

## Seasonal succession of pollinator floral resources in four types of grasslands

J. T. DELANEY,† K. J. JOKELA, AND D. M. DEBINSKI

*Department of Ecology, Evolution and, Organismal Biology, Iowa State University, Ames, Iowa 50011 USA*

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**Abstract.** Pollinators are declining globally, and this decline in ecosystem services threatens the stability of agricultural and natural systems. Pollinators depend on a diversity of floral resources that are primarily found in uncultivated areas of agro-ecosystems such as grasslands. Seasonal succession (the seasonal changes that occur in community composition and structure) of floral resources is an essential consideration for pollinator conservation within agro-ecosystems. Different types of grasslands common within agricultural landscapes could be expected to differ in their seasonal succession of floral resources. Here we investigated how different types of grasslands important for pollinator conservation in the tallgrass prairie ecoregion (remnant prairies, reconstructed prairies, conservation grazed cattle pastures, and old fields) differ in their seasonal succession of floral resources by sampling the plant community every two weeks from 3 May through 4 October 2013. We found remnant prairies had greater richness of inflorescences when summed over the growing season, and that remnants were least similar to the other grassland types in terms of composition. Reconstructed prairies had high richness of inflorescences and exhibited the most similarity in composition to remnant prairies only during the middle of the growing season. Conservation grazed cattle pastures had more periods where turnover in composition from one survey to the next was low, indicated by the coefficient of variation in turnover throughout the season. Old fields had the lowest richness of inflorescences and were significantly different from reconstructed and remnant prairies.

**Key words:** agro-ecosystems; flowering phenology; resource diversity; restoration; tallgrass prairie.

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† **E-mail:** johntdelaney@gmail.com

### INTRODUCTION

In recent decades declines in pollinators have been observed both within the Midwestern United States (Grixti et al. 2009, Swengel et al. 2011) and globally (Biesmeijer et al. 2006, Potts et al. 2010). Mitigation of these losses requires the conservation of existing habitat, creation of new habitats, and development of management practices and conservation programs that increase pollinator resources on the landscape (Isaacs et al. 2008, Bennett and Gratton 2013). Grasslands

are crucial for the conservation of pollinators in agricultural ecosystems (Öckinger and Smith 2007), because they provide nesting sites and floral resources. Given that the availability of floral resources is hypothesized to be the factor driving bee abundance and diversity in most landscapes (Roulston and Goodell 2011), the seasonal succession (the seasonal changes in community composition and structure) of these resources is an essential consideration for pollinator habitats in agricultural ecosystems (Corbet et al. 1991). However, floral resource availability

can vary among grassland types and can exhibit seasonal differences among grassland types (Parrish and Bazzaz 1979). Understanding how different grassland habitats contrast in their seasonal succession of floral resources will aid in understanding the utility of different grassland types for conservation of pollinators. It will also aid scientists and managers in developing best practices for grassland restoration and conservation.

Many pollinators depend upon floral resources to complete their life cycle (Abrol 2011, Wäckers and van Rijn 2012), and a diversity of floral resources is essential (Heinrich 2004, Tasei and Aupinel 2008, Alaux et al. 2010). The abundance, richness, and diversity of floral resources is correlated with the abundance and richness of butterflies (Shepherd and Debinski 2005) and diversity of bumble-bees (Hines and Hendrix 2005, Davis et al. 2008) in the tallgrass prairie, and similar patterns have been demonstrated in ecosystems throughout the world (Potts et al. 2003, Hegland and Boeke 2006, Holzschuh et al. 2007, Williams et al. 2012, Bennett and Gratton 2013). The seasonal succession of floral resources could be particularly relevant for the conservation of long-lived pollinators and pollinator colonies that forage throughout much of the growing season. For instance, landscapes that lack adequate floral resources during a portion of the growing season have been shown to negatively impact bumblebee numbers (Persson and Smith 2013) and colony growth (Williams et al. 2012).

Within the tallgrass prairie ecoregion, perennial grasslands are vital for providing native pollinators with the floral resources and nesting sites they require. In recent decades grassland habitats have declined throughout the Midwestern United States due to agricultural intensification and development (Wright and Wimberly 2013). In addition to typical prairie conservation and restoration projects, programs such as the U.S. Conservation Reserve Program, that provides farmers incentives to protect set-aside land, can bolster agro-ecosystems by providing habitat and resources for pollinators while still providing economic benefits to farmers (Vulliamy et al. 2006, Decourtye et al. 2010). Similarly, grazing initiatives that promote sustainable grazing practices, such as the U.S. Conservation of

Private Grazing Land Program, can also benefit pollinators and other wildlife, and contribute to the long-term stability of agro-ecosystems.

