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Compositional Shifts in Forb and Butterfly Communities Associated with Kentucky Bluegrass Invasions☆

Katherine C. Kral-O'Brien [a,*], Ryan F. Limb [a], Torre J. Hovick [a], Jason P. Harmon [b]

[a] Range Science Program, North Dakota State University, Fargo, ND 58102, USA
[b] Department of Entomology, North Dakota State University, Fargo, ND 58102, USA

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ABSTRACT

Rangeland management strategies impact biodiversity, the quality and quantity of ecosystem services, and overall rangeland resiliency. Previous management strategies, coupled with climate change, have led to widespread invasion by Kentucky bluegrass (*Poa pratensis;* bluegrass) in the Northern Great Plains, United States. Bluegrass invasions are expected to have detrimental impacts on biodiversity conservation and ecosystem services provided by rangelands. Yet none have investigated how bluegrass invasions influence pollinator populations, which are a prominent conservation concern and provide ecosystem services. We measured the impact of bluegrass invasion on mixed-grass prairie forb and butterfly communities. Obligate grassland butterflies, those that rely on grasslands, decreased as bluegrass cover increased, including the threatened *Hesperia dacotae*. Conversely, the abundance of facultative grassland butterflies, those found in grasslands but not fully dependent on them for their life history, increased as bluegrass increased. Moreover, plant species diversity and flowering forb species richness decreased as bluegrass cover increased. Overall, bluegrass invasion led to butterfly and plant community simplification, signaling a loss of biodiversity and potentially ecosystem services. Our research is the first to quantify how grassland butterflies and the floral resources they depend on are negatively impacted by bluegrass invasion. Resource managers should adopt management strategies that reduce bluegrass cover and improve nectar and host resources for obligate grassland butterflies. Management choices that removed disturbance regimes inherent to the Northern Great Plains (i.e., fire and grazing) led to bluegrass dominance in the region. Therefore, restoring disturbance regimes may be one way to reduce bluegrass and benefit pollinator populations.
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Introduction

Rangelands provide a wide array of ecosystem services including food and fiber, nutrient and water cycling, recreation, and pollination (Havstad et al., 2007). Land managers are able to capitalize on specific ecosystem services through various management strategies. However, the way in which individuals manage rangelands in the United States has changed dramatically over the past century (Fuhlendorf et al., 2012), some causing plant shifts and disruptions in ecosystem service provisioning (Grant et al., 2009). Before the Dust Bowl in the early 1930s, rangelands were commonly overgrazed to maximize livestock production (Hurt, 1985). After the Dust Bowl, overgrazing was discouraged to reduce rangeland degradation with either conservation strategies (moderate, uniform grazing) to prioritize increased rangeland sustainability or preservation strategies to remove grazing entirely (Holechek et al., 2004; Fuhlendorf et al., 2012). These management shifts were successful at reducing soil erosion, but uniform disturbance or lack of disturbance reduces heterogeneity and biodiversity (Fuhlendorf and Engle, 2001; Hovick et al., 2015). Currently, resource managers are adopting management strategies to conserve patterns and processes of rangelands by restoring interacting fire and grazing disturbances to increase heterogeneity and rangeland biodiversity (Fuhlendorf et al., 2012; Bowman et al., 2016). A large proportion of research has focused on the consequences of these broad management changes for plant communities and livestock production (see Briske, 2011), but more research is necessary to fully understand how previous management strategies impact grassland-dependent wildlife.

Idle management strategies in grasslands of the Northern Great Plains represent one example of how altering management in disturbance-prone landscapes can impact plant communities and grassland-dependent wildlife. Approximately 50% of the nation's waterfowl are produced in the prairie pothole region of the Northern Great Plains (Naugle et al., 2001), and livestock production was viewed as incompatible with increasing dense nesting cover for waterfowl and other grassland birds (Murphy and Grant, 2005; Bullock et al., 2016). Therefore, resource

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* Correspondence: Katherine C. Kral-O'Brien, 204A Hastings Hall, 1320 Bolley Dr, Fargo, ND 58102, USA. Tel.: +1 701 231 7582.
E-mail address: kralx009@gmail.com (K.C. Kral-O'Brien).

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managers on public lands removed livestock grazing and promoted rest (i.e., preservation) in the mid-1930s to improve nesting conditions for grassland birds (Grant et al., 2009; Bahm et al., 2011). Although no longer widely used after the 1990s (Grant et al., 2009), years of rest (idle management) created significant changes in these rangelands, including increased invasive plant species (Toledo et al., 2014; Limb et al., 2018). For example, plant community composition on US Fish and Wildlife Service (USFWS) properties is dominated by several invasive species, including Kentucky bluegrass (*Poa pratensis* L.), which currently composes approximately 30% of the plant community on USFWS properties in North Dakota (Kobiela et al., 2017).

Kentucky bluegrass (hereafter bluegrass) is an invasive, cool-season grass that has spread across rangelands in the Northern Great Plains over the past several decades (DeKeyser et al., 2015). Bluegrass cover has increased both in rangelands with a history of idle management commonly found on public lands (Bahm et al., 2011) and on private lands that have been continuously grazed at moderate to high levels (Murphy and Grant, 2005; Toledo et al., 2014). Bluegrass is able to outcompete native cool-season grasses in the presence or absence of grazing due to earlier spring growth activity and rapid spread associated with vegetative reproduction (Cully et al., 2003; Prosser et al., 2003). Quickly spreading rhizomes create a thick thatch layer that helps bluegrass outcompete native plant species for water, nutrients, and light (Pierson et al., 2002; DeKeyser et al., 2013). Consequently, bluegrass monocultures significantly decrease plant and animal species diversity (Cully et al., 2003; DeKeyser et al., 2015).

