Plant–pollinator networks in grassland working landscapes reveal seasonal shifts in network structure and composition

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Abstract. Declines in native bee populations can limit pollination services that support native plant communities and global food production. Mitigating the impacts on pollinators and ecosystems requires conservation actions that promote biodiversity and remain practical for producers. We investigated plant–pollinator interaction networks in working grassland landscapes, managed for cattle production and biodiversity, to advance conservation of pollinators in grazed systems. We compared and plotted interactions at the network level. We then used a regression framework to evaluate the influence of floristic availability on pollinator abundance in our system. Overall, we detected seasonal shifts at the network level, with increased specialization between flowers and bees occurring at the end of the sampling season. Furthermore, the response to floristic resources differed between honey bees (Apis mellifera) and native bees. While honey bee abundance increased with exotic floral abundance, native bee abundance showed no relationship with floral abundance and instead was positively associated with floral richness in our system. These findings could be an indication of seasonal shifts in bee activity and interactions with plants or a response to the subset of available resources in grazed systems. These interpretations, along with the detected difference in resource use between honey bees and native bees, suggest foraging preferences differ between these two groups and could influence conservation and management strategies. Furthermore, it demonstrates a need to consider how management practices could influence bee communities differentially across the growing season and suggests conservation actions should promote native floristic resources to benefit native bees.

Key words: grassland ecology; insect conservation; native bee; plant–pollinator interactions; working landscape.

INTRODUCTION

Human-induced global change has generally led to a decline in quality and extent of the world’s ecosystems (Solomon et al. 2009, Cardinale et al. 2012). Declines in genetic, species, and functional biodiversity may be the most prominent of these effects (Cardinale et al. 2012, WWF 2014). Biodiversity is fundamental for maintaining species’ interactions (Cardinale et al. 2012), along with the stability and production of ecosystem services (Hammond 1995). Declines in biodiversity can reduce the strength and number of potential species’ interactions and decrease the ability of an ecosystem to provide services society relies on such as clean water, soil retention, and pollination (De Groot et al. 2002, Cardinale et al. 2012). Thus, biodiversity conservation will be critical to maintaining ecosystem services in the future.
Pollination is an economically valuable ecosystem service, but increasing evidence suggests pollinators that sustain ecosystem stability and agricultural production are declining (Kearns et al. 1998, Grixti et al. 2009, Potts et al. 2010), although not all pollinators are in decline (e.g., Sheffield et al. 2016). Crop 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, including bees, are responsible for an estimated $3.07 billion of food production in the United States annually (Losey and Vaughan 2006). Pollinators also play a key role in maintaining biotic communities in non-agricultural areas by providing pollination services to non-crop plants and facilitating gene flow (Potts et al. 2010, Vanbergen 2013). With pollinator declines increasingly recognized as a global conservation concern (Kearns et al. 1998, Potts et al. 2010, Garibaldi et al. 2013), understanding how to maintain plant–pollinator interactions is valuable for crop production, native plant management, and overall the conservation of biodiversity (Allen-Wardell et al. 1998).

One goal of ecosystem management should be promoting native pollinator populations. Pollinator abundance and diversity have been positively correlated with pollination services (Winfree et al. 2015, Orford et al. 2016), but bee diversity can also bolster ecosystem stability (Potts et al. 2010, Orford et al. 2016). Native bees have evolved with native plants in their respective biomes (Kearns and Inouye 1997, Kearns et al. 1998), whereas non-native bees, mainly honey bees (Apis mellifera) in the United States, are often introduced for agricultural purposes and may show preference for exotic floral species and alter pollinator community composition (Goulson 2003, González-Varo et al. 2013). While honey bees are numerous and can be effective pollinators for some plants (Huryn 1997), a diverse community of bees may be required to maximize productivity within a landscape (Klein et al. 2003, Orford et al. 2016), and the diversity of plant–pollinator interactions, or networks, is important for maintaining ecosystem stability (Kearns et al. 1998, Ashman et al. 2004). In theory, increased pollinator diversity in a network equates to functional redundancy. Therefore, if one pollinator goes extinct in the network, another species will be able to fulfill the functional role in the ecosystem and maintain stability. Thus, reduced pollinator diversity reduces network stability, and increasing plant species diversity and abundance is essential for pollinator diversity and abundance (Potts et al. 2003, Hoiss et al. 2015). Additionally, competition and phenological changes can eliminate plant–pollinator interactions before actual individual species become extinct (Santamaria et al. 2016) and contribute to future species’ extinctions (Tylianakis et al. 2010). Therefore, the diversity of pollinators and their interactions with plants should be a central tenant of ecosystem conservation efforts (Carman and Jenkins 2016).