Here we compare four types of grasslands with respect to their seasonal succession of floral resources: (1) remnant prairies, (2) reconstructed prairies, (3) conservation grazed pastures, and (4) old fields. In the Midwestern U.S., the conditions of each of these grasslands are described as follows: Remnant prairies best approximate the native tallgrass prairie community because these sites have retained a high proportion of native flora. Reconstructed prairies were formerly cultivated fields and have since been seeded with native prairie plant species. Conservation grazed cattle pastures are defined by having a low stocking rate ( $\bar{x} = 2.6$  AUM/ha,  $SD = 0.95$ ) and have either never been cultivated or have been cultivated for such a brief time in their past that they maintain some remnant flora. In our region, these sites were often grazed heavily in the past and are now dominated by exotic plant species that are common agricultural weeds in our region (e.g., *Trifolium pratense*, *Lotus corniculatus*, *Bromus inermis*, and *Schedonorus arundinaceus*). Finally, old fields are plant communities that arise naturally following cessation of agricultural practices and are typical of lands owned by absentee landowners and of some lands enrolled in conservation reserve programs, and also have a high proportion of exotic plant species.

Previous comparisons of the types of grasslands outlined above have found they differ in a number of characteristics. Remnant and reconstructed tallgrass prairie can differ in terms of physical vegetation structure (Ammann and Nyberg 2005), productivity (Martin et al. 2005), as well as diversity of plants (Kindscher and Tieszen 1998, Martin et al. 2005, Polley et al. 2005), and invertebrates (Bomar 2001, Larsen and Work 2003, Shepherd and Debinski 2005, Nemecek and Bragg 2008). Grasslands with high proportions of exotic species cover, such as our conservation grazed pastures and old fields, have also been shown to differ from remnant communities in terms of biodiversity, phenology, photosynthetic mode, productivity, and ecosystem services (Wilsey et al. 2009, 2011, Isbell and Wilsey 2011, Martin et al. 2014). Additionally, old fields and reconstructed prairies have been shown to differ in terms of butterfly diversity

and floral quality index (Farhat et al. 2014).

Our goal was to characterize patterns of seasonal succession of floral resources in these four different types of grasslands, and to test hypotheses defining the specific ways that they differed in their seasonal succession of floral resources. We predicted: (1) Remnant prairies would have the greatest richness of floral resources summed over the growing season, would have the greatest difference in composition compared to other grassland types, and would show the greatest stability as measured by turnover of floral resources throughout the growing season. (2) Reconstructed prairies would be the most similar to remnant prairies in terms of composition and diversity of floral resources but floral resources would be low in the beginning of the season and relatively high in the mid-season when many of the plant species favored in seeding projects tend to bloom. (3) Cattle pastures, which are dominated by long-flowering exotic forage species, would show the lowest amount of turnover in flower composition between each sampling period over the growing season. (4) Old fields would have the lowest richness of floral resources throughout the season and would be least similar to remnant prairies in terms of composition.

## METHODS

Our study sites were located in the Grand River Grasslands, a region covering over 28,000 ha in Ringgold County, Iowa, and Harrison County, Missouri, USA. We identified sites within the Grand River Grasslands that were characteristic of four types of grasslands essential for conservation in our region based upon communication with area land managers and current features of the plant communities. Grassland types and specifications for their designations are explained in the introduction section. A total of 16 sites were selected for this study with four sites in each of the four grassland types (Fig. 1, Table 1). Eight sites utilized previously established 100 m long butterfly transects (Debinski et al. 2011) for the plant survey transects; in the eight new sites, four randomly placed transects were established. Each transect ran north to south with some slight alterations to avoid barriers within the landscape (e.g., brush

piles and drainage areas). The percent cover of native vegetation was estimated visually from 10  $1 \times 0.5$  m quadrats along each transect (five quadrats on each side of the transect one meter from the transect line at 10, 30, 50, 70, and 90 m from the start of the transect; data presented in Table 1).

Inflorescences were sampled at two week intervals over 12 sampling rounds beginning 3 May and ending on 5 October 2013. Each sampling round was completed in 1–3 days. Inflorescences were counted by species along a 1 m swath along the east side of each 100 m transect. Inflorescences were characterized as the largest consistent floral unit among individuals within a species (e.g., compound umbels in Apiaceae and capitulums in Asteraceae), similar to the methods of Rotenberry (1990). For species that produce corymbs of inconsistent structure (e.g., *Asclepias tuberosa*, *Pycnanthemum* spp., and *Vernonia* spp.) the entire corymb on an individual flowering stem was counted as one inflorescence. Panicles were not considered the largest consistent unit for any species. All species were identified in the field using regional field guides. Some species were identified only to the genus level and are counted as an individual species in the analyses (i.e., *Cirsium*, *Erigeron*, *Fragaria*, *Lonicera*, *Plantago*, *Rubus*, *Vernonia*). Although pollinators are known to collect pollen from grass flowers, we did not count inflorescences for members of the Poales. We also acknowledge that pollinators derive nutrients from other sources besides flowers that we did not quantify here, which may include extrafloral nectaries, rotting fruit, sap, dung, carrion, and wet soil (Willemstein 1987). One site in the reconstruction category was hay-mowed in the beginning of August, so this site was eliminated from all following analyses that averaged data throughout the season.

