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Evaluating Native Bee Communities and Nutrition in Managed Grasslands

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Abstract

Native pollinators are important for providing vital services in agroecosystems; however, their numbers are declining globally. Bees are the most efficient and diverse members of the pollinator community; therefore, it is imperative that management strategies be implemented that positively affect bee community composition and health. Here, we test responses of the bee and flowering plant communities to land management treatments in the context of grasslands in the upper Midwestern United States, a critical area with respect to bee declines. Twelve sites were selected to examine floral resources and wild bee communities based on three different types of grasslands: tallgrass prairie remnants, ungrazed restorations, and grazed restorations. Total bee abundance was significantly higher in ungrazed restorations than remnants, but there were no significant differences among grasslands in community composition or Shannon diversity. Across the three grassland types we also examined mass and lipid stores as nutritional health indicators in three sweat bees (Halictidae), *Augochlora pura*, *Agapostemon virescens*, and *Halictus ligatus*. Although there were no differences in lipid content, total average bee mass was significantly higher in *Ag. virescens* collected from ungrazed restorations as compared to remnants. Floral abundance of native and non-native species combined was significantly higher in grazed restorations compared to remnants and ungrazed restorations. However, ungrazed restorations had higher abundance and richness of native flowering ramets. These data suggest that bee abundance and nutrition are driven by high abundance of native flowering plant species, rather than total flowering plants.

Key words: native bees, grassland management, pollinator nutrition, prairie restoration, *Halictidae*

Pollinators provide important ecosystem services and our understanding of their contributions both ecologically and economically has been expanding over the past several decades. Among pollinators, the most efficient by far are bees (Batra 1995). Given their importance, it is concerning that native and domesticated bee populations are declining globally (Potts et al. 2010). Many factors have contributed to this unfortunate trend within native bee communities. The effects of disease, including *Nosema* and deformed wing virus, have recently been identified as potential contributors in native pollinator community declines (Otti and Schmid-Hempel 2007, Cameron et al. 2011, Vanbergen et al. 2013, Fürst et al. 2014). Insecticides such as neonicotinoids can also have detrimental effects on cognitive functions and feeding ability in native bee species (Whitehorn et al. 2012, Goulson 2013).

Although disease and insecticides have the potential to reduce populations of native bees, arguably the most important driving force of worldwide decline is habitat loss (Brown and Paxton 2009). The conversion of natural lands into agricultural systems can have wide-ranging negative impacts on native bees as well as

bee-dependent crops (Kremen et al. 2002). Thus, continued dependence of agricultural pollination on native bees makes the restoration of natural habitats imperative. This is especially true within the tallgrass prairie ecoregion of North America. Since the introduction of industrial agriculture, total land cover of native grassland in this region of the continent has declined by an estimated 99% (Samson and Knopf 1994) and recent increases in agricultural activity have only exacerbated this trend (Wright and Wimberly 2013). Restoring native prairie plant communities has the potential to slow this trend. By increasing the abundance, species richness, and diversity of flowering plants on a landscape, it is generally thought that the native bee community will respond with an increase in abundance, species richness, and diversity (Potts et al. 2003, Hines and Hendrix 2005, Roulston and Goodell 2011). However, simply planting flowering plants is not enough: the native or exotic status of flowering plants needs to be considered. Although native bees such as *Bombus* will visit exotic flowering plants and incorporate them heavily into their diets (Harmon-Threatt and Kremen 2015), preference is shown toward native plants (Morandin and Kremen 2013). Among native tallgrass

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prairie plants, bee preference is further reduced based on individual species, with bee visitation data being limited to a select list of native species (Davis et al. 2008, Holm 2017).

While bee community composition as a response to grassland management has been assessed in many studies, fewer studies have attempted to also consider health indicators, such as nutritional state, as an aspect of native bee conservation. In particular, grazing has been shown to limit the abundance and quality of floral resources on a landscape, and could lead to nutritional deficits in pollinators native to highly grazed regions (Buckles and Harmon-Threatt 2019). The Grand River Grasslands Region of Southern Iowa and Northern Missouri presents a promising opportunity for monitoring native bee community composition and health under different grassland management conditions. This region is home to a diverse matrix of agricultural, pastoral, and natural grasslands. Previous research in this region has identified three grassland types that comprise a significant portion of this landscape matrix (Delaney et al. 2015): tallgrass prairie remnants, ungrazed restorations, and grazed restorations. The mosaic of grassland types in the Grand River Grasslands provides an opportunity to assess connections between grassland management through both fire and grazing, native bee health, and flowering plant communities.

In this study, we compare the bee and flowering plant communities in these three grassland types in the Grand River Grasslands. Health of native bees was also compared among grassland management treatments. Previous grassland management studies related to health in the Grand River Grasslands have been conducted on large colonial bees such as *Apis mellifera* and *Bombus* species, and have suggested that high levels of grazing may be detrimental to the health of these social bees (Smith et al. 2016). However, data on smaller, socially variable species are lacking. Here, we compare nutritional indicators of adult bee health (average total mass, average total lipid mass, and relative lipid mass) of the three most common bee species collected during sampling, all within the family Halictidae (sweat bees): *Augochlora pura* (Say) (Hymenoptera: Halictidae), *Agapostemon virescens* (Fabricius) (Hymenoptera: Halictidae), and *Halictus ligatus* (Say) (Hymenoptera: Halictidae).