Conservation efforts focused on limiting biodiversity losses and improving the delivery of ecosystem services frequently emphasize negative impacts of invasive species (Cardinale et al., 2012; Bezemer et al., 2014). In several locations, invasive plant species have been responsible for homogenizing plant communities (Gerber et al., 2008), displacing native wildlife (Washburn et al., 2000), and reducing the delivery of some ecosystem services (Clavel et al., 2011; Hanley et al., 2015). Similarly, bluegrass invasions have been found to reduce plant diversity (DeKeyser et al., 2013), disrupt water and nutrient cycling (Pierson et al., 2002), and threaten ecosystem services (Toledo et al., 2014). Even though bluegrass can seasonally provide valuable forage for livestock (Schlaepfer et al., 2011), bluegrass invasions are expected to have severe consequences for wildlife resource availability (Toledo et al., 2014). However, no studies to date have directly assessed the impacts of bluegrass on higher trophic levels above primary producers (i.e., the plant community), such as butterflies that provide ecosystem services.

Butterflies, along with other pollinators, are a major conservation concern because they are facing worldwide declines (Lebuhn et al., 2013). Pollinator responses to invasive species are not well understood (Pejchar and Mooney, 2009), but invasive species are expected to negatively impact butterflies and may even act in synergy with other drivers of declines such as fragmentation or climate change (Keeler et al., 2006). Moreover, the impacts of invasive species on regulating services like pollination—globally valued at over $215 billion annually for crops and wild plants (Vanbergen et al., 2013) —may be more detrimental than invasive species impacts on provisioning services such as livestock production (Pejchar and Mooney, 2009). Consequently, researchers, resource managers, and policy makers need to understand how butterflies respond to invasive plant species to improve conservation efforts and more thoroughly understand the wider impacts of invasive species (Bezemer et al., 2014). In addition, butterflies can be used to identify the ecological consequences of bluegrass invasion, including impacts on biodiversity. Butterflies are regularly used as bioindicators (Thomas, 2005; Potts et al., 2010; Roy et al., 2015; Habel et al., 2015) because they are sensitive to environmental factors and respond to vegetation shifts before other organisms (Mortimer et al., 1998; Börschig et al., 2013).

Invasive plant species can impact butterflies (Bezemer et al., 2014; Hanley et al., 2015), but not all species will respond the same to invasive plant species and plant community homogenization (Filz et al., 2013; Habel et al., 2015; Kral et al., 2018b). Therefore, the overarching goal of our research was to quantify whether bluegrass invasions influence butterflies in rangelands of the Northern Great Plains. Specifically, our objectives were to evaluate the entire butterfly community to determine how species or groups of species respond to varying levels of bluegrass invasion. Our results can help determine how bluegrass has impacted biodiversity in rangelands. Moreover, our results can help identify specific butterfly species that may be useful as indicators of biodiversity or bluegrass invasion, directing management strategies and conservation planning.

Methods

Study Area

We collected butterfly and vegetation data in North Dakota, South Dakota, and Minnesota (Fig. 1). In the region, temperatures average 5.5°C, varying throughout the year from −17°C to 23°C. The majority of precipitation falls during the growing season and follows a strong gradient east to west, decreasing from 69 cm to 36 cm (USDA-NRCS, 2015). The plant community was historically tallgrass prairie in the east and mixed-grass prairie in the west. The tallgrass prairie was largely composed of native, warm-season grasses (*Andropogon gerardii* Vitman, *Schizachyrium scoparium* [Michx.] Nash), and the mixed-grass prairie was largely composed of native, cool-season grasses (*Nassella viridula* [Trin.] Barkworth, *Pascopyrum smithii* [Rydb.] Á. Löve). The forb community is similar across prairie types, being dominated by *Aster* spp. and *Solidago* spp. (USDA-NRCS, 2015). However, invasive, cool-season grasses such as *Bromus inermis* Leyss. and bluegrass have become dominant in many grasslands throughout the region (Murphy and Grant, 2005).

Survey Sites

We surveyed 20 sites in 2015, 25 sites in 2016, and 26 sites in 2017. Most sites were surveyed multiple years, but we surveyed a total of 35 unique sites over 3 yr of data collection. We selected a majority of our survey sites from USFWS refuge lands, but we also surveyed some privately owned or nongovernmental organization areas in our study region (for full details see Kral et al., 2018b). Most sites were managed with different combinations of cattle grazing (16 sites) and prescribed fire (10 sites); however, several sites had idle management (9 sites). Because of inherent differences in site history and management, bluegrass cover ranged from 3% to 36% canopy cover (Table S1; available online at https://doi.org/10.1016/j.rama.2018.10.003).

Butterfly Surveys

We collected butterfly community data including species composition, richness, diversity, and abundance using two different methods at each site. We randomly placed two, 100-m line transects (Moranz et al., 2012) and two, 4-ha visual encounter survey blocks (Hardersen and Corezzola, 2014; Harms et al., 2014) at each site. Each year, we surveyed sites three times between June and early August. We rotated the time of day and order of surveys to reduce temporal bias. Furthermore, we conducted surveys between 0900 and 1800 hours (CDT) during optimal field conditions for butterflies: air temperatures between 21°C and 35°C, winds under 25 km · hr^{-1}, and cloud cover <50% (Royer et al., 1998). During line transect surveys, observers walked at a rate of 10 m · min^{-1} and recorded all butterflies to either side of the line and ahead of the observer, with no width constraints (Moranz et al., 2012; Kral et al., 2018b). During visual encounter surveys, observers walked at a rate of 25 m · min^{-1} for 30 minutes in a back-and-forth pattern and recorded butterflies observed within the survey block (Hardersen and Corezzola, 2014). Observers would start searching approximately 25 m in from the edge of one end of the survey block and walked a straight line until approximately 25 m from the top edge of