To test for differences in the total number of inflorescences and flowering species over the sampling season, the total number of inflorescences was summed over all 12 sampling rounds for each transect, and species richness was calculated for each transect after abundances were summed. General Linear Mixed Models (GLMM) were used to test for differences among grassland types using the Poisson distribution (because data consisted of counts) with site as the

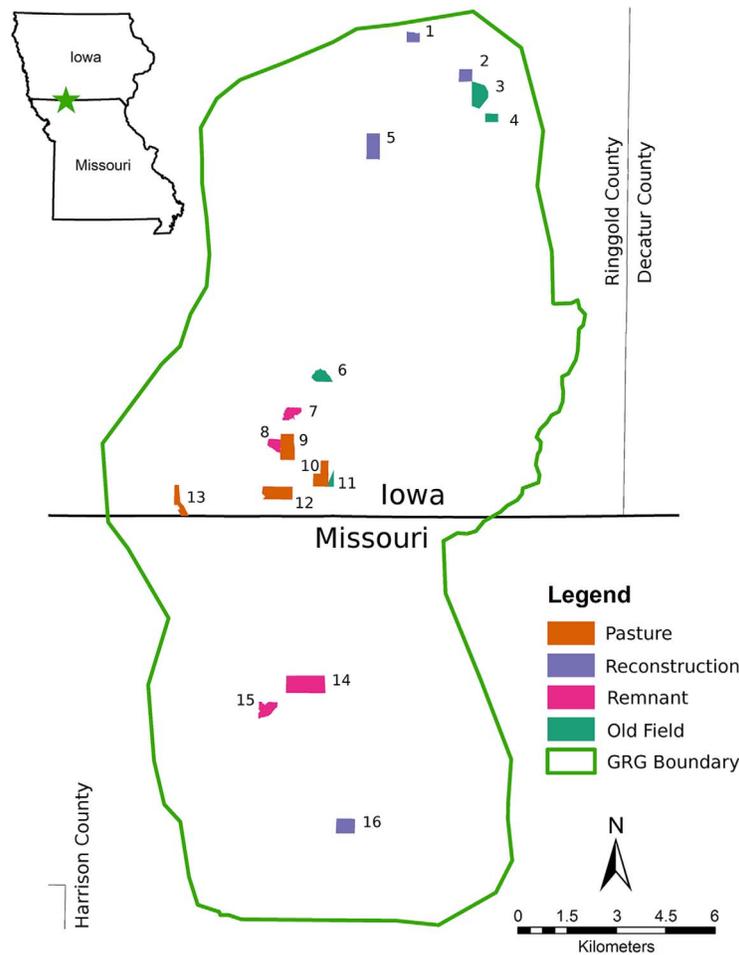


Fig. 1. Map depicting the 16 research sites in the Grand River Grasslands (GRG) of Ringgold county Iowa, and Harrison county Missouri. The thick horizontal black line is the Iowa/Missouri state border, thinner black lines are county borders. See Table 1 for details on each site.

random variable (to account for repeated measures within each site) using the nlme package (Pinheiro et al. 2013) in R (R Development Core Team 2010).

For seasonal changes in abundance of inflorescences and richness of flowering species we calculated the totals from each transect within each round. We tested for differences between grassland types within each round using GLMM with site as the random variable. To account for multiple comparisons we employed a Bonferroni correction ( $p = 0.05/72 = 6.9 \times 10^{-4}$ ) to determine whether comparisons among grassland types within each of the sampling rounds were statistically significant.

Non-metric multidimensional scaling (NMDS)

was used to observe seasonal changes in composition over time and compositional differences among grassland types. NMDS was chosen because this ordination technique has been shown to be more robust to the occurrence of rare species than other common ordination methods (Cao et al. 2001). To observe seasonal changes, species composition was averaged by each site within each round. For overall compositional differences, the total abundance of each species was calculated over all rounds for each transect and averaged by site. Ordinations were performed using the metaMDS function in vegan (Oksanen et al. 2011) in R. Difference in composition among grassland types was tested using permutational MANOVA (Anderson 2001)

Table 1. Details on sites used in this study.

Site	Type	Area (ha)	% Native cover	Longitude	Latitude
3	Old field	16.5	32.2	-94.069376	40.690143
4	Old field	9.3	51.8	-94.064491	40.683107
6	Old field	15.6	35.7	-94.124854	40.611271
11	Old field	3.5	17.2	-94.120737	40.582275
9	Pasture	32.4	47.6	-94.136821	40.591692
10	Pasture	31.2	23.1	-94.124183	40.583996
12	Pasture	34.0	52.7	-94.140074	40.579071
13	Pasture	17.8	44.5	-94.175443	40.576261
1	Reconstruction	11.5	83.3	-94.093327	40.704849
2	Reconstruction	14.5	66.6	-94.074316	40.694498
5	Reconstruction	32.4	75.0	-94.107273	40.674720
16	Reconstruction	18.7	93.5	-94.114677	40.487575
7	Remnant	15.4	88.5	-94.135568	40.601074
8	Remnant	9.0	96.7	-94.140919	40.592168
14	Remnant	40.0	95.4	-94.130453	40.527235
15	Remnant	21.8	98.7	-94.143039	40.519640

Notes: Sites are numbered based on location from north to south (1–16) Percent native cover was estimated for each transect from 10 1 × 0.5 m quadrats along each transect and averaged by site. Latitude and Longitude are represented in decimal degrees.

with the `adonis` function in `vegan` in R.