For this study, our hypotheses were as follows: 1) Tallgrass prairie remnants will support a higher abundance, higher species richness, higher Shannon diversity, and higher nutritional indicators (average total bee mass, average lipid mass, and relative lipid content) of bees compared to both ungrazed and grazed restorations. 2) Tallgrass prairie remnants will have a higher abundance, species richness, and Shannon diversity of *total* floral resources compared to both ungrazed and grazed restorations. 3) Tallgrass prairie remnants will have a higher abundance, species richness, and Shannon diversity of *native* floral resources commonly visited by native bees as compared to both ungrazed and grazed restorations.

Methods

Study Sites

In total, 12 field sites were selected within the Grand River Grasslands of Southern Iowa and Northern Missouri. Each site was categorized into one of three grassland types based on historic land use: tallgrass prairie remnant, ungrazed restoration, and grazed restoration (Table 1). Tallgrass prairie remnants are defined as areas of native tallgrass prairie cover which were never plowed and converted into agricultural lands during the settlement of Europeans in the area; these are currently managed through regular prescribed burns. Ungrazed restorations are areas of land that were once plowed to use for agricultural production but have since been cleared, reseeded with native tallgrass prairie plants; these are managed through prescribed burns to restore the original plant community. Grazed restorations are restorations (restored similarly to ungrazed restorations) where both grazing by cattle and fire are used as methods of disturbance for managing the native plant community.

Specimen Collection: Bee Bowls

Native bee sampling took place over two field seasons, 2015–2016, with each sampling period lasting from late May until early August. Bees were sampled every 2 wk within the field season. Bee specimens were captured using colored pan traps, or 'bee bowls'. A 100-m north-to-south transect which served as the bee bowl sampling area was established in a location not impeded by fences or topographic barriers within each remnant and ungrazed restoration. In grazed restorations, this transect was placed along the outside of the pasture fence to limit negative interactions from cattle. Six 1-m tall bamboo poles were placed evenly along each 100-m sampling transect and 3.25-fluid ounce plastic cups, called bee bowls, were attached to the side of each of the bamboo poles (Droege et al. 2010, Grundel et al. 2011). Bee bowls were left in the field for 24 h, after which they were collected, capped, and brought into the lab for processing and identification. The sampling of native bees only occurred when temperatures were greater than 18°C, and there was no precipitation.

After collection, specimens from each bee bowl were pooled, and bees were then sterilized using distilled water and a 75% ethanol solution and air-dried at room temperature until all moisture added during processing has evaporated, approximately 6 h. Each bee was grouped by sampling site and capture date and assigned an identification number for future analysis. Bees were identified to species level using identification keys created by discoverlife.org, except for individuals belonging to genus *Lasioglossum*, which were identified to subgenus. Following identification, specimens were frozen until lipid analysis or pinning.

Specimen Collection: Hand Netting

Hand net sampling was used to only sample large bees that generally do not get captured through bee bowl sampling *Bombus*, and *Xylocopa* (Roulston et al. 2007). Hand net sampling events occurred once during the 2015 field season in late July, and twice during the 2016 field season in late June and late July. Hand net sampling events were not conducted during the first half of June, to avoid the capture of emerging *Bombus* queens, and disrupting new colony formation. Hand net sampling events occurred over a standardized 20-min sampling period, where two observers would walk throughout a site, in a nonspecific pattern, seeking out large bees. Bees were captured using a hand net, and then transferred into site-labeled 'kill jars' where specimens were euthanized using diluted ethyl acetate. Sampling time was paused while capturing and handling bees. After capture, bees were immediately brought back to the lab and frozen until identification could occur.

Measurement of Nutritional Indicators

Bees species were selected for lipid analysis based on having a minimum abundance (16 individuals) within each of the three grasslands. Only female bees were selected for lipid analysis. Three species captured through bee bowl sampling met this criterion in the 2015 field season, *Au. pura*, *Ag. virescens*, and *H. ligatus*. No bees were selected from the 2016 field season due to low numbers of captured specimens. We randomly chose 64 individuals from *Au. pura*, 66 individuals from *Ag. virescens*, and 60 individuals from *H. ligatus*

Table 1. Experimental sites used in bee and floral resource sampling

Experimental site	Treatment	Location	Area (ha)
Luisi	Tallgrass prairie remnant	Harrison Co., MO	156
Parsons	Tallgrass prairie remnant	Harrison Co., MO	6.80
Ringgold North	Tallgrass prairie remnant	Ringgold Co., IA	17.8
Ringgold Southeast	Tallgrass prairie remnant	Ringgold Co., IA	12.0
Kellerton House	UnGrazed restoration	Ringgold Co., IA	11.8
Kellerton Tauke	UnGrazed restoration	Ringgold Co., IA	31.6
TNC Cemetery	UnGrazed restoration	Harrison Co., MO	3.60
TNC Forb	UnGrazed restoration	Harrison Co., MO	32.7
Kellerton North	Cattle-grazed restoration	Ringgold Co., IA	32.0
Lee Trail Road	Cattle-grazed restoration	Ringgold Co., IA	31.0
Pyland North	Cattle-grazed restoration	Ringgold Co., IA	32.0
Sterner	Cattle-grazed restoration	Ringgold Co., IA	46.9

from the pool of sampled specimens for lipid analysis. Before lipid extraction, whole bees were weighed using a microbalance to provide total mass. Lipids were extracted and quantified using methods adapted from those described in Toth and Robinson (2005).