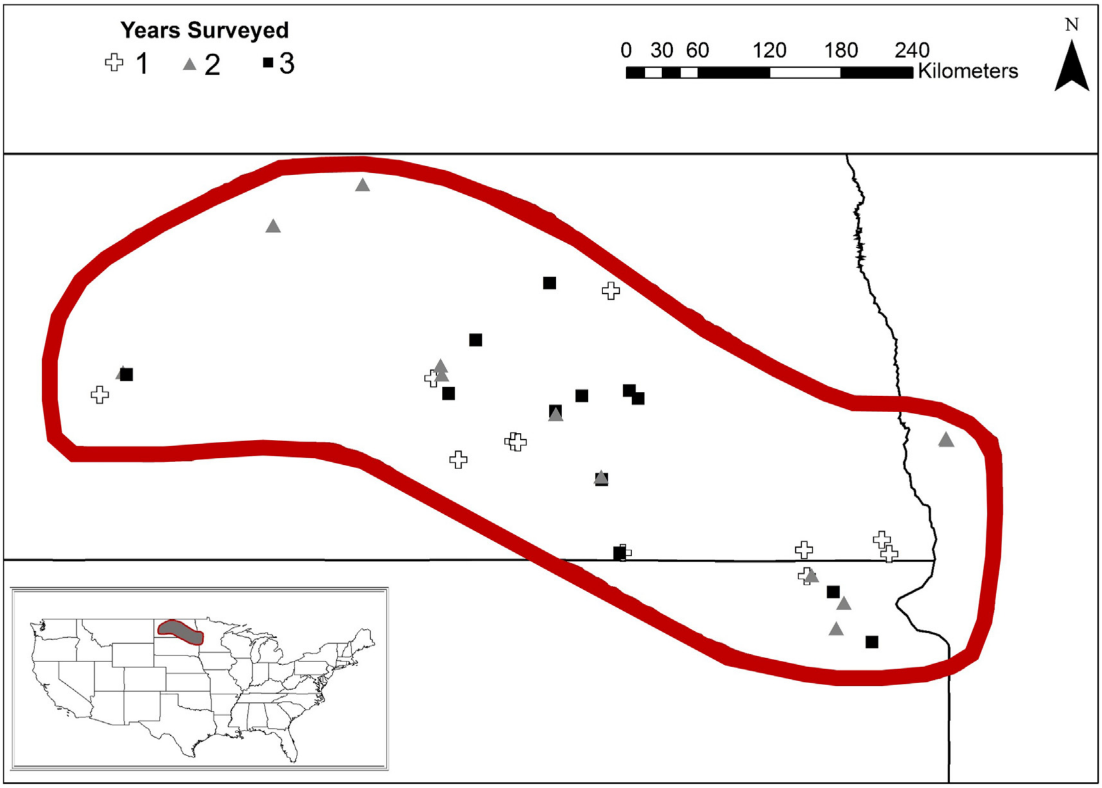

Figure 1. Location of butterfly surveys conducted from 2015 to 2017 in North Dakota, South Dakota, and Minnesota, United States (Geographic Coordinate System, World Geodetic Survey 1984 Projection). Thirty-five sites were surveyed over 3 yr, with each site surveyed at least 3 times in the yr(s) it was surveyed.

the block. The observer would then walk approximately 50 m perpendicular from the end of the first "transect" searched in the survey block, taking care to only record individuals on their first detection. This process was repeated until observers were at the opposite end of the survey block from where they started. If a butterfly could not be identified, observers suspended their survey, took a picture or attempted to capture the butterfly with a net, and then resumed the survey at the stopped point. During each site visit, two observers surveyed one line transect and one survey block each. On subsequent visits, observers rotated to reduce observer bias.

Vegetation Surveys

We collected plant community data to quantify cool-season grass invasion and resource availability for butterflies. We recorded species and counted the number of flowering ramets along eight, 100-m transects in 5-m belts during each site visit to obtain nectar resource density (Moranz et al., 2012). We established belts around the 100-m line transect and three more belts in each 4-ha survey block, which were also 100 m in length. During peak plant production in late July, we estimated average plant species canopy cover at each site using 30, 1-m^2 quadrat frames. We placed six evenly distributed quadrat frames along each line transect and nine evenly distributed quadrat frames within survey blocks. We then visually estimated absolute canopy cover to the nearest percent and placed each species in cover classes (0 — 5, 5 — 10, 10 — 20, 20 — 30, 30 — 40, 40 — 50, 50 — 60, 60 — 70, 70 — 80, 80 — 90, 90 — 95, and 95 — 100). Although we were largely interested in the cover of invasive cool-season grasses, we collected composition and canopy cover for all plant species.

Landscape Cover

We collected landscape cover data around each site to quantify the influence on the butterfly community. We buffered each site with a radius of 1 000 m around a point in the middle of each pasture (Pocewicz et al., 2009; Perović et al., 2015) and determined land cover, including each survey site, using USGS National Land cover datasets in ArcGIS v. 10.2 (ESRI, 2013). We only buffered to 1 000 m because we previously found this distance to be more influential for a larger proportion of the butterfly community, and most landcover variables were correlated with each other at larger buffer sizes (e.g., 2 500 m) (Kral et al., 2018b). Within each buffer, we calculated the percentage of major cover types including perennial grassland, wetland, hay ground, open water, cropland, and development (roads, buildings, etc.).

