. 2013, Moranz et al. 2012). We sampled each

floral-visitor transect for eight minutes attempting to collect all flower visitors within 1 m of the

transect on either side. Handling time was not included in the eight minutes. Every specimen was

collected, so we were able to move forward and backward on the transect without double

sampling. For the focus of this study, we targeted bees while collecting, but used post-sampling identification in the lab to refine our analysis to exclusively bees.

In order to identify specific bee-flower interactions, we collected floral-visitors using a standard 1 m aerial insect net with a 40 cm diameter bag. After netting insects, we transferred them to a 50 mL plastic collecting tube with approximately 5 mL of ammonium carbonate in the bottom to euthanize individuals. We only collected floral-visitors touching the reproductive parts of a flower. Actively collecting floral-visitors from individual flowers provides information about plant-pollinator interactions and more accurately reflects use of a resource (Popic et al. 2013). We also recorded the associated flower species each specimen(s) was collected from, and this information was stored with the euthanized specimens in a 5 dram plastic tube. During each floral-visitor sampling round, we recorded the number and species of flowering stems within 2 m of each 25 m transect to make correlations between plants and pollinators. This information was also necessary to calculate selectiveness of resources by species among available resources over time, and among management practices.

Bee identification

We prepared specimens for identification by pinning them in a Cornell pinning tray with #2 stainless steel pins at the end of each sampling day. They were stored in plastic bags indoors at room temperature for the remainder of the field season which helped prevent specimens from being parasitized. We assigned each specimen a unique identification code that related them to the flower, transect, pasture, and date they were collected on. At the end of the field season, we used UNITRON © Z10 Stereo microscopes and the key *The Bee Genera of North and Central America* to identify specimens down to the lowest taxonomical class practical (Michener et al.

1994). We additionally sought assistance from entomologists and reference collections at USGS

Northern Prairie Wildlife Research Center.

Data Analysis

Bee and floral richness

To see broad patterns between floral availability and the bee community, we calculated

floral and bee richness among sampling rounds (Early-Late). We used the function *c2cv* in the R

package 'rich' to determine statistical differences in bee richness between rounds by means of

randomization (Rossi 2011). We also compared this richness data to the plant-pollinator

networks in each sampling round to determine the influence of resource availability on these

interactions

Network analyses

Ecological networks encompass the interactions of species within an ecosystem and the

direct and indirect links between them and thereby aid in assessing the stability of an ecosystem

(Montoya et al. 2006). We evaluated plant-pollinator interactions across the growing season by

calculating the species-level specialization index (*d'*) for each bee species. In a bee (columns) by

plant (rows) matrix, let p'_{ij} be the proportion of the frequency of interactions between a plant ($_j$)

and bee species ($_i$) in respect to the total interactions of that plant species (row total). Let q_j be

the availability of that plant species. Thus the specialization index d_i calculates the distribution of

a bees' interactions in comparison to the availability of those plants (Blüthgen et al. 2006).

$$d_i = \sum_{j=1}^{c} \left(p'_{ij} \cdot \ln \frac{p'_{ij}}{q_j} \right)$$

We present the normalized index *d'* which ranges from 0, indicating a bee equally used

all resources relative to their availability, to 1, indicating a bee used only one resource (Blüthgen

et al. 2006). Thus d' can be interpreted as how much a bee species deviated from one of these extremes (Blüthgen et al. 2006). Previous analyses of plant-pollinator interactions used the number of partnerships that existed in a network as a response variable, however this only evaluates whether or not a relationship is present in a community (Blüthgen et al. 2006). The index d' accounts for the proportional use of a resource relative to its abundance and can therefore assess the selectivity of a species (Blüthgen et al. 2006).

We also calculated the quantitative network-level index H_2, similar to the species-level index d, H_2 assesses the specialization at the network level. In a bee (columns) by plant (rows) matrix, let p_{ij} be the proportion of the frequency of interactions between a plant (j) and bee species (i) in respect to the total number of interactions (sum of rows and columns) in the network (Blüthgen et al. 2006).

$$H_2 = - \sum_{i=1}^{r} \sum_{j=1}^{c} \left(p_{ij} \cdot \ln p_{ij} \right)$$

We present the standardized index H_2' which again ranges from 0 (most generalized) to 1 (most specialized) network (Blüthgen et al. 2006). The index also allows us to evaluate nestedness where 0 represents a perfectly nested network (e.g. each bee species visits a subset of flower species of the most generalized bee), and 1 is the greatest deviation from this nested assemblage (e.g. each bee species has a mutually-exclusive interaction with a flower species) (Blüthgen et al. 2008, Hülsmann et al. 2015). The index H_2' gives us a more valuable biological analysis of the pollinator networks. We generated these specialization indices as well as plotted the networks to visually evaluate differences in networks across the growing season. These analyses were conducted in the package 'bipartite' in R (version 3.3.1., R Core Team 2016).