We calculated the change in species composition from round to round for each transect using the `vegdist` function in `vegan` in R, employing Bray-Curtis Dissimilarity as the dissimilarity measure. The coefficient of variation ( $CV = \sigma/\mu$ ) was calculated across all round to round comparisons throughout the season for each transect. Differences in the coefficient of variation among grassland types was tested using a mixed effects-model using the `lme` function in the `nlme` package in R with site as a random variable. Finally, figures in this manuscript were constructed using the `ggplot2` package (Wickham 2009) in R.

## RESULTS

We counted 296,256 inflorescences from a total of 142 species across the 12 sampling rounds; 113 of the species were native and 29 were classified as exotic. Total abundance of inflorescences did not differ among grassland types ( $F = 0.4$ ,  $p = 0.78$ ; Fig. 2A), but richness did ( $F = 6.1$ ,  $p = 0.0005$ ; Fig. 2B). Remnants and reconstructions supported the highest species richness of flowering plants and differed from the richness of old fields ( $p < 0.001$  and  $p = 0.028$ ; respectively), using Tukey’s multiple comparison test. Pastures exhibited a marginally statistically significantly greater richness as compared to old fields ( $p = 0.051$ ), using Tukey’s multiple comparison test. Native species richness differed among all

Tukey’s multiple comparison tests ( $p < 0.05$ ) except for the contrast between reconstructions and pastures ( $p = 0.772$ ). Specifically, native richness was greatest in remnant prairies and lowest in old fields, while native richness in reconstructions and pastures was intermediate between the two.

Within individual sampling rounds, grassland types showed few differences in abundance and richness of floral resources (Fig. 3A, B). In terms of abundance, there were no statistically significant differences among grassland types within individual rounds after Bonferroni correction for multiple tests ( $p < 0.05/72 = p < 6.9 \times 10^{-4}$ ). In terms of richness, there were several differences among grassland types within individual rounds following Bonferroni correction ( $p < 6.9 \times 10^{-4}$ ) as follows: richness was greater in pastures than in old fields in rounds 3 and 4 ( $p = 4.5 \times 10^{-5}$  and  $p = 8.6 \times 10^{-6}$ , respectively), in round 11 richness was higher in remnants than pastures and old fields ( $p = 3.0 \times 10^{-4}$  and  $p = 5.7 \times 10^{-5}$ , respectively). In round 4, pastures had marginally significantly greater richness than reconstructions ( $p = 7.1 \times 10^{-4}$ ).

NMDS ordination indicated that composition showed similar trajectories among all four grassland types over the course of the season ( $k = 2$ , stress = 9.74%; Fig. 4A). Sites were least similar at the beginning of the season and became more similar over time. Reconstructed prairies were the most dissimilar from remnant prairies during the first three sampling rounds (3

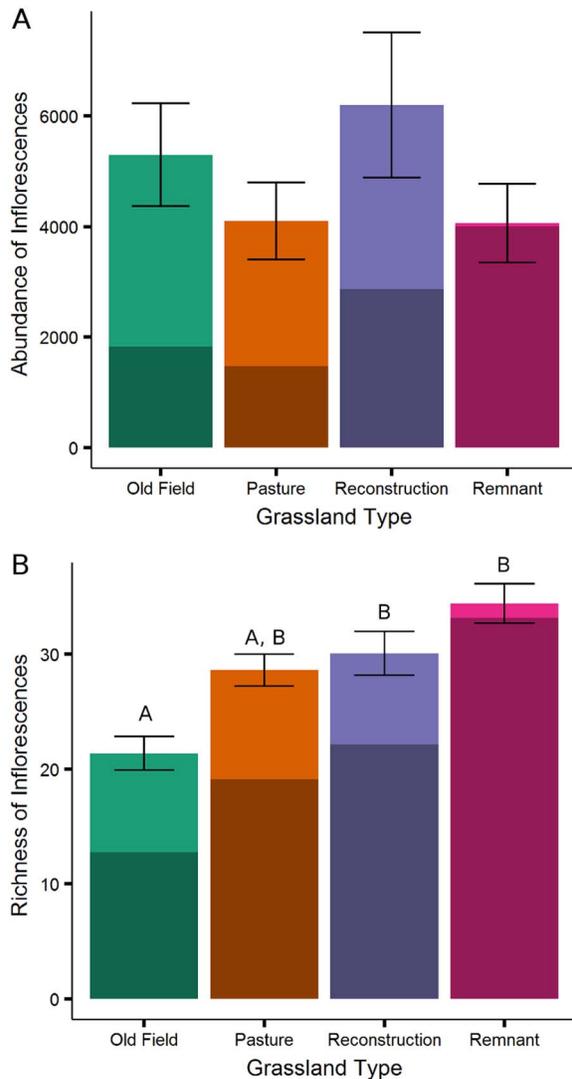


Fig. 2. The average seasonal total abundance (A) and seasonal total richness (B) of inflorescences among grassland types with four transects within each site. Seasonal total of abundance (A) did not differ among grassland types. Statistically significant differences in seasonal total of richness of inflorescences are indicated by different letters. Shaded portions of each bar represent the proportion of native inflorescences. Error bars depict standard error of the mean.