Current pollinator research has mainly focused on managed honey bees (Aizen and Harder 2009, Pettis and Delaplane 2010, Mogren and Lundgren 2016, Smart et al. 2016). This research generally drives policy initiatives, and a honey bee centric focus can have indirect negative consequences on other, native bee species (Colla and Maclvor 2016). Recent research suggests that the addition of honey bee hives to a landscape results in native bumble bee declines (Herbertsson et al. 2016), and honey bees have been found to negatively impact bumble bee populations via resource competition (Thomson 2016). Therefore, specific management strategies beneficial for the non-native honey bee may not promote native bee populations. While honey bees are effective pollinators of certain monoculture crops, maintaining diverse native bee communities likely has greater benefit to agricultural yields (Klein et al. 2003, Garibaldi et al. 2015, Orford et al. 2016). However, decreases in floral resource availability and distribution are contributing to native pollinator declines (Potts et al. 2010). Even moderate increases in flowering resources in agricultural landscapes (e.g., alfalfa) could promote pollinator populations while simultaneously promoting biodiversity that sustains ecosystem stability and native plant communities (Kearns et al. 1998, Ashman et al. 2004, Orford et al. 2016).

Our study examined plant–pollinator interactions in grazed working landscapes—ecosystems managed for both biological and economic objectives (Polasky et al. 2005). Efforts to effectively
conserve biodiversity will inevitably need to incorporate these types of landscapes because the majority of grasslands are in private ownership that rely on livestock production for income (Herrero et al. 2009, Mora and Sale 2011). Our objectives were to (1) describe plant–pollinator interactions in working grassland landscapes at the network level and (2) quantify the relationship between floral availability and bee abundance. We hypothesized that floral resource availability would positively influence network-level interaction metrics as well as pollinator abundance due to other evidence of bee communities’ responses to floral availability and bee abundance (Ebeling et al. 2011, Wray et al. 2014, Goulson et al. 2015). This information will be important for understanding bee resource use and will improve management that can effectively support native bee communities in working landscapes.

**Methods**

**Site description**

From 2015 to 2016, we evaluated the influence of floral availability on pollinator communities and foraging in the Sheyenne National Grasslands (SNG) and surrounding area located in Richland and Ransom counties, North Dakota, USA (46.3815° N, 97.2760° W). These areas are located in the tallgrass prairie ecoregion and characterized by sandy soils and native grasses such as big bluestem (*Andropogon gerardii*), switchgrass (*Panicum virgatum*), and prairie cordgrass (*Spartina pectinata*), but they are heavily invaded by Kentucky bluegrass (*Poa pratensis*) and smooth brome (*Bromus inermis*). Common native forbs include leadplant (*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. The average annual precipitation is 52.6 cm, and average annual temperatures are 5.5°C (NDAWN 2015). During the growing season (June–August), the historical average temperatures are 19.4°C, 22.2°C, and 21.1°C, and rainfall totals are 9.8, 8.9, and 5.4 cm, respectively (NDAWN 2015). The SNG and surrounding area are managed with a combination of fire, mowing, and grazing leases (United States Department of Agriculture 2008).

We selected eight pastures comprising a variety of grazing management strategies 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 located adjacent to the SNG and managed by North Dakota State University. Pastures ranged in size from 54 to 484 ha. All pastures were working landscapes managed for cattle production with similar stocking rates, but different cattle management strategies were utilized at each site (two pastures per strategy). Our initial study was designed to test for differences between management strategies. However, due to logistical constraints, treatments were not fully implemented to correspond with the timing of this study. Moreover, management strategies did not influence floral resources and the butterfly community over the same time period that bee data were collected (Bendel et al. 2018), and we therefore did not evaluate changes in the pollinator and floral community across management strategies.