<u>Linear regressions</u>

To quantify relationships between floral availability and bee abundance we conducted generalized linear mixed-effect regressions in 'lme4' package in R (version 3.3.1., R Core Team 2016). Regressions were conducted using transect-level data that included site as a mixed effect. We investigated relationships between bee abundance and density of floral resources as well as the availability of native vs. exotic flowering plants. We analyzed responses between native bees and honey bees separately in order to disclose differences in resource use that inform native bee conservation.

Results

Bee and floral richness

We collected 1,111 bee specimens from the summers of 2015-2016. In total, 68 unique bee species were identified. The most abundant species was the *Apis mellifera* (European honey bee) which comprised 647 of the total specimens. The second most abundant species was *Lasioglossum perpunctatum* (sweat bee; $n = 43$), and we made 35 observations of *Bombus griseocollis* (Brown-belted bumblebee). Overall, bee abundance was greatest in the first round of sampling, but bee richness was the highest in the last round of sampling (Table 2.1., Figure 2.1.), but the only significant difference in bee richness was between the first and last rounds ($p = 0.005$, $n = 999$ permutations).

We detected 82 different flowering plant species on the landscape, 5 of which were exotic. We found that invasion by exotic species such as leafy spurge, white clover, and sweet clover formed extensive patches in most pastures and accounted for 85% of the total number of flowering stems. Overall, floral abundance was on average highest in the first round, but floral richness was highest in the second round of sampling (Table 2.1., Figure 2.1.).

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Table 2.1. Total flowering stems, bee abundance, and bee richness. Data are presented by sampling round and year collected at the Sheyenne National Grassland, ND from 2015-2016. Abundance peaked early but was mainly driven by exotic species whereas richness peaked later in the growing season.

	Floral		Bee	
	Abundance	*Richness*	*Abundance*	*Richness*
(June 10- June 30)	42405	24	100	18
(July 1- July 20)	60133	42	180	12
(July 21- August 10)	50185	36	162	25
2015 Total	152723	82*	442	36*
(June 10- June 30)	62697	31	294	25
(July 1- July 20)	36391	37	204	23
(July 21- August 10)	12382	36	171	31
2016 Total	111470	82*	669	49*

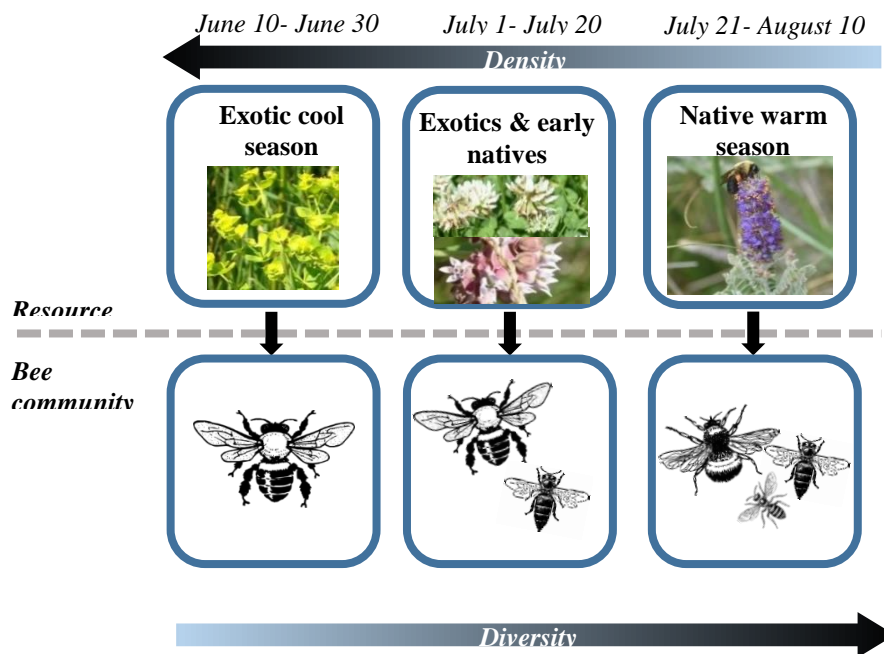* Total richness values are the sum of unique species found that year