Floral Resource Sampling

Floral resources were estimated to provide information about resource availability in bee sampling areas. To estimate floral resources, we recorded flowering plants along transects in 2015 and 2016, with sampling events taking place every 2 wk, at the same time as bee bowl sampling. Floral resource sampling was conducted using a modified Pollard walk technique (Pollard 1977). A 1- × 100-m quadrat was constructed on one side of the permanently established bee sampling transect. Observers travelled from one end of the transect to the other, counting every flowering ramet that was located within the sampling quadrat, and identifying plants to species (Moranz et al. 2012, Delaney et al. 2015). Plants commonly used by bees according visitation records in previous literature were referred to as 'bee floral resources' (Davis et al. 2008, Holm 2017). Plants that could not be identified in the field were collected, and later identified in the lab.

Statistical Analysis: Community Data

The goal of statistical analysis was to compare the total abundance, species richness, and Shannon diversity of native bees and flowering plants on each of the grasslands over 2 yr. To calculate abundance, bee specimens collected through bee bowl and hand net sampling were summed across temporal replicates within a season and across years for each experimental site. Species richness was defined as the total number of species or members of *Lasioglossum* subgenera collected in each site and grassland management treatment within each sampling year. We used the Shannon diversity index to calculate native bee diversity by sampling site for each year (Smith et al. 2016). Flowering ramet abundance was calculated similarly to native bee abundance. The total number of flowering ramets counted were summed across experimental site and treatment for both field seasons. Species richness was defined as the total number of flowering plant species identified in each experimental site and each management treatment. The Shannon diversity index was used to calculate flowering plant diversity (as in Smith et al. 2016). Statistical analysis for flowering plant data was repeated and applied only to native plant species that are commonly visited by bees (Davis et al. 2008, Holm 2017) (Table 2).

We used the R software package (R 3.3.1) to construct generalized linear mixed effects models (GLMER) assuming a Poisson distribution, using site and year as random effects to test for significant differences in native bee and flowering plant abundances and species richness among remnants, ungrazed restorations, and grazed restorations. Shannon diversity for each grassland management treatment for native bees and flowering plants was compared using linear mixed effects models (LMER) using site and year as random effects. All results from GLMER and LMER tests were graphed using the R-package 'ggplot2' for visual interpretation. This process was repeated for flowering plants commonly visited by bees. Ordination of community composition of bees and flowering plants was conducted using the PC-ORD software package (PC-ORD 6.08) to visualize community relationships in two-dimensional space. For the ordination analysis, 2015 and 2016 data were summed. Significant differences in species composition among grassland type were determined through the Permutational Multivariate Analysis of Variance (PERMANOVA) function within PC-ORD.

Statistical Analysis: Lipid Data

The goal of statistical analysis of lipid data was to compare average total bee mass, average total lipid mass, and average relative lipid content for *Au. pura, Ag. virescens*, and *H. ligatus* among grassland type. Concentration of lipids within extract solutions was estimated by fitting absorbance readings along a standard curve for pure cholesterol. Estimated concentrations of total lipids within the extract solutions allowed for total lipid mass to be calculated for each bee specimen. Relative lipid content was calculated by dividing lipid mass, by the total mass of each specimen. We used the R software package (R 3.3.1) to construct linear mixed effects models (LMER) using site as a random effect, for each individual species to test for significant differences in average total bee mass, average total lipid mass, and average relative lipid content among each grassland management treatment. Results from the constructed linear mixed effects models were graphed using the R-package 'ggplot2' for visual interpretation.

Results

Bee Data

Over two sampling seasons, 292 bee specimens belonging to 26 species were collected from remnants, the most common of which was *Au. pura*, comprising 28.0% of bees collected. In total, 625

Table 2. Abundances of flowering ramets found in three grassland management treatments collected in 2015 and 2016