**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 09:00 and 17:30 hours on sunny days with temperatures ≥17°C and sustained winds <15 km/h (Moranz et al. 2012, Popic et al. 2013). We sampled each floral visitor transect for eight minutes attempting to collect all flower visitors within 1 m of either side of the transect. 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 laboratory to refine our analysis to exclusively bees.

In order to identify specific bee–flower interactions, we collected floral visitors using an aerial insect net. We only collected floral visitors
touching the reproductive parts of a flower. After an individual was netted on a flower, we recorded the associated flower species each specimen was collected from and euthanized specimens with ammonium carbonate in a vial. 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). Additionally, we recorded the number and species of flowering stems within 2 m of each 25 m transect (modified from Moranz et al. 2014) during each floral-visitor sampling round to make predictions between floral abundance (the total number of flowering stems counted in belt transects), floral richness (the total number of unique species detected in belt transects), and pollinators. This information was necessary to create plant–pollinator networks and foraging preference among available resources over time.

*Bee identification.*—We stored specimens in plastic bags indoors at room temperature for the remainder of the field season which helped prevent specimen damage. We assigned each specimen a unique identification code that related them to the flower, transect, pasture, and date they were collected. At the end of the field season, we used UNITRON Z10 Stereo microscopes and the key from *The Bee Genera of North and Central America* (Michener et al. 1994) to identify specimens down to the lowest taxonomical class practical. 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 basic metrics of the floral and bee communities including abundance, richness, and number of flowering species used by bees among sampling rounds (Early–Late). We used these data for evaluating differences in plant–pollinator interaction networks from each sampling round.

*Network analyses.*—Ecological networks encompass the interactions of species within an ecosystem and act as a proxy to assess the stability of an ecosystem (Montoya et al. 2006). We conducted all network analyses using the statistical software R (version 3.3.1., R Core Team 2016) and the package bipartite (Dormann et al. 2018). We pooled data at the pasture level for each observation period resulting in three plant–flower interaction webs (Ebeling et al. 2011). We generated both quantitative indices as well as qualitative metrics in the form of interaction plots to visually evaluate differences in networks across the growing season.

We evaluated plant–pollinator interactions across the growing season by calculating the quantitative network-level index $H_2$ for the eight pastures in each sampling period both years. $H_2$ assesses the specialization at the network level. In a bee ($c =$columns) by plant ($r =$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 $[r]$ and columns $[c]$ in the network (Blüthgen et al. 2006).

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

We present the standardized index $H_{2}'$ which ranges from 0 (most generalized) to 1 (most specialized) network (Blüthgen et al. 2006). In the index, 0 represents a perfectly nested network (e.g., progressively specialized bee species visit a subset of flower species visited by the most generalized bee), and 1 is the greatest deviation from this assemblage (e.g., each bee species has a mutually exclusive interaction with flower species; Blüthgen et al. 2008, Hülsmann et al. 2015). The index $H_{2}'$ accounts for the frequency of interactions and thus gives a more quantitative analysis of the pollinator network which can then be compared to other networks of varying composition and interactions, instead of just comparing the number of links in the network or connectance (proportion of realized vs. potential links; Blüthgen et al. 2006).

To quantify differences in the pollinator networks, we used analysis of variance (ANOVA) in R (version 3.3.1.; R Core Team 2016). The $H_{2}'$ followed a normal distribution, so we did not transform the data. We evaluated changes in the index $H_{2}'$ over sampling periods with year and site as random factors. For any significant differences ($P \leq 0.05$), we used post hoc Tukey tests for pairwise comparisons.
Linear regressions.—To quantify relationships between floral resources and bee abundance, we used generalized linear mixed-effect modeling using the lme4 package in R (version 3.3.1.; R Core Team 2016). Our response variables were honey bee abundance and native bee abundance. The a priori floral resource variables (explanatory variables) were total floral abundance, native floral abundance, exotic floral abundance, total floral richness, and native floral richness. We tested for correlations and removed variables that were highly correlated \( (r \geq 0.60) \). Exotic floral abundance was correlated with total floral abundance, but neither variable was highly correlated with native floral abundance. Total floral richness was highly correlated with native floral richness. Final explanatory variables were exotic floral abundance, native floral abundance, and total floral richness.