Analysis

We conducted all our statistical analyses in the R (v. 3.1.3) statistical environment for Windows (R Development Core Team, 2015). We determined butterfly community composition at each site by identifying all species detected by either method within each year. In addition, we categorized species on the basis of their dependence on grasslands (facultative or obligate) using descriptions from Glassberg (2001) and Royer (2003). To be included in our community analysis, a species had to be detected at least twice because we were interested in rarer species but wanted to remove species with limited detections (Blanchet et al., 2014). Species with limited detections may be rare, but they may also be anomalies associated with weather patterns or irruptions and not indicative of sites supporting rare species. Then we summed abundance data for each species over site visits in each year (Davis et al., 2008) and averaged species site abundance over the 3 yr of data collection for our multivariate analysis. We used nonmetric multidimensional scaling (NMDS) with Bray-Curtis distance measures to create community ordination plots in the *vegan* package (Kindt and Coe, 2005; Oksanen, 2015). In NMDS, site scores are plotted as points, and the distances between sites allow us to determine the similarity or dissimilarity of the butterfly community (Moranz et al., 2012; Oksanen, 2015). Sites that are closer together in ordination space are more similar.

Moreover, species are also plotted as points and are plotted next to sites where they are relatively more abundant. We considered three-dimensional ordinations with stress values under 0.20 to be acceptable (Clark, 1993).

We used the function "envfit" within the *vegan* package to test how the ordinated butterfly community was influenced by vegetation variables (ramet density, bluegrass canopy cover, flowering forb species richness, flowering forb species diversity, plant species richness, and plant species diversity); landscape variables (perennial grassland, wetland, hay ground, open water, cropland, and development cover; see Table S1); and management strategies. Before variables were used in our community analysis, we tested for correlations and eliminated correlated variables ($r \geq 0.60$; Marini et al., 2009; Harms et al., 2014). Flowering forb species richness and diversity were highly correlated ($r^2 = 0.60$), along with plant species richness and diversity ($r^2 = 0.72$). However, flowering forb species richness and diversity were not correlated with plant species richness and diversity ($r^2 = 0.31$ and 0.27, respectively). We chose to include forb species richness and plant species richness in our analysis, eliminating forb and plant diversity, on the basis of previous research (see Moranz et al., 2012). At the landscape scale, perennial grassland and cropland cover were negatively correlated ($r^2 = -0.78$). If vegetation or landscape variables were significantly related with the butterfly community ($\alpha \leq 0.05$), we included them as vectors in our ordination plots (Moranz et al., 2012).

Next, we used generalized linear mixed-effect modeling (GLMM) to quantify the influence of bluegrass (fixed effect) on single variables. Whereas other studies have used univariate analyses to inform individual species responses or treatment effects (e.g., Moranz et al., 2012; Hovick et al., 2015), we used GLMM to determine relationships with variables of interest (i.e., plant and butterfly community metrics and bluegrass cover). GLMM allowed us to determine how single vegetation variables used in the community ordination and butterfly variables including butterfly species richness, butterfly species diversity, total butterfly abundance, obligate grassland butterfly richness, obligate grassland butterfly abundance, and facultative grassland butterfly abundance responded to bluegrass cover (see Table S1). Using the *lattice* package, we created GLMMs with Gaussian and Poisson distributions, depending on variable distribution, to compare univariate variables to bluegrass cover at the site level (Bates et al., 2015). We used log-transformations as needed to normalize variables in models with Gaussian distributions (Crawley, 2013). Similar to the multivariate analysis, we summed abundance data for each species over site visits in each year to get an average site abundance (Davis et al., 2008), but instead of averaging at the site level, we incorporated year and site as random factors in GLMMs (Price et al., 2005) to account for sites surveyed multiple years. In addition to our main models, we used analysis of variance to test for differences in bluegrass cover between management strategies (burned, grazed, or idled). For each analysis, we set an $\alpha \leq 0.05$ to indicate statistically significant differences between factors.

Results

We detected > 11 000 butterflies representing 45 species from 2015 to 2017. Of these 45 species, we used 39 species that met our minimum threshold of being detected at least twice (Table 1). Overall, we detected 12 obligate grassland butterflies (4 173 detections) and 27 facultative grassland butterflies (6 917 detections; see Table 1).

Butterfly Community Responses

The butterfly community was significantly influenced by three vegetation variables including bluegrass cover ($R^2 = 0.23$, $P = 0.02$); flowering forb species richness ($R^2 = 0.52$, $P = 0.001$), and plant species richness ($R^2 = 0.28$, $P = 0.004$; Fig. 2). In general, sites with relatively greater abundance of obligate grassland butterflies were associated with greater plant species richness and flowering forb species richness and less bluegrass cover (see Fig. 2). Specifically, *Hesperia dacotae* (HESDAK), a threatened butterfly species, was associated with greater flowering forb richness (see Fig. 2). Similarly, *Speyeria idalia* (SPEIDA), a species of conservation concern, was associated with greater plant species richness and less bluegrass cover (see Fig. 2). *Danaus plexippus* (DANPLE), a facultative species considered for listing under the Endangered Species Act, was not associated with any significant vectors and therefore not influenced by bluegrass cover (see Fig. 2).

Sites with a larger proportion of facultative butterfly species, such as *Colias philodice* (COLPHI) and *Pieris rapae* (PIERAP), were associated with decreasing flowering forb and plant species richness and increasing bluegrass cover (see Fig. 2). Although most obligate grassland species were associated with decreasing bluegrass cover, two obligate species, *Cercyonis pegala* (CERPEG) and *Coenonympha tullia* (COETUL), were associated with less forb species richness compared with other obligate species that were correlated with greater flowering forb richness (see Fig. 2). However, *C. pegala* and *C. tullia* were the most abundant obligate grassland species (see Table 1) and may respond differently to plant community dynamics compared with other obligate species that occur at lower abundances.

As bluegrass cover increased, facultative grassland butterflies became dominant and obligate grassland butterflies decreased. The community was not influenced by management strategies. However, the

Table 1
Species list, 6-letter codes, classification (obligate or facultative), and total detections for each yr and cumulative 3-yr total for all butterflies detected at least twice in butterfly surveys conducted in the Northern Great Plains, United States, 2015 − 2017. Classifications are based on species' dependence on grasslands using descriptions from Glassberg (2001) and Royer (2003).

