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Plant Community Composition Following Adaptive Management

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Abstract – The United States Fish and Wildlife Service's Native Prairie Adaptive Management (NPAM) program utilizes natural disturbance regimes to increase native species diversity on native prairie within the Prairie Pothole Region. We compared species composition from 2012 and 2020 and employed distance-based redundancy analysis (dbRDA) to relate species composition to explanatory variables and determined species composition was significantly correlated with northing, years since a site was grazed most recently, and the number of times a site was burned. Paired *t*-tests revealed overall floristic quality increased from 2012 to 2020 despite no apparent change in species richness. *Poa pratensis* L. (Kentucky Bluegrass) cover decreased from 2012 to 2020 while *Bromus inermis* Leyss. (Smooth Brome) and *Melilotus officinalis* (L.) Lam. (Sweetclover) cover increased.

Introduction

The prairies of central North America are among the world's most converted and least protected ecosystems (Hoekstra et al. 2005). The United States' portion of the Prairie Pothole Region (PPR) is a particularly wetland-rich region of central North America that once contained millions of acres of tallgrass and mixed-grass prairie. Tallgrass and mixed-grass prairies have declined in area by 99% and 70%, respectively, primarily due to agricultural conversion following Euro-American settlement in the 1800s (Samson and Knopf 1994). Today, the native biodiversity of remnant prairies continues to be threatened by agricultural conversion, urbanization, climate change, fire suppression, certain grazing practices, and the establishment and expansion of invasive plants (Dennhardt et al. 2021; Doherty et al. 2013; Grant et al. 2020a, 2020b; Samson and Knopf 1994; Samson et al. 2004). Introduced species invasions and disrupted disturbance regimes are implicated in the loss of native biodiversity in remnant tallgrass and mixed-grass prairies (DeKeyser et al. 2009; Grant et al. 2020a, 2020b). The invasion of introduced species and resulting loss of native species has negative implications for preserving the ecological integrity, function, and services provided by remnant native prairies (Printz and Hendrickson 2015, Toledo et al. 2014).

The historic ecological processes that characterized the region's tallgrass and mixed-grass prairie communities were disrupted following Euro-American settlement (Samson and Knopf 1994). Resilient, disturbance-adapted plant communities were shaped by interactions between climate, herbivory, and fire (Higgins 1986). The region supported year-round migratory herds of bison and elk (Hanson 1984), and natural and anthropogenic fires likely occurred every 5–6 years (Bragg 1995). Following Euro-American settlement in the late 1800s, native herbivores were replaced with domestic livestock and naturally occurring fires were suppressed, resulting in a pronounced shift in tallgrass and mixed-grass prairie plant

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communities from diverse assemblages of numerous native species toward plant communities dominated by a few introduced species (DeKeyser et al. 2009; Dixon et al. 2019; Grant et al. 2020a, 2020b; Stotz et al. 2017). In the Northern Great Plains and throughout the PPR, *Poa pratensis* L. (Kentucky Bluegrass), and/or *Bromus inermis* Leyss (Smooth Brome) have become prevalent and impact native plant diversity and ecological processes by altering nutrient, light, and soil moisture conditions such that they suppress native species germination and growth (Dillemuth et al. 2009, Toledo et al. 2014). Genera and specific epithets follow the United States Department of Agriculture PLANTS Database (USDA-NRCS 2022a).

The United States Fish and Wildlife Service (USFWS) manages more than 100,000 ha of native prairie within the PPR through the National Wildlife Refuge System (Gannon et al. 2013). Prairies owned by the USFWS were traditionally managed (ca. 1930s–1990s) to increase waterfowl production (Dixon et al. 2019). Waterfowl nesting density was determined to be highest in prairies with tall, dense herbaceous vegetation (Naugle et al. 2000). Thus, fire was suppressed, and livestock grazing occurred infrequently and at light intensities (Murphy and Grant 2005) to promote the desired nesting structure. These management practices persisted through the 1990s and are implicated in the widespread proliferation of introduced species on tallgrass and mixed-grass prairies managed by USFWS (Gannon et al. 2013, Grant et al. 2020a). Kentucky Bluegrass and Smooth Brome now comprise more than 50% of vegetative cover on USFWS-owned prairies in the Northern Great Plains (Grant et al. 2020a, Murphy and Grant 2005). Both species are associated with declines in native species diversity and abundance (Cully et al. 2003, DeKeyser et al. 2013, Fink and Wilson 2011, Williams and Crone 2006) and altered ecosystem function (Printz and Hendrickson 2015, Toledo et al. 2014). Thus, the prevalence of Kentucky Bluegrass and Smooth Brome on USFWS-owned prairies indicates native plant diversity may be imperiled on tallgrass and mixed-grass prairies throughout the region.