Figure 2.1. Density vs. diversity. A landscape-level schematic representing relationships between floral resources and bee communities in the Sheyenne National Grasslands throughout the growing season. Early in the year, total bee and flower abundance were at their highest due to exotic species which form large, dense resource patches that attract almost exclusively honey bees. As the summer progressed, floral richness was at its highest as both natives and exotics were in bloom but bee richness was low. At the end of the growing season, bee richness greatly increased. During this period exotics had finished blooming and a diverse assemblage of native warm season flowers were in bloom. While floral density attracts an abundance of honey bees in the early summer, the availability of diverse native resources found in the last round promoted pollinator diversity.

Network analyses

From 2015-2016 we detected 215 unique plant-pollinator interactions, bees made use of only 39 species of the 82 available flowering plants on the landscape throughout the summer (Figure 2.2.). The most frequently used native floral species were Flodman's thistle (*Cirsium flodmanii*), lead plant (*Amorpha Canescens*), and Missouri goldenrod (*Solidago missouriensis*). Honey bees were disproportionately represented in the network and were highly specialized on leafy spurge and white clover in the beginning of the summer (Figure 2.2.) and transitioned to use of the exotic flowers white and yellow sweet clover during the second sampling round. As summer plant phenology progressed and native warm-season floral species became available, native bee richness greatly increased and the proportional abundance of honey bees decreased (Figure 2.2.).

We found that at the species-level, specialization indices (*d'*) varied across the growing season (Table 2.2.). We were able to identify trends across the growing season for 27 bee species, 11 species decreased specialization across the season, 11 species fluctuated, and five species increased specialization (Table 2.2.). Our most abundant native species, *Bombus bimaculatus, B. griseocollis, Colletes aberrans, Halictus confusus, Halictus ligatus, Lasioglossum pectorale,* and *L. perpunctatum,* increased specialization from the first to second round, but were then less specialized again in the last round of sampling (Table 2.2.). At the network level, specialization (H_2') also followed this fluctuating pattern with the highest specialization occurring in the middle of the summer, representing the most exclusiveness in interactions between the three plant-pollinator networks (Blüthgen et al. 2008, Figure 2.2.).
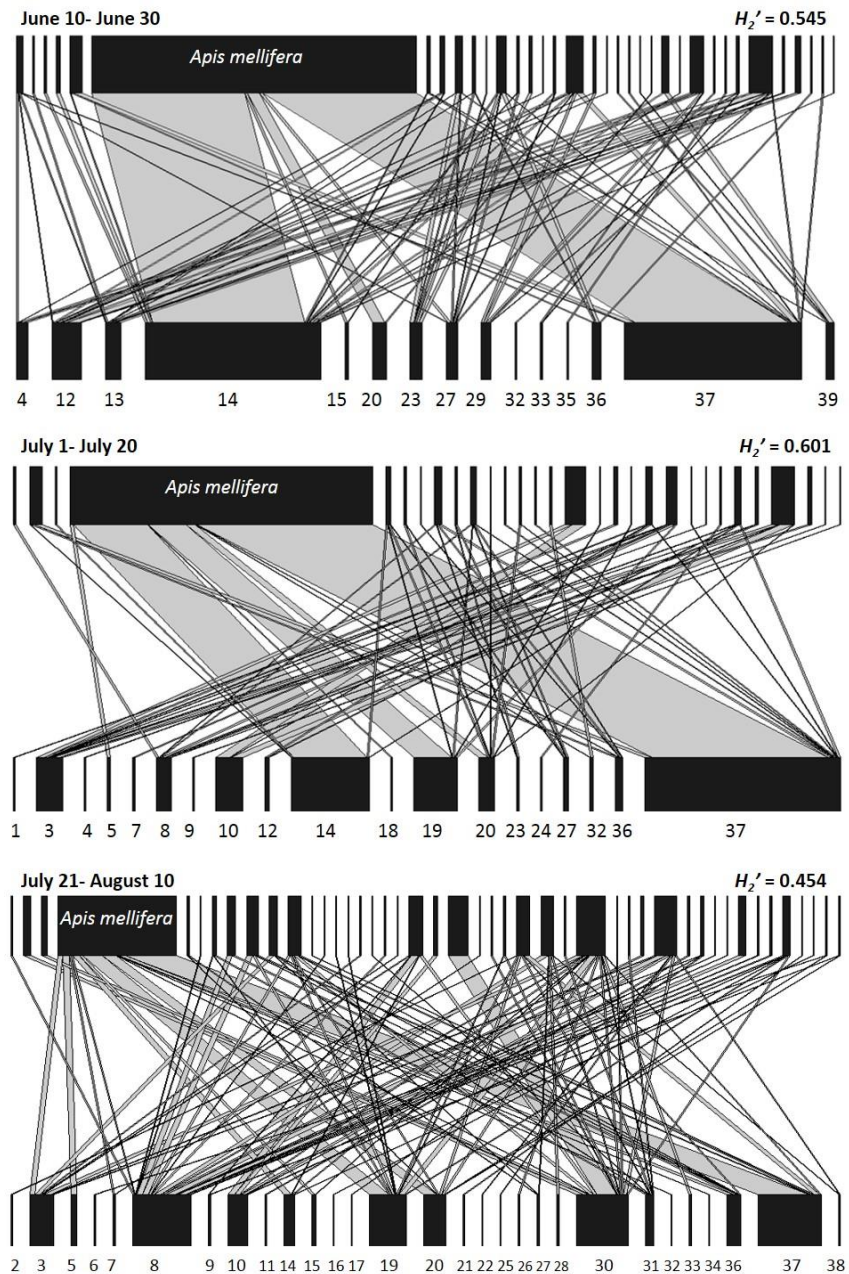
Figure 2.2. Plant-pollinator networks. Plotted interaction networks from bees sampled in 2015-2016 in the Sheyenne National Grasslands. The top bars represent all bee species and bottom bars represent individual flowers species. Two species are connected by a bar if an interaction occurred (i.e., the bee was collected from that flower). For ease of interpretation, only honey bee (*Apis mellifera*) is labelled. This exotic bee species is disproportionately represented in the networks, notably in the beginning of the growing season. The networks are plotted for each sampling round and indicate increased network interactions, nestedness (indicated by the lower H_2' specialization index), and overall complexity.