We conducted regressions using transect-level data that included site as a random factor. Additionally, we used Poisson distributions when creating models for honey bee and native bee abundance to account for the skewedness in the count data. During floral visitor surveys, we occasionally had no bee captures, resulting in zero count data. We considered any results with a \( P \)-value \( \leq 0.05 \) to be significant.

**Results**

**Bee and floral richness**

We collected 1111 bee specimens and 68 species over 153 h of bee sampling. We observed at least one bee on 171 of 192 transects throughout the study, but frequently encountered transects with no individuals. The most abundant species was the honey bee which comprised 647 of the total specimens. The second most abundant species at 43 observations was a sweat bee \( (Lasioglossum perpunctatum) \), and we made 35 observations of brown-belted bumble bees \( (Bombus griseocollis) \). Overall, bee abundance across sampling rounds varied between 2015 and 2016, but bee species richness was the highest in the last round of sampling in both years (Table 1).

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 79% of the total number of flowering stems over the entire study. During each sampling round, exotic species varied in their percentage of total floral abundance at the site level \( (0–100\%) \), with an average of 68% of floral abundance compromised of exotic species. Overall, floral abundance across rounds varied between 2015 and 2016 (Table 1). However, in both years, floral species richness was lowest in the first round and highest in the second round of sampling, and the number of flowering species that bees were collected from generally increased throughout the season (Table 1).

**Network analyses**

From 2015 to 2016, we detected 215 unique plant–pollinator interactions, and bees made use of only 39 of the 82 flowering plants available throughout the sampling period (Table 1, Fig. 1).

Table 1. Total flowering forb abundance, floral richness, floral species bees were collected from, bee abundance, and bee richness by sampling round (1–3), and year collected at the Sheyenne National Grassland and surrounding areas, ND, from 2015 to 2016.

| Sampling round | Exotic abundance | Native abundance | Richness | No. species used by bees | Abundance | Richness |
|----------------|------------------|------------------|----------|-------------------------|-----------|----------|
| 1 (June 10–June 30) | 30,420           | 11,819           | 24       | 8                       | 100       | 18       |
| 2 (July 1–July 20)  | 49,694           | 10,363           | 42       | 10                      | 180       | 12       |
| 3 (July 21–August 10) | 35,317          | 14,852           | 36       | 21                      | 162       | 25       |
| 2015 Total        | 115,431          | 37,034           | 63†      | 27†                     | 442       | 36†      |
| 1 (June 10–June 30) | 53,291           | 9406             | 31       | 14                      | 294       | 25       |
| 2 (July 1–July 20)  | 31,756           | 4635             | 37       | 15                      | 204       | 23       |
| 3 (July 21–August 10) | 6807            | 5575             | 36       | 16                      | 171       | 31       |
| 2016 Total        | 91,854           | 19,616           | 82†      | 32†                     | 669       | 49†      |