Species	6-letter code	Classification	2015	2016	2017	3-Yr total
Boloria bellona	BOLBEL	Obligate	31	215	104	350
Boloria selene	BOLSEL	Obligate	1	1	4	6
Celastrina neglecta	CELNEG	Facultative	0	2	1	3
Cercyonis pegala	CERPEG	Obligate	477	1104	809	2390
Charidryas gorgone	CHAGOR	Obligate	0	19	13	32
Coenonympha tullia	COETUL	Obligate	167	275	201	643
Colias eurytheme	COLEUR	Facultative	60	1437	204	1701
Colias philodice	COLPHI	Facultative	429	568	538	1535
Danaus plexippus	DANPLE	Facultative	124	104	109	337
Epargyreus clarus	EPACLA	Facultative	0	1	2	3
Euptoieta claudia	EUPCLA	Obligate	0	45	48	93
Glaucopsyche lygdamus	GLALYG	Facultative	31	57	23	111
Hesperia dacotae	HESDAK	Obligate	0	1	1	2
Junoia coenia	JUNCOE	Facultative	0	2	0	2
Limenitis archippus	LIMARC	Facultative	0	0	25	25
Limenitis arthemis	LIMART	Facultative	0	1	2	3
Lycaena hyllus	LYCHYL	Facultative	0	6	9	15
Oeneis uhleri	OENUHL	Obligate	0	2	14	16
Papilio glaucus	PAPGLA	Facultative	0	2	5	7
Papilio polyxenes	PAPPOL	Facultative	0	22	37	59
Phyciodes batesii	PHYBAT	Facultative	0	13	9	22
Phyciodes cocyta	PHYCOC	Facultative	13	76	55	144
Phyciodes tharos	PHYTHA	Facultative	186	208	69	463
Pieris rapae	PIERAP	Facultative	190	224	127	541
Plebejus melissa	LYCMEL	Facultative	83	136	251	470
Polites mystic	POLMYS	Obligate	71	120	70	261
Polites peckius	POLPEC	Obligate	6	2	8	16
Polites themmistocles	POLTHE	Obligate	10	22	18	50
Pyrgus communis	PYRCOM	Facultative	0	1	13	14
Pontia protodice	PONPRO	Facultative	0	1	2	3
Satyrodes eurydice	SATEUR	Facultative	10	15	3	28
Satyrium titus	SATTIT	Facultative	4	27	6	37
Speyeria aphrodite	SPEAPH	Facultative	44	308	298	650
Speyeria atlantis	SPEATL	Facultative	0	0	5	5
Speyeria cybele	SPECYB	Facultative	15	51	33	99
Speyeria idalia	SPEIDA	Obligate	10	151	153	314
Vanessa atalanta	VANATA	Facultative	22	54	31	107
Vanessa cardui	VANCAR	Facultative	1	2	528	531
Vanessa virginiensis	VANVIR	Facultative	0	2	0	2

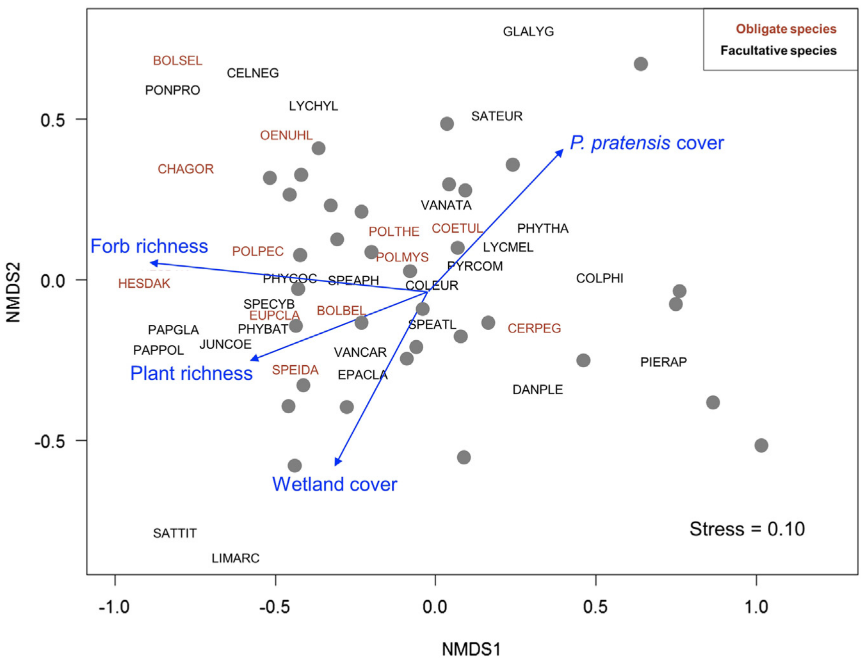

Figure 2. Nonmetric multidimensional scaling ordination for the butterfly community detected from 2015 to 2017 in the Northern Great Plains, United States. Six-letter codes for obligate grassland species (displayed in red) and facultative grassland species (displayed in black) are shown (see Table 1 for full scientific names) along with site scores *(gray circles)*. Species nearest to sites represent which species were more prominent at those sites. We then used "envfit" to determine if vegetation vectors were correlated with site butterfly community. Flowering forb richness (Forb richness), plant species diversity (Plant diversity), and Kentucky bluegrass canopy cover (*P. pratensis* cover) were statistically significant ($P \leq 0.05$) vegetation vectors for the community. In addition, the percent cover of wetlands (Wetland cover) was also a statistically significant landscape vector ($P \leq 0.05$). The plant community and nectar resources became more homogenized as Kentucky bluegrass cover increased. The butterfly community correspondingly went from more obligate grassland species to more facultative grassland species as bluegrass cover increased.

butterfly community was influenced by wetland cover at the landscape level ($R^2 = 0.30$, $P = 0.005$; see Fig. 2). Notably, sites with a larger abundance of *Satyrium titus* (SATTIT) and *Limenitis arthemis* (LIMART), two facultative species, were associated with greater wetland cover (see Fig. 2).