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Table 2.2. Species specialization indices. The species-level specialization index (d') for bee species collected from 2015-2016 in the Sheyenne National Grasslands and Albert Ekre Grassland Preserve. The index compares the division of floristic resource use by a bee to the availability of that resource, it ranges from 0 (most generalized selection) to 1 (most specialized selection). We calculated this index by round for each species that was present in more than one round. We reveal whether species' were increasing (↑), decreasing (↓), or fluctuating (↑↓, ↓↑) specialization across the growing season. If a species was not detected in a round, we were not able to calculate an index (-).

Bee species	Species-level specialization index (d')			Trend
	June 10- June 30	July 1- July 20	July 21-August 10	
Agapostemon angelicus	0.26	-	0.02	↓
Andrena wilkella	0.17	0.22	-	↑
Apis mellifera	0.61	0.66	0.55	↑↓
Augochloropsis sumptuosa	0.29	0.29	0.49	↑
Bombus bimaculatus	0.43	0.57	0.34	↑↓
Bombus borealis	0.50	0.62	0.40	↑↓
Bombus fervidus	0.54	0.25	0.19	↓
Bombus griseocollis	0.52	0.78	0.51	↑↓
Bombus huntii	-	0.49	0.00*	↓
Bombus ternarius	0.28	0.17	0.24	↓↑
Bombus vagans	0.73	0.00*	0.49	↓↑
Ceratina dupla	0.36	-	0.18	↓
Colletes aberrans	-	0.69	0.60	↓
Colletes americanus	0.28	0.29	-	↑
Colletes spp.	-	0.91	0.46	↓
Epeolus spp.	-	0.49	0.05	↓
Halictus confusus	0.11	0.37	0.29	↑↓
Halictus ligatus	0.56	0.60	0.46	↑↓
Hoplitis pilosifrons	0.61	0.00*	-	↓
Hoplitis truncata	0.00*	0.39	-	↑
Hylaeus affinis	0.61	-	0.49	↓
Hylaeus mesillae	0.54	1*	-	↑
Lasioglossum paraforbesii	0.42	-	0.49	↓
Lasioglossum pectorale	0.45	0.48	0.27	↑↓
Lasioglossum perpunctatum	0.42	0.60	0.34	↑↓
Lasioglossum pictum	0.61	0.54	1.00*	↓↑
Lasioglossum spp.	0.55	0.37	0.23	↓
Melissodes communis	-	0.50	0.02	↓