† Values are the sum of unique species found that year or unique species used by bees.
Fig. 1. Plant–pollinator networks sampled from 2015 to 2016 in the Sheyenne National Grasslands and surrounding areas. Networks were combined over the two years and plotted for each sampling round. The top bars represent pollinator species and bottom bars represent individual flowers species. A pollinator species is connected by a line to a flower if an interaction occurred (i.e., the bee was collected from that flower). For ease of interpretation, only the honey bee (Apis mellifera) is labeled on the graphic, but bee species are listed from left to right.
right for each round below. Species in bold are non-bee species that collected from the reproductive parts of the flower. Specimens from the families Icethonidae and Tephridae could not be identified to genus. Flower species are labeled as numbers on the bottom of each graph, with the key for each number found below. Bar width increases as the relative number of interactions between the same bee and flower species increases. Additionally, the $H^2$ for each round is included to indicate the level of network interactions. A higher $H^2$ indicates higher network specialization. Plants: 1, Achillea millefolium; 2, Allium cernuum; 3, Amorpha canescens; 4, Anemone canadensis; 5, Asclepias syriaca; 6, Asclepias stenophylla; 7, Cirsium discolor; 8, Cirsium flodmanii; 9, Dalea candida; 10, Dalea purpurea; 11, Dalea villosa; 12, Eriogonum strictum; 13, Erysimum capitatum; 14, Euphorbia esula; 15, Glycyrrhiza vulgaris; 16, Helianthemum autumnae; 17, Liatris aspera; 18, Lythrum alatum; 19, Melilotus albus; 20, Melilotus officinalis; 21, Mentha arvensis; 22, Oenothera biennis; 23, Onosmodium virginianum; 24, Potentilla arguta; 25, Pycnanthemum virginianum; 26, Ratibida columnifera; 27, Rosa arkansana; 28, Rudbeckia hirta; 29, Senecio plattensis; 30, Solidago missouriensis; 31, Spiraea alba; 32, Symphoricarpus albus; 33, Taraxacum officinale; 34, Teucrium canadense; 35, Tragopogon dubius; 36, Trifolium pretense; 37, Trifolium repens; 38, Vernonia fasciculata; 39, Zizia aptera. Pollinators: (June 10–June 30): Agapostemon angelicus, Andrena nasonii, Andrena nivalis, Andrena vicina, Andrena wilkella, Apis mellifera, Augochloropsis sumptuosa, Bombus bimaculatus, Bombus borealis, Bombus auricomus, Bombus bimaculatus, Bombus griseocollis, Bombus huntii, Bombus rufocinctus, Bombus ternarius, Bombus vagans, Colletes aberrans, Colletes americanus, Colletes robertsonii, Epeolus scutellaris, Halictus confuses, Halictus ligatus, Hylaeus cristatus, Hylaeus annulatus, Hylaeus mesillae, Ichneumonidae., Lasio glossum spp., Lasio glossum cressoni, Lasio glossum nelsoni, Lasio glossum parrarbei, Lasio glossum pectoral, Lasio glossum perpunctatum Lasio glossum pictum, Megachile brevis, Osmia distincta, Vespula vidua. (July 1–July 20): Agapostemon virescens, Andrena wilkella, Andrena ziziae, Apis mellifera, Augochloropsis sumptuosa, Bombus borealis, Bombus fideus, Bombus griseocollis, Bombus huntii, Bombus rufocinctus, Bombus ternarius, Bombus vagans, Colletes aberrans, Colletes americanus, Colletes robertsonii, Epeolus spp., Halictus confuses, Halictus ligatus, Hylaeus ptilipes, Hylaeus truncatus, Hyleca mesillae, Lasio glossum spp., Lasio glossum pectoral, Lasio glossum perpunctatum, Lasio glossum pictum, Melissodes communis, Nomia univittatiss. (July 21–August 10): Agapostemon angelicus, Andrena krigiana, Andrena nubecula, Apis mellifera, Augochloropsis sumptuosa, Bom bus auricomus, Bombus borealis, Bombus fideus, Bombus griseocollis, Bombus huntii, Bombus impatiens, Bombus nevadensis, Bombus sandersoni, Bombus ternarius, Bombus vagans, Ceratina dupla, Cerceris spp., Colletes aberrans, Colletes solidaginis, Ectemnius maculosus, Epeolus spp., Epeolus scutellaris, Halictus confuses, Halictus ligatus, Hyleca affinis, Lasio glossum spp., Lasio glossum forbesi, Lasio glossum pararbei, Lasio glossum pectoral, Lasio glossum perpunctatum, Lasio glossum pictum, Megachile latinunitas, Melissodes agilis, Melissodes communis, Melissodes magister, Melissodes subillata, Melissodes trinitis, Philanthus bilunatus, Polistes fuscatus, Tachytes spp., Tephiidae, Melissodes subillata, Melissodes trinitis, Philanthus bilunatus, Polistes fuscatus, Tachytes, Tephiidae.