	Status	Remnant		Ungrazed restoration		Grazed restoration	
		2015	2016	2015	2016	2015	2016
Achillea millefolium*	N	32	12	14	24	27	21
Agrimonia gryposepala	N	1	26	0	0	0	0
Asclepias purpurascens	N	2	0	0	0	0	0
Asclepias incarnata*	N	0	0	0	2	0	0
Asclepias verticillate*	N	0	0	0	0	3	0
Asclepias hirtella	N	0	0	0	0	1	0
Asclepias syriaca*	N	0	295	0	0	0	0
Asclepias tuberosa*	N	35	0	8	2	0	0
Baptisia alba*	N	0	1	0	0	3	6
Brassica napus	E	0	0	0	0	0	1
Chamaecrista fasciculata*	N	269	28	615	62	5	25
Cichorium intybus	E	0	0	2	0	0	6
Cirsium discolor*	N	0	0	1	0	0	0
Coreopsis palmata*	N	0	0	42	1	0	0
Coreopsis tripteris	N	0	0	0	1,044	0	0
Dalea purpurea*	N	0	0	17	94	0	0
Daucus carota	E	62	1,458	244	275	457	620
Desmodium canadense*	N	14	0	20	87	0	0
Dianthus armeria	E	0	6	22	0	9	72
Drymocallis arguta*	N	0	5	10	3	0	23
Echinacea pallida*	N	0	0	8	0	0	0
Erigeron strigosus*	N	6	270	125	478	513	668
Eryngium yuccifolium*	N	0	0	5	38	0	0
Euphorbia corollate*	N	49	0	0	0	0	0
Helianthus grosseserratus*	N	1	3	5	227	0	0
Heliopsis helianthoides*	N	0	0	0	3	0	0
Hypericum punctatum	N	12	57	7	0	0	0
Leucanthemum vulgare	E	0	0	0	64	1	6
Liatris spicata*	N	0	0	97	105	0	0
Lobelia spicate*	N	1	83	0	12	1	20
Lotus corniculatus	E	0	0	13	29	4,872	6,915
Medicago lupulina	E	0	20	0	28	0	630
Melilotus albus	E	11	131	1	3	0	105
Melilotus officinalis	E	9	0	6	91	44	38
Monarda fistulosa*	N	129	127	267	801	0	28
Oxalis stricta	N	0	1	0	0	82	3
Parthenium integrifolium*	N	0	0	0	3	0	0
Pastinaca sativa	E	3	46	0	2	0	0
Penstemon digitalis*	N	0	0	0	27	0	0
Persicaria maculosa	E	0	0	0	0	0	6
Plantago lanceolata	E	0	0	0	0	0	474
Potentilla recta	E	0	0	0	0	1	0
Prunella vulgaris*	N	0	19	0	0	62	22
Pycnanthemum pilosum	N	296	38	31	4	0	0
Pycnanthemum tenuifolium	N	0	3,189	0	177	85	54
Ratibida pinnata*	N	428	1,181	241	1,537	3	1
Rosa arkansana*	N	0	26	0	0	0	0
Rubus sp.	N	0	14	0	0	0	0
Rudbeckia hirta*	N	304	200	261	227	154	56
Ruellia humilis	N	0	5	0	0	24	2
Silphium integrifolium	N	52	0	21	238	0	0
Silphium laciniatum*	N	0	2	0	0	0	0
Silphium perfoliatum*	N	0	0	28	19	0	0
Sisyrinchium angustifolium	N	0	4	0	0	0	2
Solanum carolinense	N	0	17	0	16	11	235
Solidago canadensis*	N	0	0	13	75	0	0
Stellaria graminea	E	0	0	0	0	0	63
Taraxacum officinale*	N	0	0	0	0	0	4
Teucrium canadense*	N	0	4	0	0	9	8
Tradescantia bracteata*	N	8	16	39	43	0	0
Trifolium hybridum	E	0	0	0	29	1	12
Trifolium pretense	E	33	45	90	138	1,479	1,167
Trifolium repens	E	0	89	10	2	3,948	4,138
Verbena hastata*	N	0	0	0	0	0	27
Verbena stricta*	N	0	1	0	0	118	101
Verbena urticifolia	N	0	0	0	0	1	20
Vernonia fasciculata*	N	0	4	2	3	14	13
Veronica arvensis	E	0	0	0	0	60	0

Status indicated whether a plant species is native or exotic. N indicates a native flowering plant species. E indicates an exotic flowering plant species. Asterisks (*) indicate native plant species commonly visited by bees (Davis et al. 2008, Holm 2017).

specimens belonging to 41 species were collected from ungrazed restorations, the most common of which was the *Lasioglossum* subgenus, *Lasioglossum (Dialictus)*, comprising 29.4% of bees collected. In total, 446 specimens belonging to 37 species were collected from grazed restorations, the most common of which was again the *Lasioglossum* subgenus *Lasioglossum (Dialictus)*, comprising 34.8% of bees collected. Bee bowl sampling over two sampling seasons accounted for 1,290 collected individuals or 94.6% of total specimens (Supp Table 1 [online only]). Hand net sampling over two sampling seasons accounted for 73 collected individuals or 5.4% of total specimens. Samples from bowls and netting were pooled for all subsequent analyses.