Univariate Responses

Bluegrass canopy cover was significantly correlated with plant and butterfly community metrics (Fig. 3). Plant species diversity ($t = -3.16$, df = 66, $P \leq 0.002$; see Fig. 3A) and flowering forb species richness ($t = -1.97$, df = 66, $P = 0.05$; see Fig. 3B) decreased as bluegrass cover increased. In addition, butterfly species richness ($t = -2.27$, df = 66, $P = 0.03$; Fig. 3C) and obligate butterfly species abundance ($z = -8.65$, df = 66, $P \leq 0.001$; Fig. 3D) decreased as bluegrass cover increased. We did not find a statistically significant relationship between bluegrass cover and the other plant and butterfly variables including total butterfly abundance and facultative species abundance, but total butterfly abundance showed a declining trend as bluegrass cover increased (Fig. S1, available online at https://doi.org/10.1016/j.rama.2018.10.003).

We did not find significant differences in bluegrass cover due to management strategies ($F_{2, 32} = 2.08$, $P = 0.11$). However, bluegrass cover tended to be lower on recently burned sites (within the past 3 yr). Average bluegrass cover on burned sites was 14.2% (±1.99 SE), whereas average bluegrass cover on grazed and idled sites tended to be higher at 21.1% (±1.72 SE) and 22.6% (±3.14 SE), respectively.

Discussion

Idle management strategies previously used in the Northern Great Plains have had considerable ramifications for the plant community, ecosystem services, and ecosystem processes (Toledo et al., 2014; Limb et al., 2018). As a result, bluegrass invasions are widespread and pervasive, as upwards of 30% bluegrass canopy cover is now common on public lands (Kobiela et al., 2017). However, little is known about how plant invasions influence pollinator communities (Pejchar and Mooney, 2009). Our research examining grassland butterflies in the Northern Great Plains found that increasing bluegrass cover had a strong negative influence on obligate grassland butterflies including *H. dacotae* and *S. idalia*, species of conservation concern, although *D. plexippus*—a facultative grassland butterfly of conservation concern—was unaffected by bluegrass. As bluegrass cover increased, facultative grassland butterflies became dominant and obligate grassland butterflies decreased. Negative responses to bluegrass in the butterfly community were mirrored in the plant community. Sites with higher bluegrass cover had lower plant species diversity and flowering forb richness. Collectively, more bluegrass translated to reduced plant species diversity (potential host and nectar resources for butterflies) and homogenized butterfly communities. Similar results have been reported for native plants and arthropods in Europe (Gerber et al., 2008) and could signal homogenization in other taxa as well. Consequently, management strategies with goals of conserving obligate grassland butterfly populations and biodiversity more generally should focus on reducing invasive bluegrass cover.

We found a correlation between butterfly communities and bluegrass canopy cover, with communities transitioning from more facultative species and fewer obligate grassland species as bluegrass cover increased. We expected the plant community, specifically the cover of bluegrass, to influence butterflies because plants create a bottom-up effect on the butterfly community (Keeler et al., 2006; Vilà et al., 2011). Bluegrass was negatively correlated with plant species richness, so the butterfly community shifted from obligate to facultative grassland butterflies that could tolerate plant community changes as observed in other grassland systems (Moranz et al., 2012; Farhat et al., 2014). Conversely, increased plant and forb richness can provide necessary host and nectar resources for obligate species with stricter resource requirements (Ekroos et al., 2010). This could explain why more butterfly species, including facultative species, were found as plant and forb richness increased.

The only landscape variable we found to be correlated with the grassland butterfly community was wetland cover. Obligate grassland