May–1 June), and then shifted to being the most similar to remnant prairies beginning in round four (14 June). When we compared composition based on seasonal total inflorescences there were differences among grassland types ( $F = 2.60, p = 0.001$ ), with remnant prairies being the least

similar to the other three grassland types ( $k = 3, \text{stress} = 7.43\%$ ; Fig. 4B).

All grassland types showed similar change in composition from round to round over the course of the study (Fig. 5). Only the fifth comparison between rounds showed differences among grassland types after Bonferroni correction ( $p < 0.05/66 = p < 7.6 \times 10^{-4}$ ). Specifically, Bray-Curtis dissimilarity between rounds was greater in remnants than old fields and pastures ( $p = 3.7 \times 10^{-5}$  and  $p = 1.8 \times 10^{-4}$ , respectively). Grassland types differed in terms of variability indicated by the coefficient of variation in change in composition from round to round throughout the season ( $F = 4.90, p = 0.02$ ; Fig. 6), with remnant prairies having less variability than pastures after Tukey’s multiple comparison test ( $p = 0.02$ ).

## DISCUSSION

Our results have demonstrated differences in the availability of floral resources among grassland types of the Upper Midwest, and these differences could have implications for pollinators. The importance of a diverse diet has been verified for some pollinators. For example, Alaux et al. (2010) found that honeybees fed diets of pollen from multiple sources had greater immunocompetence than honeybees who fed on pollen from a single flower source. Similarly, Tasei and Aupinel (2008) demonstrated that bumblebee larvae were heavier when fed a diet from multiple pollen sources than when fed pollen with greater protein content that came from a single flower source. The importance of diverse diet is even evident in foraging data. Bumblebees have been shown to travel farther to forage in species-diverse floral patches even when less diverse but florally dense patches are available at shorter distances from the nest (Jha and Kremen 2013).

### Species richness

Consistent with our prediction of cross-season total species richness, old fields had the lowest richness and differed from remnant and reconstructed prairies. Kwaiser and Hendrix (2008) found similar results wherein the abundance, richness, and diversity of floral resources was lower in old fields compared to remnant prairies.

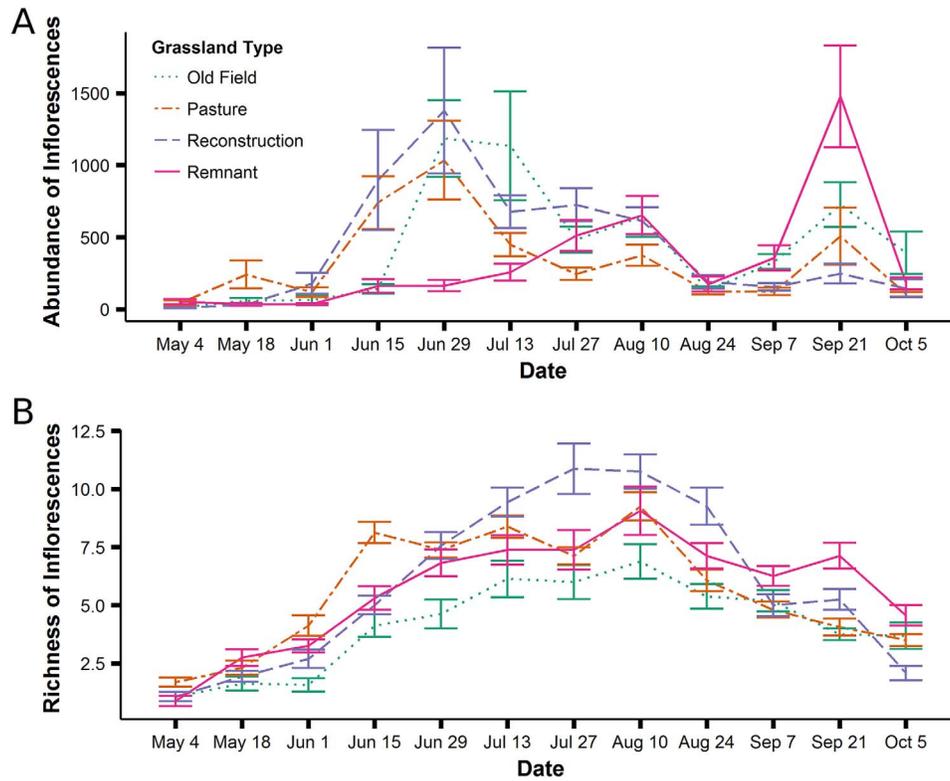


Fig. 3. Seasonal changes in the average abundance (A) and richness (B) of inflorescences for each grassland type, with four transects within each site. Each round was sampled at a two week interval beginning on a Friday or Saturday and ending on a Saturday or Sunday beginning on 3 May and ending on 5 October in 2013. Dates listed on this graph are the Saturday date of each sampling round. There were no differences with comparison among grassland types within a single round in terms of the abundance of inflorescences. Richness was statistically significantly greater in pastures than in old fields in rounds 3 and 4, in round 11 richness was statistically significantly higher in remnants than pastures and old fields. See results for specific details on specific statistics. Error bars depict standard error of the mean.