The total abundance of bees was significantly higher in ungrazed restorations as compared to remnants ($z = 1.98$, residual df = 19, $P = 0.05$) (Fig. 1). However, no significant differences were found in grazed restorations compared to remnants ($z = 1.53$, residual df = 19, $P = 0.13$) or grazed restorations compared to ungrazed restorations ($z = -0.46$, residual df = 19, $P = 0.65$). No significant differences were found in species richness for ungrazed restorations ($z = 1.53$, residual df = 19, $P = 0.13$) or grazed restorations ($z = 1.47$, residual df = 19, $P = 0.14$) compared to remnants, or for ungrazed restorations and grazed restorations compared to each other ($z = -0.06$, residual df = 19, $P = 0.96$). Similarly, no significant differences were found in Shannon diversity for ungrazed restorations ($t = 1.18$, df = 21, $P = 0.25$) or grazed restorations ($t = 1.19$, df = 21, $P = 0.25$) compared to remnants, or for ungrazed restorations and grazed restorations compared to each other ($t = 0.10$, df = 21, $P = 0.99$). Differences in the bee community composition did not show any significant differences among grassland type ($F = 0.83$, df = 23, $P = 0.68$).

Average total bee mass was significantly higher in *Ag. virescens* collected from ungrazed restorations compared to those collected from remnants ($t = 3.11$, df = 2.41, $P < 0.01$). There were no significant differences in total bee mass for *Au. pura* or *H. ligatus* among

the three grasslands. Average total lipid mass was marginally significantly higher in *H. ligatus* collected from ungrazed restorations as compared to those collected from remnants ($t = 1.70$, df = 57.00, $P = 0.09$). No significant differences in average total lipid mass were observed for *Au. pura* or *Ag. virescens* among the three grasslands. No significant differences were found when comparing relative lipid content among the three grasslands for any of the bee species examined (Table 3).

Flowering Plant Data

Over two sampling seasons, remnants had a total of 9,180 flowering ramets, with native species comprising 79.2% of total floral abundance. Ungrazed restorations over 2 yr had a total of 8,278 flowering ramets, with native species comprising 87.3% of total floral abundance. Grazed restorations over 2 yr had a total of 27,580 flowering ramets, with native species comprising 8.9% of total floral abundance. The total abundance of flowering ramets was significantly higher in grazed restorations compared to both remnants ($z = 2.72$, residual df = 19, $P < 0.01$), and ungrazed restorations ($z = 2.50$, residual df = 19, $P = 0.01$) (Fig. 2). No significant differences were found in Shannon diversity for ungrazed restorations ($t = 1.82$, df = 9, $P = 0.10$) or grazed restorations ($t = 0.08$, df = 9, $P = 0.94$) compared to remnants, or for ungrazed restorations and grazed restorations compared to each other ($t = 1.75$, df = 9, $P = 0.12$). Differences in plant community composition, however, can be seen in ordination space between ungrazed and grazed restorations. The plant communities in remnants and ungrazed restorations were similar in species composition, while grazed restorations remained distinct, indicating a unique community composition of floral resources. PERMANOVA analysis of the ordination data showed that the flowering plant community in grazed restorations was significantly different compared to both remnants ($t = 2.33$, df = 23, $P < 0.01$) and ungrazed restorations ($t = 2.41$, df = 23, $P < 0.01$) (Fig. 2).

When floral analysis was restricted to native flowering plant species commonly used by bees as a source of nectar, native flowering ramet abundance was significantly lower in grazed restorations as compared to ungrazed restorations ($z = -2.22$, residual df = 19, $P = 0.03$) (Fig. 3). Species richness of flowering plants was also significantly lower in grazed restorations compared to ungrazed restorations ($z = -2.78$, residual df = 19, $P = 0.01$). Shannon diversity was significantly higher in ungrazed restorations than cattle grazed restorations. Ungrazed restorations were numerically higher in native flowering plant abundance, species richness, and diversity as compared to tallgrass prairie remnants, although there were no statistically significant differences.

Discussion

The results of this study indicate that grasslands under different management regimes support different native bee communities. In contrast to our original hypothesis, bees were more abundant in ungrazed restorations than tallgrass prairie remnants, and grazed restorations were intermediate. Also, contrary to our prediction that bee species richness and Shannon diversity would be highest in tallgrass prairie remnants, we found no significant differences among any of the grassland types. Mirroring the bee abundance result, we found some indication that ungrazed restorations best supported the nutritional health of two sweat bee species. Specifically, average total mass of *Ag. virescens* from ungrazed restorations was significantly higher than from remnants. Similarly, total average lipid mass was marginally significantly higher in *H. ligatus* collected in
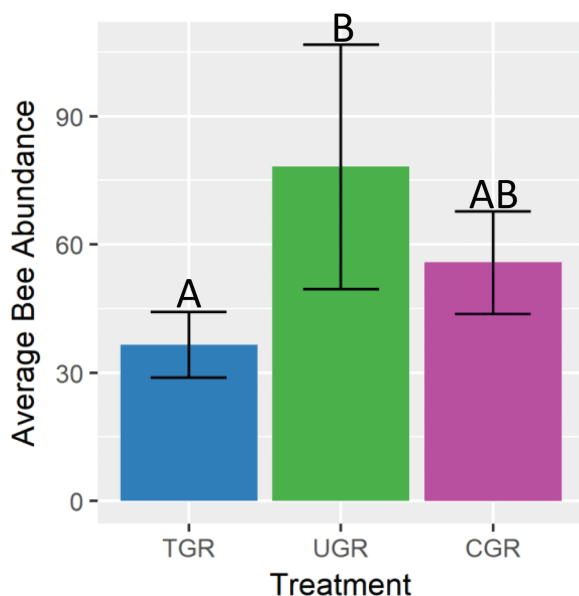

Fig. 1. Measures of average bee abundance among three grassland management treatments for 2015 and 2016. TGR indicates tallgrass prairie remnants, UGR indicates ungrazed restorations, and CGR indicates cattle-grazed restorations. Different letters indicate statistically significant differences at the *P* < 0.05 level. Bars indicate standard error.