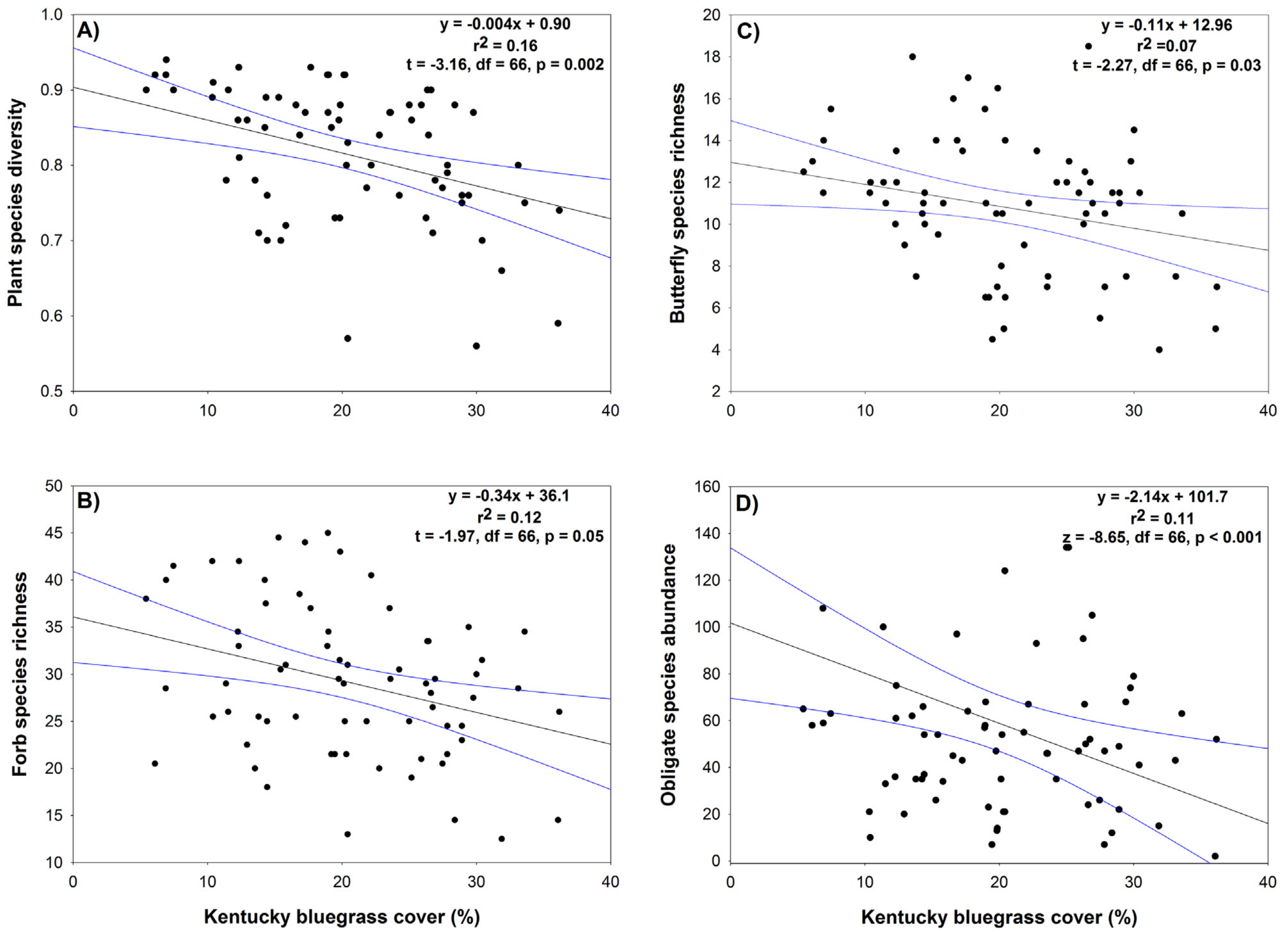

Figure 3. Plant and butterfly community responses to Kentucky bluegrass *(Poa pratensis)* canopy cover from butterfly and vegetation surveys completed in the Northern Great Plains, United States, from 2015 to 2017. Kentucky bluegrass cover had a negative relationship with plant species Simpson's diversity (**A**), flowering forb species richness (**B**), butterfly species richness (**C**), and obligate species abundance (**D**). Generalized linear model results are included for each variable, along with 95% confidence bands. Models for plant species diversity, flowering forb species richness, and butterfly species richness were created using the Gaussian distribution, but the obligate species abundance model used the Poisson distribution. Note differing scales of each dependent variable. As Kentucky bluegrass cover increased, the plant and butterfly communities became more homogenized and the abundance of obligate grassland butterfly species declined.

butterfly species and overall butterfly species richness increased as wetland cover increased. Wetland cover offers another form of perennial cover and increases compositional heterogeneity at the landscape scale to create more niches (Fahrig et al., 2011; Perović et al., 2015), much like plant diversity and flowering forb richness increase heterogeneity at the local scale. Therefore, obligate grassland species that require mesic prairie, such as *S. idalia* (Glassberg, 2001; Royer, 2003), and facultative species that require willows (*Salix* spp.), a common wetland plant (Royer, 2003; van der Kamp and Hayashi, 2009), such as *S. titus* and *L. arthemis,* increased in landscapes with increasing wetland cover. Unexpectedly, crop cover did not influence the butterfly community. We expected increasing crop cover would shift the community from obligate to facultative species as observed in other agroecosystems (e.g., Ekroos et al., 2010; Börschig et al., 2013), but crop cover may be too low or irregular to detect in our study region. Across our study, crop cover averaged 11% (see Table S1), whereas studies where crop cover significantly impacted the butterfly community averaged 51% (see Ekroos et al., 2010).

Butterfly species richness was negatively correlated with increasing bluegrass cover. Invasive species are expected to negatively impact butterfly abundance (Kalarus and Nowicki, 2015), but we only observed negative influences on obligate grassland species. Moreover, total butterfly abundance was not significantly correlated with bluegrass cover. Therefore, although butterfly species richness declined, we did not detect a significant decrease in overall abundance due to either increased abundance of facultative species or because obligate species declines were too variable among sites to detect significant differences. Similar patterns of reduced richness, declines in specialist species, and stable or fluctuating overall abundance have been observed for butterfly communities responding to human disturbance gradients in Japan (Kitahara and Fujii, 1994) and butterflies across the United Kingdom (Brereton et al., 2011).

When invasive plants reduce butterfly species richness, especially obligate species, functional homogenization reduces biodiversity and diminishes the ability of the butterfly community to provide ecosystem services (Clavel et al., 2011; Börschig et al., 2013). For example, invasive woody plants reduce pollination services in forested systems with reduced pollinator diversity (Pejchar and Mooney, 2009; Florens et al., 2010). Although bees contribute more to pollination (Rader et al., 2016), butterflies are still important for pollination (Szigeti et al., 2018) and some grassland forbs may be exclusively pollinated by butterflies, as in the case with *Dianthus carthusianorum* (Bloch et al., 2006). We did not measure ecosystem services like pollination directly, but we can infer from our results potential declines in other ecosystem services provided by butterflies. With increased bluegrass cover, fewer butterfly species are observed and nonmarket cultural services—services not easily quantified monetarily such as aesthetics and recreation—are reduced (Hanley et al., 2015). Although invasions may simply displace obligate species to other areas (Gurevitch and Padilla, 2004), an eventual threshold will be reached where populations do begin to decline (Clavero and García-Berthou, 2005). Consequently, obligate grassland butterfly declines and shifts in the community could threaten ecosystem services provided by rangelands and the biodiversity found within.