Linear regressions

We found that honey bee abundance increased with total floral density ($p < 0.001$, $r^2 =$ 0.474), but native bee abundance did not follow this relationship ($p = 0.494$, Figure 2.3.). We then broke down the floral community into exotic and native resources and tested correlations with bee abundance and found that as native floral abundance increased, native bee abundance also increased ($p = 0.0093$, $r^2 = 0.05$). We found a similar relationship between and exotic resources and honey bee abundance ($p < 0.001$, $r^2 = 0.538$). No correlations were found between native bees and exotic flowers or honey bees and native flowers ($p>0.05$).
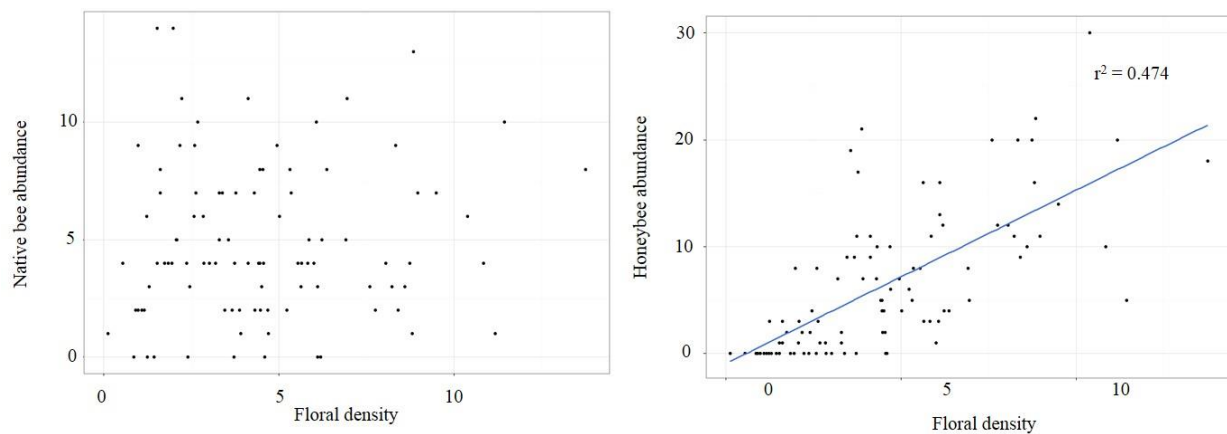
Figure 2.3. Bee response to floral density. Mixed-effect linear regressions that compare relationships between bee abundance and resource availability in the Sheyenne National Grasslands from 2015-2016. As floral density increased at the transect level, honey bee abundance increased, indicating a response to dense patches of resources. Native bee abundance showed no response to floral density, suggesting that native bees are not responding at this scale.

Discussion

Ecosystem degradation coupled with homogenous management that is practiced on many remaining landscapes has led to declines in the world's biodiversity (Cardinale et al. 2012, Briske et al. 2008, WWF 2014). As a result, provision of necessary ecosystem services such as pollination, are imperiled (Kearns and Inouye 1997, Kearns et al. 1998, Potts et al. 2010). Reconciling production and conservation of biodiversity is crucial to effective ecosystem management. To address this, we investigated interactions between plants and pollinators in grassland working landscapes and found resource availability was influencing the specialization of native bees within plant-pollinator networks at the species-level. At the network-level, floristic resource availability resulted in the increased specialization seen in the middle of the summer, and decreased floral richness may have contributed to the limited specialization in the first and final rounds of sampling. At the end of the summer, we saw a decrease in honey bee dominance and the greatest bee richness resulting in the most complex plant-pollinator network. These relationships between resources and bee specialization are corroborated by our findings that native bee abundance was being driven by the availability of native floral resources. Our results are similar to other studies that have reported bottom-up effect of resource diversity on pollinators in grazed systems (Orford et al. 2016). Together these results suggest that honey bees and native bees are using resources across the landscape differentially, resulting in changes in the pollinator community across the growing season. By implementing management practices that promote diverse floral resources throughout the entire growing season, grassland working landscapes can simultaneously support livestock production and native pollinator communities.