Farhat et al. (2014) did not find differences in richness of flowers between old fields and reconstructed prairies, but did find differences in terms of floral quality index. The differences in richness of floral resources among grassland types found in this study concur with other research demonstrating differences in terms of biodiversity, productivity, phenology, ecosystem services etc. when conducting comparisons between remnant grasslands and grasslands that consist of a mix of native and exotic species such as our old fields and conservation grazed cattle pastures (Wilsey et al. 2009, 2011, Isbell and Wilsey 2011, Martin et al. 2014).

When comparing richness of native forb species, all grassland types differed from each

other except for reconstructed prairies and pastures. The proportion of native flower species was particularly high in the remnants and comparatively lower in the other three grassland types. The degree to which exotic plant species may benefit pollinators is currently unclear (Palladini and Maron 2014). Exotic nectar and pollen sources are thought to be potentially valuable supplemental resources for native pollinators (Bjerknes et al. 2007, Tepedino et al. 2008). However, this pattern may only apply to generalists; pollinators that specialize on native plants may be negatively affected by the presence of exotic plant species (Stout and Morales 2009). We included both native and exotic species in our analyses because we expected the exotic species

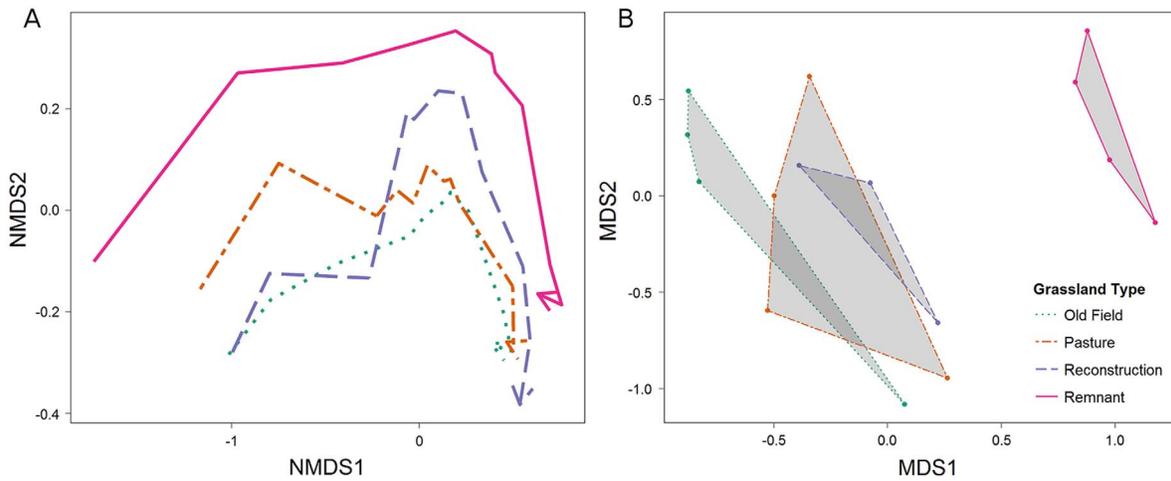


Fig. 4. Ordination diagrams showing seasonal changes in composition (A) and differences among grassland types in total composition (B). Lines in diagram A follow the centroids (average) of each of the four sites within a treatment through each round across the season. See methods and results for details.

to represent adequate resources for many of our pollinator species (Tepedino et al. 2008) and because interactions between pollinators and plants tend to be fairly generalized (Burkle and Alarcón 2011).

Despite our predictions, the four different grassland types that we examined showed surprising similarity in their seasonal succession of both abundance and richness of inflorescences. At no point in the growing season did the

abundance of inflorescences differ among grassland types but it became markedly greater for all grassland types except remnant prairies from rounds four through six (14 June to ~15 July). This pattern was primarily driven by flowering of *Erigeron* spp., *Lotus corniculatus*, *Melilotus officinalis*, and *Trifolium* spp. With the exception of *Erigeron* spp., these are species commonly introduced in agricultural landscapes (Stubben-dieck et al. 1994), and were found less frequently

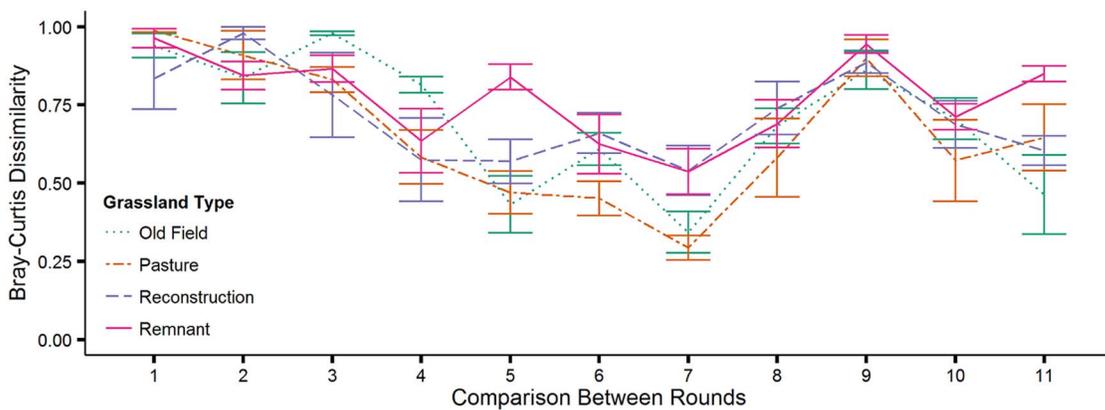


Fig. 5. Seasonal changes in turnover in species composition from one round to the next for each of the grassland types. Remnants differed statistically significantly from pastures and fallow fields in round 5. Difference in composition is measured using Bray-Curtis dissimilarity where 1.0 indicates no species were shared and 0.0 indicates no difference in composition (i.e., both identical species and abundances for each species). Error bars depict standard error of the mean.