The most frequently used native floral species were Flodman’s thistle (Cirsium flodmanii), lead plant, and Missouri goldenrod (Solidago missouriensis). Honey bees were highly specialized on leafy spurge and white clover in the beginning of the summer (Fig. 1), but then transitioned to the exotic white and yellow sweet clover during the second sampling round. As plant phenology progressed, we observed an increase in native floral resources which corresponded with an increase in native bees and the overall number of flowering species used by bees in the networks (Fig. 1).

At the network level, specialization ($H^2$) was significantly different ($F_{2,31} = 15.94, P < 0.001$) between sampling rounds combined over both years. Specialization increased over the field season with the highest specialization occurring at the end of the summer, representing the most exclusiveness in interactions between the three plant–pollinator networks (Fig. 1). However, the first two rounds of sampling were not significantly different from each other (Fig. 1).

**Linear regressions**

We found honey bee abundance increased with increasing exotic floral abundance ($z = 21.04, df = 182, P < 0.001, r^2 = 0.53$), but native bee abundance did not follow this relationship ($z = 0.68, df = 182, P = 0.50, r^2 = 0.0002$; Fig. 2).
Additionally, honey bee abundance was not predicted by total floral richness ($z = -0.20$, $df = 182$, $P = 0.84$, $r^2 = 0.0003$). Conversely, we found a positive relationship between native bee abundance and total floral richness ($z = 4.85$, $df = 182$, $P \leq 0.001$, $r^2 = 0.11$; Fig. 2). Neither honey bee abundance ($z = -0.68$, $df = 182$, $P = 0.50$, $r^2 = 0.03$) nor native bee abundance ($z = -1.41$, $df = 182$, $P = 0.16$, $r^2 = 0.0001$) was predicted by native floral abundance alone.

**DISCUSSION**

Ecosystem degradation coupled with intensive agricultural practices has led to declines in the world’s biodiversity (Briske et al. 2008, Cardinale et al. 2012, WWF 2014) and could threaten the provision of pollination services and food security (Kearns and Inouye 1997, Kearns et al. 1998, Potts et al. 2010). Reconciling agricultural production and conservation of biodiversity is
crucial to effective ecosystem management. We examined plant–pollinator interactions in grasslands actively grazed by livestock to investigate plant–pollinator relationships within agroecosystems and found that the network structure and composition shifted across the growing season with an increase in native bee species later in the growing season. Furthermore, we detected differences in native bee and honey bee responses to floral resources. Native bee abundance increased as total floral richness increased, whereas honey bee abundance increased as exotic floral abundance increased. Our results are similar to other studies that have reported bottom-up effects of resource diversity on pollinators in grazed systems (Orford et al. 2016) and differences in honey bee and native bee foraging preferences (Otto et al. 2017). Together, these results suggest that bee species are using resources differentially in working landscapes, resulting in the spatial-temporal fluctuations observed in the plant–pollinator networks in this study and elsewhere (see Lopez et al. 2017).

Honey bees were a prominent part of plant–pollinator networks we observed. North Dakota has the most commercial honey bee colonies in the country, with several hundred colonies residing in our study area alone (USDA 2016). Nonetheless, plant–pollinator networks for both honey bees and native bees changed over the season, and floral resource availability, both abundance and richness, appears to be influencing pollinator abundance. Phenology of floral resources, along with native and exotic bee phenology and biology, likely influenced our network results. Life history traits and evolutionary relationships with plants can influence the timing of plant–pollinator interactions, all of which can be altered by land use (Geslin et al. 2016, Ogilvie and Forrest 2017). Furthermore, grazed systems in this study may only offer a subset of floral resources due to historical land management affecting floral resource availability and pollinator abundance. Generally, increases in floral diversity can increase pollinator diversity (Potts et al. 2010, Ebeling et al. 2011, Venjakob et al. 2016), but the identity of those floral resources may be of importance for managing particular groups of bees (Sutter et al. 2017), especially in working landscapes.