Table 3. Average nutritional indicator values for three bee species among three grassland management treatments

Bee species	Treatment	Average bee mass (mg)	Average total lipid mass (mg)	Average relative lipid content (mg/mg)
Agapostemon virescens	Tallgrass prairie remnant	17.94 (SE = 0.88a)	1.54 (SE = 0.25)	0.09 (SE = 0.01)
	Ungrazed restoration	*22.05 (SE = 1.26b)*	1.93 (SE = 0.36)	0.09 (SE = 0.02)
	Cattle grazed restoration	19.67 (SE = 1.23ab)	1.56 (SE = 0.36)	0.08 (SE = 0.02)
Augochlora pura	Tallgrass prairie remnant	7.15 (SE = 0.48)	2.04 (SE = 0.24)	0.30 (SE = 0.49)
	Ungrazed restoration	7.57 (SE = 0.67)	2.11 (SE = 0.33)	0.31(SE = 0.69)
	Cattle grazed restoration	7.50 (SE = 0.63)	2.00 (SE = 0.33)	0.28 (SE = 0.64)
Halictus ligatus	Tallgrass prairie remnant	8.13 (SE = 0.68)	1.24 (SE = 0.31)	0.16 (SE = 0.03)
	Ungrazed restoration	9.84 (SE = 0.90)	1.94 (SE = 0.41)	0.20 (SE = 0.04)
	Cattle grazed restoration	9.62 (SE = 0.89)	1.78 (SE = 0.41)	0.19 (SE = 0.04)

SE indicates standard error, and letters (a, b) indicate significance at the *P* < 0.05 level. Data in bold and italics indicates a significantly higher value for bees found in the treatment.
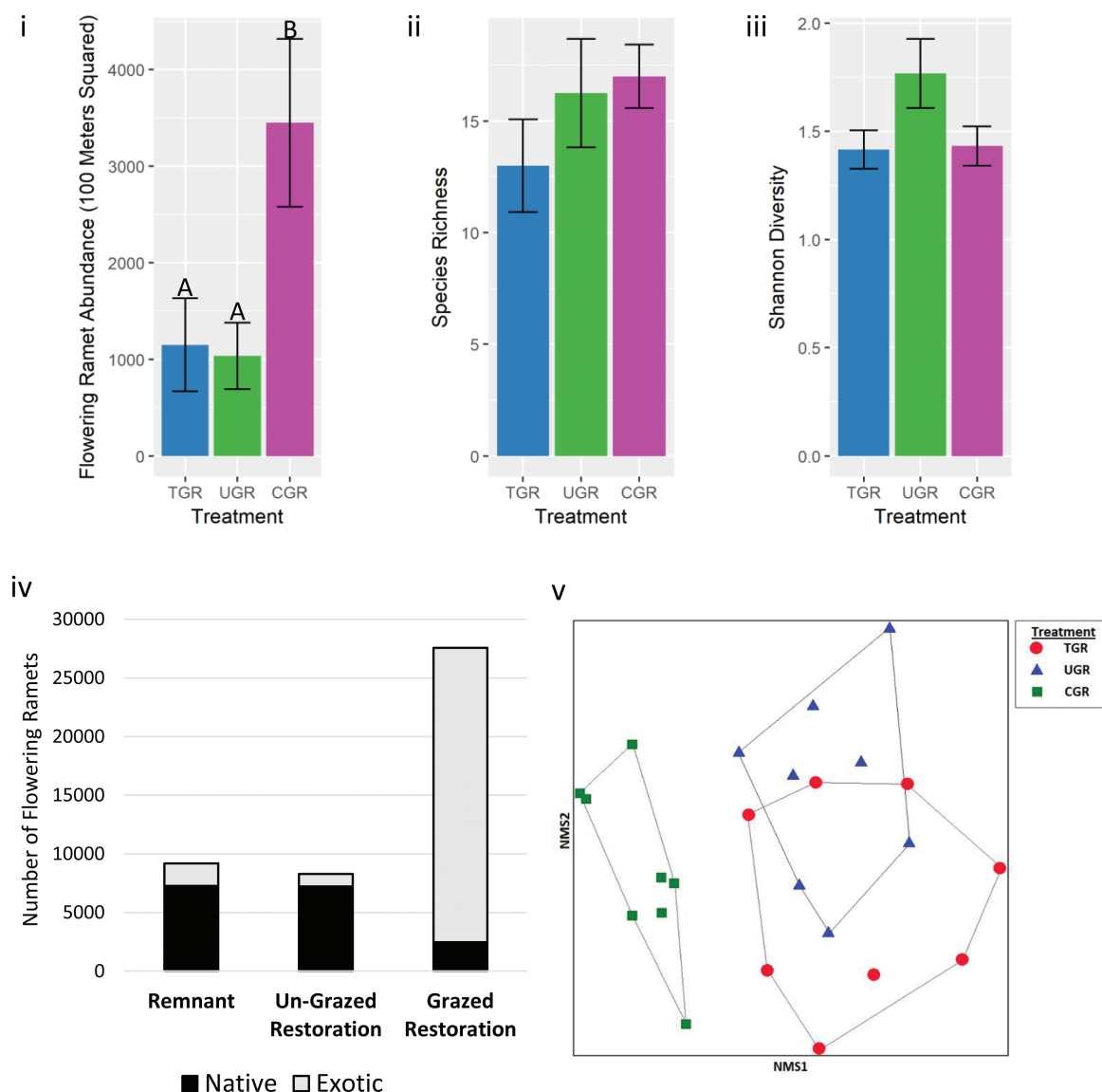