At the species-level, floristic resource availability influenced bees' selectivity across the growing season. The most common pattern was increased specialization from the first to second

round of sampling, with a decrease again in the last round of sampling (i.e. species were most selective in the middle of the growing season). In theory, a species would decrease specialization (i.e. become less selective) in a landscape with limited resources (Fontaine et al. 2008). This is because low diversity landscapes may not offer species' preferred resources, thus they are forced to broaden their diet (Fontaine et al. 2008). We propose this may have accounted for the lower specialization indices seen in the beginning of the season when floral richness was at its lowest. Then when floral richness was at its highest in the middle of the growing season, we saw increases in specialization. Therefore, management practices which promote temporally diverse resources could effectively mitigate this impact on bee selectivity.

It is also possible that decreases in specialization by bee species could be stimulated by increased displacement or competition (Fontaine et al. 2008). With the increase in total bee richness at the end of the growing season, displacement could have contributed to the decreased specialization of many species (Fontaine et al. 2008). Furthermore, low specialization in the first round may have been driven by bees avoiding honey bee dominated resources in combination with the overall lack of floral diversity. To evade competition with honey bees, this same shift in interactions was seen in species with similar functional traits to the honey bee (Montero-Castaño and Vilà 2016). This avoidance behavior could then lead to decreases in native bee abundance in the presence of honey bee colonies (Thomson et al. 2016). However, we observed other patterns in specialization across the growing season as well, including a consistent increase in specie-level specialization, and consistent decrease. This variability in specialization patterns is most likely a result of niche partitioning in response to the availability of individual species' resource needs across the summer (Samnegård et al. 2015, Venjakob et al. 2016). Overall, pollinator

conservation initiatives can moderate any competition by broadening their focus from just one species (e.g. honey bees), to bolstering diverse bee communities.

When we incorporate patterns between all species at the broader network level, we observed a consistent pattern to the species-level indices. The least specialized and most nested plant-pollinator network occurred at the end of the summer, whereas the most specialized network occurred in the middle of the summer. Due to the dominance honey bees have on plant pollinator networks (Carman and Jenkins 2016), and their abundance in our sampling, we can again make connections between network-level specialization patterns and availability of resources. In the middle of the summer, the most mutually exclusive plant-pollinator interactions were occurring (Blüthgen et al. 2008). Floral richness was the highest during this sampling period and species could be more selective (Fontaine et al. 2008). In the final round of sampling, we saw that specialization decreased as the network became more nested (Blüthgen et al. 2008). Honey bees became less abundant and expanded their diet breadth in this final round and we saw an increase in bee richness. While richness can be a biased response representing presence of species but unsuccessful foraging (Carman and Jenkins 2016), the increase in interactions and complexity of the plant-pollinator network seen at the end of the summer suggests this is not the case. Overall, plant-pollinator networks had the greatest specialization in the middle of the summer as high floristic resource availability mitigated potential for displacement, but networks were the most complex and the bee community most diverse at the end of the summer.

Regressions analyses investigating floristic availability and bee abundance complement our network analyses but reveal that honey bees and native bees are responding to different resources. We found that honey bee abundance increased with floral density, specifically exotic floral resources. It is common for *Apis* species to focus on abundant and dense resources,

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whereas solitary bee species favor floral richness (Ebeling et al. 2011, Thomson et al. 2016).

Thus, it is unsurprising that honey bees focused on leafy spurge and sweet clover, which form in

dense patches on the landscape (Lym and Kirby 1987, Wolf et al. 2003). Conversely, native bee

abundance showed a significant relationship with native floral abundance. Though this

relationship wasn't as strong, this is likely attributed to partitioning of specific floral resources

among these bees (Venjakob et al. 2016), and the overall increase in bee richness and

specialization in response to native floral availability found in the network analyses supports this

relationship. While an Iowa study found that floral richness alone did not lead to increased

nutritional status of bees, they hypothesized native bees could be attracted to a high abundance of

resources, only to find that they were flowers with low nutritional value (Smith et al. 2016).

Thus, exotic flowers have the capacity to attract native bees to an area, but it is the availability of

native resources which we found to influence their abundance.

Overall, both floral resource availability and the non-native honey bee are influencing

plant-pollinator networks and native bee communities in working grassland landscapes.