Our results are most likely a reflection of bee phenology and niche partitioning between species (Samnegård et al. 2015, Venjakob et al. 2016). Regression analyses investigating floristic availability and bee abundance complement our network analyses but reveal that honey bees and native bees are responding to different resources. Factors such as size and sociality can drive temporal variation in bee species’ presence (Ogilvie and Forrest 2017). We found that the social honey bee increased with exotic floral abundance, an indication of total floral abundance. *Apis* species commonly focus on abundant and dense resources, whereas solitary bee species favor floral richness (Ebeling et al. 2011, Thomson 2016). Thus, it is unsurprising that honey bee abundance was predicted by areas dominated by leafy spurge and sweet clover, two exotic species that form dense patches on the landscape compared to native species (Lym and Kirby 1987, Wolf et al. 2003). Conversely, solitary bees may respond to resources at a smaller scale (Gathmann and Tscharntke 2002). For example, specialist bees in the northeastern United States may rely on just one host–plant or nectar source and thus have a limited period to be observed (Fowler 2016). This could explain our finding between native bee abundance and total floral richness as well as the increase in native bee species seen at the end of the growing season when floral richness was at its highest. However, it is important to point out that we did not further categorize native bees as solitary vs. social or generalist vs. specialist. All of these variations in resource use and network structure can fluctuate between seasons (Geslin et al. 2016) and be altered by land use and climatic changes (Ogilvie and Forrest 2017). Therefore, it will be important to conduct longer term studies of plant–pollinator networks to best inform conservation in modern-day working landscapes.

The observed plant–pollinator network shifts in our study may be the result of the limited resource availability in moderately grazed pastures or phenological changes in resource availability. Grazing can impact bee communities indirectly through changes to the floral community (Lazaro et al. 2016). Often, grazing reduces the availability of floral resources, unlike fire which can increase floral density (Moranz et al. 2017).
Grazing has been shown to be compatible with pollinator conservation (Potts et al. 2006, Williams et al. 2010, Moranz et al. 2012), but landscapes impacted by humans can be resource-limiting during certain times of the year and require bees to travel long distances (Olsson et al. 2015). In particular, early season grazing has been shown to be harmful to bee communities because fewer resources are blooming during this time (Lazaro et al. 2016). We observed similar patterns among pastures used in this research. In general, fewer flowering species were available early in the season, but floral density was relatively high due to exotic species. This is one explanation for the simplified network seen in our first sampling period.

Plant-pollinator networks may also change throughout the growing season due to resource availability in adjacent landscape types. Both native bees and honey bees may utilize crops grown in the surrounding area (Garibaldi et al. 2013) such as edible beans and peas, sunflower, and soybeans (North Dakota Agricultural Statistics 2017). Additionally, honey bees may use wooded areas to collect resin for propolis later in the growing season (Simone-Finstrom and Spi vak 2010). However, bees will still need access to semi-natural habitat for supplemental resources within a reasonable foraging distance (Olsson et al. 2015, Senapathi et al. 2016). Additionally, pollinator communities need these resources to be temporally distributed (Leong et al. 2016). We found that floral availability was predictive of the bee community but differed between native bees and honey bees. Entire bee communities may shift throughout the season as a result of niche partitioning among the resources available (Venjakob et al. 2016, Lopez et al. 2017), but a suite of flower species should be available to support a diverse pollinator community throughout the season and across the landscape (Samnegård et al. 2015, Venjakob et al. 2016). Other researchers found that rarer bees used a subset of resources from more abundant native bees and honey bees (Sutter et al. 2017). Managing for these key resources can result in increases in total bee abundance (Sutter et al. 2017), but management strategies would undoubtedly change for social vs. solitary bee species due to differences in dispersal range and communication abilities (Tscharntke et al. 2005). Overall, management practices which emphasize the spatial-temporal distribution of key floristic resources will not only bolster pollinator diversity but the services they provide (Fründ et al. 2013).

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. A study greater than two years may help to 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 may only provide one or the other (Robertson 1925, Baude et al. 2016), influencing species’ resource use. 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 ecosystem services, responses which forego production entirely are impractical. Rather, management practices which can simultaneously achieve both, need to be researched and applied. 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 floral resource availability (abundance and richness) was influencing plant-pollinator networks and bee abundance throughout the summer. By managing for diverse spatial-temporal floristic resources, the potential to support native bee species across the entire growing season can increase. Developing innovative management practices which can provide this floristic diversity will be imperative to conserving native bee species and industries which support global food production.
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