Fig. 2. Measures of (i) abundance, (ii) species richness, (iii) Shannon diversity, (iv) abundance of native and exotic flowering ramets, and (v) Bray–Curtis ordination for all species of flowering ramets among three grassland management treatments. TGR indicates tallgrass prairie remnants, UGR indicates ungrazed restorations, and CGR indicates cattle-grazed restorations. Different letters indicate statistically significant differences at the *P* < 0.05. Bars indicate standard error.
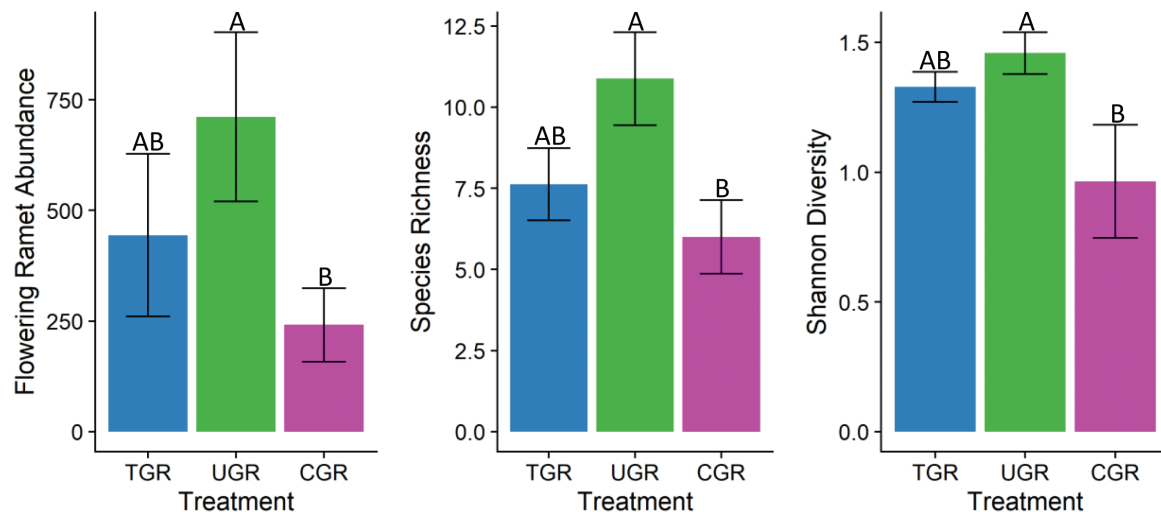
Fig. 3. Measures of (i) average ramet abundance, (ii) average species richness, and (iii) Shannon diversity for native flowering ramets among three grassland management treatments. TGR indicates tallgrass prairie remnants, UGR indicates ungrazed restorations, and CGR indicates cattle-grazed restorations. Different letters indicate statistically significant differences at the $P < 0.05$ level. Bars indicate standard error.

ungrazed restorations as compared to those collected in remnants. Taken together, these data suggest ungrazed restorations may provide good-quality habitat to support native bee abundance and nutritional health.

These findings are similar to results from some other insect communities, namely beetles, which also had greater abundances in restorations than remnant prairies (Larsen and Work 2003). In contrast, these findings are a departure from other previous insect community studies within tallgrass prairies, where tallgrass prairie remnants generally contained the highest number of species and the greatest level of diversity (Bomar 2001, Nemec and Bragg 2008). Similarly, studies of butterfly pollinators often show greater numbers of species and diversity in tallgrass prairie remnants rather than restorations (Shepherd and Debinski 2005, Moranz et al. 2012). However, community trends of butterflies are not always accurate predictors of bee community responses in grassland systems (Davis et al. 2008), and our data confirm this is also the case in the context of tallgrass prairie restoration. Although causes of differential insect responses to grassland management are not known, they may relate to how these insects use the flowering plant community within these grasslands.