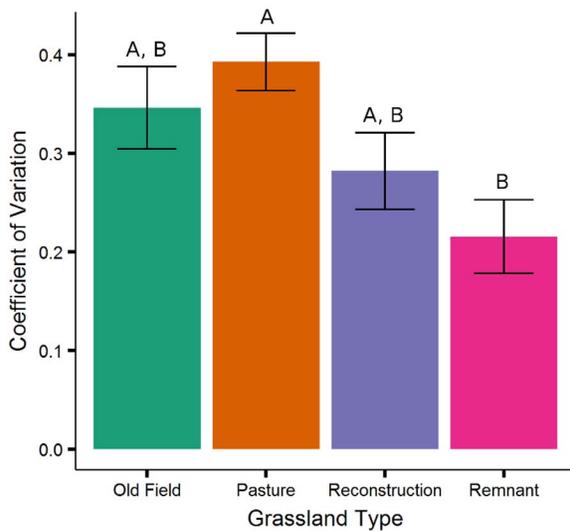


Fig. 6. Coefficient of variation ( $CV = \sigma/\mu$ ) in turnover in species composition across the season for each of the grassland types. Statistically significant difference in the coefficient of variation among grasslands types are indicated by letters above each bar. Error bars depict standard error of the mean.

in remnant prairies. Another observation of note is that abundance of inflorescences was highest in round two (18 May) in cattle pastures and highest in round 11 (21 September) in remnant prairies. The early spring and early fall periods are important foraging times for both honey bee and bumblebee colonies. Based upon the abundance of inflorescences, pollinators may benefit from nearby conservation grazed cattle pastures in the spring and remnant prairies in the fall.

All four of the grassland types showed a general pattern of highest richness in the mid-season, which has been observed in other regions of the tallgrass prairie (Anderson and Adams 1981, Craine et al. 2012). Reconstructed prairies exhibited a distinctive mid-season peak in richness of inflorescences, which was more pronounced compared to other grassland types. This pattern coincides with our prediction that reconstructed prairies would show a strong midseason peak with lower richness early and late in the season because of the observation that prairie reconstruction plantings favor species that flower mid-summer. Species most frequently encountered in reconstructed prairies in this study included *Dalea purpurea*, *Heliopsis helian-*

*thoides*, *Hypericum ascyron*, *Liatris pycnostachya*, *Melilotus officinalis*, *Monarda fistulosa*, *Oligoneuron rigidum*, *Penstemon digitalis*, *Potentilla arguta*, *Silphium perfoliatum*, and *Trifolium hybridum*, most of which reached peak bloom in the middle of the season between the fifth and ninth sampling rounds (~29 June to ~24 August). Reconstructed prairie plantings may be an important resource for pollinators foraging in the middle of the season and their integration within agricultural landscapes is likely to benefit pollinators. Alternatively, highly attractive floral displays may act as a sink (Thomas and Kunin 1999) if adequate resources for larval stages are absent (e.g., nesting sites for bees or larval host plants for butterflies).

### Community composition

With respect to the overall community composition of flowering plants across the season, remnant prairies were the most dissimilar to the other grassland types, as we had predicted. In our ordination illustrating seasonal change in composition, we see several patterns that were not testable, but are validated in the context of what is commonly known about our four grassland types. Grassland types showed the greatest dissimilarity in ordination space early in the season. Common early blooming exotic species included *Barbarea vulgaris* and *Taraxacum officinale*, and these species were encountered in all grassland types except for remnant prairies. Early blooming native tallgrass prairie species in this study included *Antennaria neglecta*, *Comandra umbellata*, *Fragaria* spp., *Oxalis violacea*, *Pedicularis canadensis*, *Sisyrinchium campestre*, *Viola pedatifida*, and *Viola sororia*. None of these species occurred in reconstructed prairies or old fields with the exception of *V. pedatifida* that was found in reconstructed prairies. This highlights why reconstructions and old fields were most dissimilar from remnant prairies at the beginning of the season.

Reconstructed prairies became more similar to remnant prairies beginning in round four (~15 June), and remained that way for 14 weeks and then became less similar in mid-September onwards (the last two rounds). This pattern could indicate that (1) previous disturbance, perhaps early in the establishment phase, may have excluded early and late blooming species,

(2) establishment of prairie species in reconstructions favors native species that flower in the middle of the season, or (3) that seed mixes at these sites were deficient in early and late flowering native species. The inability of reconstructed prairies to mimic the diversity of remnant prairies has been previously recognized (Polley et al. 2005). Our results demonstrate that greater attention to early and late blooming species establishment and persistence in reconstructed prairies is needed in order to better mimic floral resource composition of remnant prairies throughout the entire growing season.