Our results show the value of reducing bluegrass cover to improve obligate grassland butterfly species richness and rangeland biodiversity. Invasive species are difficult to remove once they have been introduced, but reducing invasive species cover in a tropical forest and prairie fen wetland was successful at increasing butterfly species richness and diversity (Florens et al., 2010; Fiedler et al., 2012). Nevertheless, selecting appropriate management strategies to reduce invasive species and promote the butterfly community can be difficult. Resource managers regularly use herbicides to reduce bluegrass cover (Bahm et al., 2011), but herbicides also reduce the cover of desirable plants and butterfly survival and fitness (Russell and Schultz, 2010; Wagner et al., 2017). Alternatively, restoring historic disturbance regimes (fire and grazing) is one way to reduce bluegrass cover in rangelands with a history of rest (Bahm et al., 2011; Kral et al., 2018a) and increase vegetation and structural heterogeneity (Diacon-Bolli et al., 2012) while maintaining livestock production (Fuhlendorf et al., 2012). Historic disturbance regimes increase native plant diversity and forb richness, and they benefit butterfly diversity when applied at the correct spatial-temporal scale (Kral et al., 2017), but fire and grazing may also cause direct mortality and displace butterflies (Kral et al., 2017; Moranz et al., 2012). Therefore, management decisions must carefully consider the benefits of reducing bluegrass and apply management at the appropriate spatial and temporal scales to minimize collateral damage to pollinator populations in the short and long term. We found a trend of reduced bluegrass cover on sites managed with prescribed fire, aligning with research conducted in the region on reducing bluegrass cover with fire (Kral et al., 2018a). Nonetheless, management changes may not produce immediate results in heavily invaded rangelands without additional efforts such as reseeding native plants (Fiedler et al., 2012) because land-use legacies have lasting impacts on plant communities (Moranz et al., 2012).

We can use our results to suggest butterfly communities that can be used as indicators of functioning rangelands with increased biodiversity. For instance, butterfly communities with obligate species such as *S. idalia* would be expected to have increased butterfly and plant species richness and less bluegrass cover. However, butterflies are not always accurate indicators for certain taxa and more specific relationships need to be established (Brereton et al., 2011). For example, bee diversity may be expected to increase with butterfly diversity, but butterfly diversity was negatively correlated with bee diversity in Iowa (Davis et al., 2008). Nonetheless, developing trends and potential insights for how the butterfly community relates to biodiversity in rangelands and bluegrass cover is imperative for identifying consequences of invasion, encouraging proactive management, and restoring ecological processes to increase the delivery of ecosystem services and conserve biodiversity.

Conclusions

Rangelands can be used to support biodiversity and provide a variety of ecosystem services (Havstad et al., 2007), but management strategies to simultaneously benefit multiple ecosystem services are often viewed as contradictory (e.g., wildlife habitat or livestock production; Bullock et al., 2016). Management decisions on public lands in the Northern Great Plains assisted widespread invasion of exotic grasses like bluegrass (Grant et al., 2009). We surveyed the butterfly community, acting as an indicator of biodiversity, along a gradient of bluegrass invasion (3 − 36% canopy cover) to determine how bluegrass invasions have impacted imperiled pollinators like butterflies and overall biodiversity. The butterfly community transitioned from more obligate and facultative grassland species to being dominated by several facultative species as bluegrass cover increased. We found significant decreases in butterfly species richness and obligate grassland species abundance along the same gradient. In addition, forb richness decreased as bluegrass cover increased, which may impact the availability of host and nectar resources necessary for butterflies (Kral et al., 2018b). Even though bluegrass provides some benefits to rangelands (e.g., early spring forage), it negatively impacts the butterfly community and plant species diversity. We can infer from our results that cultural ecosystem services provided by butterflies are reduced when butterfly communities are homogenized. This could signal reduced biodiversity of other taxa essential for biodiversity conservation. Therefore, management strategies that promote decreasing bluegrass cover while increasing plant species diversity and flowering forb richness are necessary for conservation of obligate grassland butterflies, such as *S. idalia* and *H. dacotae,* and continued ecosystem services in rangelands.

Implications

As previously predicted, bluegrass negatively impacted grassland butterfly communities. Obligate grassland butterflies that rely on diverse, native rangelands for resources declined in abundance and diversity as bluegrass canopy cover increased. In contrast, facultative grassland butterfly species that use but do not rely on grasslands did not significantly decline in abundance as bluegrass cover increased. However, more facultative species were present in the community as bluegrass cover decreased. Reduced butterfly community diversity in response to increasing bluegrass cover was mirrored in the plant community as sites with more bluegrass cover had reduced diversity of plant species, including reduced diversity of flowering forbs. Butterflies and other pollinators are a major conservation concern for many rangeland managers, but it will be an ongoing challenge to manage for reductions in bluegrass and other invasive plant species while simultaneously improving resource availability for pollinators. Moreover, no single management strategy will simultaneously benefit all butterfly species, not even all butterfly species that rely on grasslands. That being said, management should focus on strategies that 1) reduce bluegrass canopy cover, 2) improve native grass and forb diversity used by immature and adult butterflies, and 3) limit mortality or exposure to harmful control mechanisms (e.g., broad herbicide application or annual, widespread burning). Varying the type and spatial distribution of disturbance is one way to benefit multiple butterfly species and reduce the likelihood of negative impacts to a particular species or population (Bendel et al., 2018). Although strategies that meet these conditions may not quickly reduce bluegrass cover, they will help alleviate trade-offs between butterfly resource availability and bluegrass cover to improve the diversity and abundance of grassland butterflies.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.rama.2018.10.003.

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