Specifically, honey bee abundance could be contributing to indirect competition for the few

floristic resources available in the beginning of the summer, generating decreased specialization

in pollinators at the species and network levels. This research took place in North Dakota, which

is the leading state for honey production and has the most commercial honey bee colonies in the

country (USDA 2016). Richland and Ransom counties, where our study was conducted, have

several hundred colonies alone (USDA 2016). Thus, honey bees are a prominent part of these

plant-pollinator networks. However, these non-native bees can have negative effects that range

from competition with large native bee species, reduced pollen and nectar availability, and

negative correlations with native bee density (Klein et al. 2003, Torné-Noguera et al. 2016,

Thomson 2016). Our study adds that honey bees may be altering resource selection of native bee species. Furthermore, the attraction of honey bees to exotic resources we observed could facilitate invasions by exotic plants that sexually reproduce (Barthell et al. 2001), and bring about conservation initiatives that then promote plantings of exotic resources (e.g. Decourtye et al. 2010), both further reducing floral diversity. In combination with intensive agricultural practices that limit resource availability, competition for conservation action with honey bees is threatening native bee diversity and reducing the pollination services provided to agricultural systems (Colla and MacIvor 2016, Landaverde-González et al. 2016). This problem is exacerbated when more honey bees are needed to compensate for pollinator diversity because honey bees are less efficient pollinators than many native bees (Garibaldi et al. 2013, Goulson et al. 2015). Effective pollinator conservation in working landscapes should therefore focus on managing for diverse native resources to both alleviate any displacement by honey bees and bolster pollination services (Potts et al. 2003, Blüthgen and Klein 2011, Orford et al. 2016).

Landscape heterogeneity has been shown to promote biodiversity, pollinator diversity, and even mitigate competition between native bees and honey bees (Fuhlendorf et al. 2006, Fahrig et al. 2011, Hovick et al. 2015, Herbertsson et al. 2016, Senapathi et al. 2016). Furthermore, bees have shown resilience to anthropogenic disturbances as long as diverse floristic resources are available (Hülsmann et al. 2015). However, landscapes heavily impacted by humans (i.e. agricultural) can be resource-limiting during certain times of the year and require bees to travel long distances (Olsson et al. 2015). Bees in these systems need access to semi-natural habitat for supplemental resources and it needs to be within a reasonable foraging distance (Senapathi et al. 2016, Olsson et al. 2015). Additionally, pollinator communities need these resources to be temporally distributed (Leong et al. 2015). We found that floristic

availability was predictive of the bee community but differed between native bees and honey bees. This is because plant composition shapes niche partitioning between pollinator species (Venjakob et al. 2016). Entire bee communities may shift throughout the season as a result of the resources available, but there always needs to be access to a suite of flower species so that a diverse pollinator community is present throughout the season, and across the landscape (Samnegård et al. 2015, Venjakob et al. 2016). Management which emphasizes the spatial-temporal distribution of floristic resources will not only bolster pollinator diversity and abundance but populations' persistence as well (M'Gonigle et al. 2015).

We recognize that our study has limitations as a consequence of being conducted over two variable growing seasons and other challenges of conducting research in working landscapes. Pollinator specialization and plant-pollinator networks have been known to change over time with pollinators foraging opportunistically as resource availability allows (Petanidou et al. 2008). A study greater than two years may help to improve specialization indices and delineate interactions further. Additionally, we did not differentiate between floral resources being used for nectar or pollen. Often species have more nectar than pollen hosts, and some flower species are only providing one or the other (Robertson 1925, Baude et al. 2016), this could have influenced species' resource use and specialization indices. Finally due to much of the landscape being leased to private ranchers, we had insufficient knowledge of current and historic land use practices to make connections between management practices and floristic resource availability. Nevertheless, this research contributes to the limited understanding of native plant-pollinator networks in grassland working landscapes and presents a very realistic outlook of how pollinator communities interact with the floral resources that remain after decades of intense land use.

While the conservation of biodiversity is imperative to supporting the ecosystem services that sustain society, responses which forego production entirely are impractical. Rather, management practices which can simultaneously achieve both, need to be researched and endorsed. In the case of pollinators, the grassland ecosystems that provide the bulk of their resources are also essential landscapes for agriculture and livestock production. We investigated plant-pollinator networks in grassland working landscapes grazed by cattle and found that native resource availability and non-native honey bees were influencing plant-pollinator networks and native bee abundance throughout the summer. By managing for diverse spatial-temporal floristic resources, displacement by honey bees can be mitigated across the entire growing season while bolstering provision of pollination services to natural and managed landscapes. Developing innovative management practices which can provide this floristic diversity will be imperative to saving the species and industries which support global food production.