Flowering plant communities in the different grassland types were assessed with the goal of providing insights into the bee responses we observed. In contrast to our original hypothesis, grazed restorations had significantly higher abundances of flowering ramets compared to both remnants and ungrazed restorations. However, the majority of these ramets were exotic species, primarily *Lotus corniculatus* and *Trifolium* species. Some of these exotic plants may provide forage for native bee species. For example, legumes such as *Trifolium* have been shown to provide high-quality forage for wild *Bombus* and *Osmia* species (MacIvor et al. 2013). Also, in contrast to our original hypothesis, remnants did not have higher levels of floral diversity than restorations. Instead, ungrazed restorations, although not significantly, had higher levels of floral diversity compared to remnants and grazed restorations, departing from previous literature (Polley et al. 2005). A reason for this increased diversity in ungrazed restorations could be a result of 1) seeding involved in the restoration of these sites which was not present in remnants,

and 2) grazing that may be removing both plant biomass and diversity. The flowering plant abundances found in the different grassland types did not reflect the patterns of bee abundance, mass, and lipid content.

We further investigated a subset of the plant community that may be more relevant to native bees, specifically native species of flowering plants commonly used by bees as sources of nectar (Davis et al. 2008, Holm 2017). This flowering plant abundance was significantly higher in ungrazed restorations as compared to grazed restorations. This follows a similar trend to the bee abundance results, suggesting that high floral abundance of native flowering plant species can result in high bee abundance. Species richness of native plants showed similar results. Ungrazed restorations had the highest number of native flowering plants among each grassland type, and was significantly higher than grazed restorations, illustrating that areas with high abundance and richness of native flowering plant species that bees commonly use also had high levels of bee abundance. This could explain why grazed restorations, with higher total floral resources but fewer native floral resources, had lower average bees collected compared to ungrazed restorations. Further, higher levels of abundance and species richness of native flowering plants may also explain the results of the bee nutritional analyses, in which *Ag. virescens* had significantly higher total mass, and *H. ligatus* had marginally higher lipid mass in specimens collected from ungrazed restorations.

This study provides a foundation for describing the community composition and health of bees within a grassland matrix of the tallgrass prairie ecoregion. Although cattle-grazed sites had high flowering plant abundance, they were predominantly exotic plants, whereas ungrazed restorations had the highest native flowering resources, in terms of total native flowering ramets and total native flowering plant species. Thus, although a site may appear full of flowers, this is not necessarily an indicator of its value as bee forage; in fact, we found a negative correlation between total average floral abundance and bee abundance. Instead, native bees responded positively to ungrazed grasslands with higher levels of native flowering resources. These results concur with Smith et al. (2016) who found that bee nutritional indicators were negatively correlated with cattle

stocking rate. Thus, cattle grazing, at least at the moderate to high stocking rates (0.98–1.72 Animal Unit Months [AUM]) in our study sites, may shift flowering plant communities in ways that reduce forage availability for bees. It is worth noting that Smith et al. (2016) focused on *Apis melifera* and *Bombus*, bees which forage regularly on exotic plants which are highly abundant in cattle-grazed sites. However, in this study these bees were only a minority of what was sampled, and thus did not drive total bee abundances.

A common theme among the flowering plant and native bee community results from this study is the seemingly lower quality of the remnants compared to the restorations. The remnant sites were significantly lower in bee abundance as compared to ungrazed restorations, and significantly lower in flowering ramet abundance compared to grazed restorations. Additionally, remnants had a significantly lower number of native flowering ramet species than restorations. On the face of it, such findings of this study seem to indicate that the tallgrass prairie remnants we examined are not as valuable for conserving for native bees. However, the remnant sites in this study had a lower density of flowering plants compared to the other treatments (Moranz et al. 2012). These grass-dominated sites are expected to provide less forage for bees across the landscape. Additionally, the sheer number of flowering ramets, even including some exotic plants, in the grazed grasslands may have provided some advantage over the remnants.

This study shows the potential value of integrating bee nutritional health indicators into studies of bee conservation. In this study, we measured only three such indicators (mass and lipid content) in a small subset of species. In future studies, several variables could be considered to better understand nutritional responses of bees to different habitats. A shortcoming of the methods used in this study might explain the low pollinator richness in remnants and grazed restorations. Bee bowls which were used to collect the majority of our native bee specimens only account for the capture of approximately half of the native bee species found in an area (Grundel et al. 2011). Additionally, observed species are confounded by abundance (Gotelli and Colwell 2001). To avoid these shortcomings, future studies will need to have bee bowl sampling paired with extensive sweep and hand net collection as well as statistical species richness estimation through rarefaction as opposed to simple observed species counting. Temporal analysis could be applied to assess the shifting levels of nutritional quality in native bees across multiple sampling events. Seasonal floral resource can be present for a longer period of time in prairie remnants as compared to restorations (Delaney et al. 2015). Thus, it is important to examine pollinator responses throughout the season. Similarly, average levels of floral abundance, species richness, and diversity during sampling events could provide further insight into the shifting levels of relative lipid content in captured specimens, considering that constant floral resources must be available throughout the season to provide adequate forage for native bees (Williams et al. 2012, Persson and Smith 2013). Finally, moving forward it will be important to consider how different bees species representing different functional groups related to nesting, feeding, and social strategy respond to availability of floral resources in the context of different grassland management strategies.

Supplementary Data

Supplementary data are available at *Environmental Entomology* online.

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