The cattle pastures used in this study are believed to have experienced minimal disturbance in the past aside from heavy cattle grazing and interseeding of exotic forage species. Thus, they retain some remnant flora and this may explain why they were more similar to remnant prairies at the beginning of the season. For early flowering native species, *Comandra umbellata*, *Oxalis violacea*, and *Pedicularis canadensis* were only encountered in remnant prairies, *Antennaria neglecta*, *Fragaria* spp., and *Viola pedatifida* were found in remnants and pastures, while *Sisyrinchium campestre* and *Viola sororia* were more common in pastures than they were in remnant prairies.

The convergence among all grassland types later in the season is likely explained by the tendency for later flowering species to be common species across all four grassland types. For example, species that were common later in the season tend to occur in a range of habitats from high-quality to degraded. The most abundant late season species in this study (i.e., making up 94% percent of total abundance of inflorescences of the 35 blooming species encountered in the last two rounds) were *Solidago canadensis*, *Symphotrichum ericoides*, *Symphotrichum lanceolatum*, and *Symphotrichum oolentangiense*, most of which have low coefficient of conservatism values (0, 3, 4, and 7 respectively; Drobney 2014).

Composition turnover was not consistently lower in conservation grazed cattle pastures as we predicted, but the variability in composition turnover was greater in cattle pastures than in remnant prairies. Although the richness of inflorescences between remnant prairies and cattle pastures was equivalent throughout much

of the season, the resources that were available to pollinators did not change from round to round as consistently in cattle pastures as they did in remnant prairies. The lowest period of turnover in pastures occurred during comparisons five through seven. It is possible that the variability in turnover in pastures could be reduced by the establishment of native species. Based on our data, potential candidate species that could increase diversity over this time period include *Chamaecrista fasciculata*, *Dalea purpurea*, *Desmodium canadense*, *Heliopsis helianthoides*, *Monarda fistulosa*, *Parthenium integrifolium*, *Potentilla arguta*, *Ratibida pinnata*, and *Rudbeckia hirta*. However, further research is required to investigate the ability of these species to persist in a managed grazing system.

Rotenberry (1990) found a similar variability in turnover of inflorescence composition in an old field dominated by exotic species in northern Michigan, USA. In our study, old fields had the second highest (but not statistically significantly higher) variability in composition turnover. Recent studies have demonstrated the importance of floral resource diversity for pollinator health of honey bees and bumble bees (Tasei and Aupinel 2008, Alaux et al. 2010, Jha and Kremen 2013). Thus, it seems reasonable to assume that periods of low turnover in floral resources (i.e., lower diversity over time) could be problematic for long-lived pollinators that require a diverse diet. However, we are not aware of any study that specifically investigates the effect of floral resource diversity over time on the health of long lived pollinators such as honey bees or bumble bees.

#### Future research

While the importance of abundant and diverse sources of floral resources for pollinators has been demonstrated in multiple studies (Tasei and Aupinel 2008, Alaux et al. 2010, Jha and Kremen 2013), the degree to which the differences among grassland types found in this study translate to ecologically significant influences on different pollinator taxa is beyond the scope of this paper. Likewise, differences among grassland types that did not fall below the stringent significance thresholds could still have important ecological implications. Understanding how pollinator communities differ among grassland types is an

essential next step and necessary to demonstrate whether differences are truly ecologically significant. This study provides a valuable baseline for studies in the tallgrass prairie ecoregion to investigate the responses of various pollinator taxa to differences in floral resource availability among grassland types.

An important next step in understanding seasonal succession patterns in floral resource availability would be to quantify interannual variation among grassland types. It would also be valuable to investigate the degree to which pollinators switch between grassland types throughout the season in response to floral resource availability. For example, the abundance of floral resources was very high in non-remnants from rounds four through six (~15 June to ~13 July), and as such, these sites may have attracted pollinators from remnants.

Finally, future research should consider how short or infrequent sampling periods could bias scientific interpretation of the availability of floral resources and pollinator responses. For example, our ability to detect statistically significant differences among grassland types within some rounds but not others (even with very low significance threshold used to account for multiple tests) illustrates the importance of considering how sampling time within the season could influence interpretation of floral resource availability.

#### *Implications for conservation and management*

(1) *Old fields* were the grassland type most consistently different from remnant prairies. Given these findings, our results indicate that targeted efforts to enhance floral diversity on old fields could accomplish the largest potential change in resources for pollinators.

(2) *Conservation grazed cattle pastures* showed the greatest variability in composition turnover throughout the growing season. Interseeding native plant species that are tolerant of grazing and bloom during periods of low turnover could improve pollinator resources in conservation grazed cattle pastures.

(3) *Reconstructed prairies* showed the strongest midseason peak in richness of inflorescences, and differed in composition from remnants at the beginning and end of the season. Greater efforts to establish early and late blooming species to

better mimic remnant composition would enhance pollinator resources at these sites.

(4) *Remnant prairies* showed the largest difference in composition compared to the other three habitat types and supported the greatest abundance and richness of flowering native plants. The preservation of remnants will be essential for maintaining native pollinator diversity, particularly for insect and plant species with specialized plant-pollinator interactions.

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

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