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Table A1. Pasture-level characteristics. Pastures used in study, pasture size and location, as well as abundance and richness of grassland butterflies detected during line-transect distance sampling conducted from 2015-2016 in the Sheyenne National GRASSLANDS AND Albert Ekre Grassland Preserve.

Pasture Name	Size (ha)	Management	Location	Abundance	Richness
Bachelor Yearling (BAY)	125	Season-long	Sheyenne	8412	32
Schultz (SCHU)	54	Season-long	Sheyenne	16182	31
North S (NS)	480	Rotational	Sheyenne	20739	47
Ekre Rotational (ER)	65	Rotational	Albert Ekre	27223	35
Carlson (CA)	187	Rotational w/ mowing	Sheyenne	25864	42
Sohljem (SO)	484	Rotational w/ mowing	Sheyenne	17484	42
Ekre PBG NE (EPNE)	65	Patch-burn	Albert Ekre	24934	34
Ekre PBG SW (EPSW)	65	Patch-burn	Albert Ekre	33645	27

Table A2. Butterfly abundance and richness by round. Total abundance and richness of the grassland butterfly community during line-transect distance sampling conducted in three sampling rounds (Early- June 10-June 30, Middle- July 1-July 20, Late-July 21-August 10) from 2015-2016 in tallgrass prairie landscapes grazed by cattle.

Year	Round	Abundance	Richness
2015	Early	98	10
2015	Middle	244	19
2015	Late	385	17
	Total	*727*	*25*
2016	Early	421	20
2016	Middle	713	25
2016	Late	717	18
	Total	*1851*	*32*
TOTAL		**2578**	**34**

Table A3. Butterfly species detected. List of all grassland butterfly species detected and their abundance during line-transect distance sampling conducted from 2015-2016 in the Sheyenne National Grasslands and Albert Ekre Grassland Preserve.

Common Name	Scientific Name	2015	2016	Pooled
Acadian Hairstreak	*Satyrium acadica*	2	6	8
American Copper	*Lycaena phlaeas*	-	5	5
American Lady	*Vanessa virginiensis*	1	10	11
Black Swallowtail	*Papilio polyxenes*	1	1	2
Bronze Copper	*Lycaena hyllus*	-	12	12
Cabbage White	*Pieris rapae*	6	57	63
Checkered White	*Pontia protodice*	9	15	24
Clouded Sulphur	*Colias philodice*	279	748	1027
Common Buckeye	*Junonia coenia*	-	1	1
Common Ringlet	*Coenonympha tullia*	50	16	66
Common Wood Nymph	*Cercyonis pegala*	29	28	57
Delaware Skipper	*Anatrytone logan*	5	3	8
Eastern-tailed blue	*Cupido comyntas*	-	48	48
Eyed Brown	*Satyrodes eurydice*	4	1	5
Gorgone Checkerspot	*Chlosyne gorgone*	-	43	43
Great Spangled Fritillary	*Speyeria cybele*	-	1	1
Least Skipper	*Ancyloxypha numitor*	1	15	16
Long Dash	*Polites mystic*	28	37	65
Meadow Fritillary	*Boloria bellona*	80	252	332
Monarch	*Danaus plexippus*	56	32	88
Mourning Cloak	*Nymphalis antiopa*	-	1	1
Northern Crescent	*Phyciodes cocyta*	1	4	5
Orange Sulphur	*Colias eurytheme*	38	3	41
Painted Lady	*Vanessa cardui*	1	-	1
Pearl Crescent	*Phyciodes tharos*	18	145	163
Peck's Skipper	*Polites peckius*	55	66	121
Purplish Copper	*Lycaena helloides*	-	78	78
Red Admiral	*Vanessa atalanta*	9	14	23
Red-spotted Purple	*Limenitis arthemis*	1	0	1
Regal Fritillary	*Speyeria idalia*	9	60	69
Silver-bordered Fritillary	*Boloria selene*	42	123	165
Tawny-edged Skipper	*Polites themistocles*	1	4	5
Variegated Fritillary	*Euptoieta claudia*	-	4	4
Viceroy	*Limenitis archippus*	1	18	19
Total	**34**			**2578**