Following the outcomes of regional floristic assessments (Grant et al. 2009, Murphy and Grant 2005), the USFWS partnered with the United States Geological Survey (USGS) to develop an adaptive process to guide management of tallgrass and mixed-grass prairies (Gannon et al. 2013, Grant et al. 2009). The Native Prairie Adaptive Management (NPAM) program emerged to evaluate strategies intended to increase native species abundance while minimizing costs. The program provides annual decision support for tallgrass and mixed-grass prairie units in the face of biological or environmental uncertainty by utilizing site-specific information and annual vegetation monitoring to develop management recommendations each year. Management recommendations for tallgrass sites are undergoing revisions based on recent research but consisted of: burning within Smooth Brome elongation period; grazing within Smooth Brome elongation period; defoliating by burning, grazing, or haying anytime outside of the Smooth Brome elongation period), and resting for the years evaluated in this study. Annual management actions for mixed grass sites included: grazing; prescribed burning; prescribed burning and grazing within the same management year; and resting.

The establishment of the NPAM program marked a formal shift in management paradigms on USFWS lands with burning and grazing becoming more commonplace. Restoring periodic disturbances to historically idle native prairie has demonstrated promise for improving floristic composition; notably, prairies enrolled in the NPAM program and burned at greater frequencies were found to have greater native species richness and lower Smooth Brome relative cover when compared to unburned prairies (Dixon et al. 2019, Kobiela et al. 2017). Results of annual belt-transect monitoring conducted by USFWS staff indicated native species abundance increased at sites enrolled in the NPAM program between 2010 and

2016 (Dixon et al. 2019). However, potential changes in relative abundances of individual native species remained unclear due to the relatively coarse annual monitoring built into the NPAM program that was intended to detect broad patterns in the plant community (i.e., Smooth Brome and/or Kentucky Bluegrass prevalence), rather than monitor individual native species.

In 2012 we established permanent monitoring plots across a subset of tallgrass and mixed-grass units enrolled in the NPAM program to periodically assess plant community composition. We revisited these plots in 2020 to evaluate changes in species composition from 2012 to 2020. We used distance-based redundancy analysis (dbRDA, Legendre and Anderson 1999) to relate environmental and management variables for each site to species composition, and to determine whether changes were associated with the NPAM program's management recommendations. Though the principal goal of the NPAM program is to increase native species cover, implied within that is control of introduced invasive species. Thus, we included two predominant introduced species, Kentucky Bluegrass and Smooth Brome, in our assessment. Additionally, we examined certain species assemblages and a subset of species of special interest to USFWS personnel (established a priori based on the species' sensitivity to management).

Methods

Study area

The PPR spans approximately 750,000 km^2 in the center of the North American continent, extending through six U.S. states and three Canadian provinces (Millett 2004, Millett et al. 2009). The landscape within the PPR is characterized as flat to gently rolling and contains millions of small wetlands or potholes, formed by glacial activity in the late Wisconsin glaciation (Johnson et al. 2008). The region's land use is generally dominated by agriculture, typically cropping in the flatter areas and livestock grazing on steeper slopes. The PPR's climate is semi-arid to sub-humid with cyclic deluge and drought periods (Winter and Rosenberry 1998). Precipitation and temperature vary along orthogonal latitudinal and longitudinal gradients. Annual precipitation ranges from 30 cm in the western extent to 90 cm in the eastern extent, with the majority (70%) falling during the growing season between April and September (Millett 2004, Millett et al. 2009). Mean annual temperatures range from 10° C in the southern extent of the PPR to 1° C in the northern extent, while daily temperatures fluctuate to above 40° C or below −40° C (Millett 2004, Millett et al. 2009).

Site selection

We selected 30 native prairie sites on USFWS lands in North Dakota and South Dakota that were enrolled in the NPAM program (Fig. 1). Site selection was based on site history, accessibility, and soil characteristics. Upon enrollment in NPAM, sites were managed with various combinations of rest, grazing, burning, or a combination of burning and grazing following NPAM guidance and based on annual monitoring. When recommended by the NPAM program and feasible to conduct in the field, prescribed burning was primarily conducted in early- to mid-May at our study sites. When grazing was the selected management action recommended by the NPAM program the actual timing and stocking density varied considerably across our 30 study sites between seasons and years due to site-specific constraints faced by managers.

The 30 tallgrass and mixed-grass sites included in this study were remnants of native prairies. As such, these sites were never cultivated. We limited site selection to prairie remnants with predominantly loamy soils because loamy soils are the predominant soil type in the region and are vulnerable to invasion by introduced cool-season grasses (i.e., Kentucky Bluegrass and Smooth Brome; DeKeyser et al. 2009; DeKeyser et al. 2013). Limiting site selection to loamy ecological site types was intended to help control potential variability resulting from the large geographical extent of this study (Sedivec and Printz 2012). Plant communities associated with loamy ecological sites throughout our study area were expected to have comparable species compositions (Sedivec and Printz 2012; USDA-NRCS 2022b, 2022c, 2022d). The major components of the typical plant communities encountered at loamy ecosites are similar throughout our study area while there may be potential differences in less prevalent species.

In 2012 we established permanent plots and conducted vegetation monitoring at our study sites (Kobiela et al. 2017). We randomly placed 3 to 5 1000 m^2, long-term Modified-Whittaker plots (Stohlgren et al. 1995) in loamy soil types at each unit. The number of plots established was proportional to the area of the unit being surveyed. After initial monitoring, we determined that 3 Modified-Whittaker plots per site was sufficient to capture plant species composition at each site. In 2020 we re-monitored the plots at each site established in 2012 by randomly selecting 3 plots for inclusion in 2020, at sites where more than 3 plots were established originally.

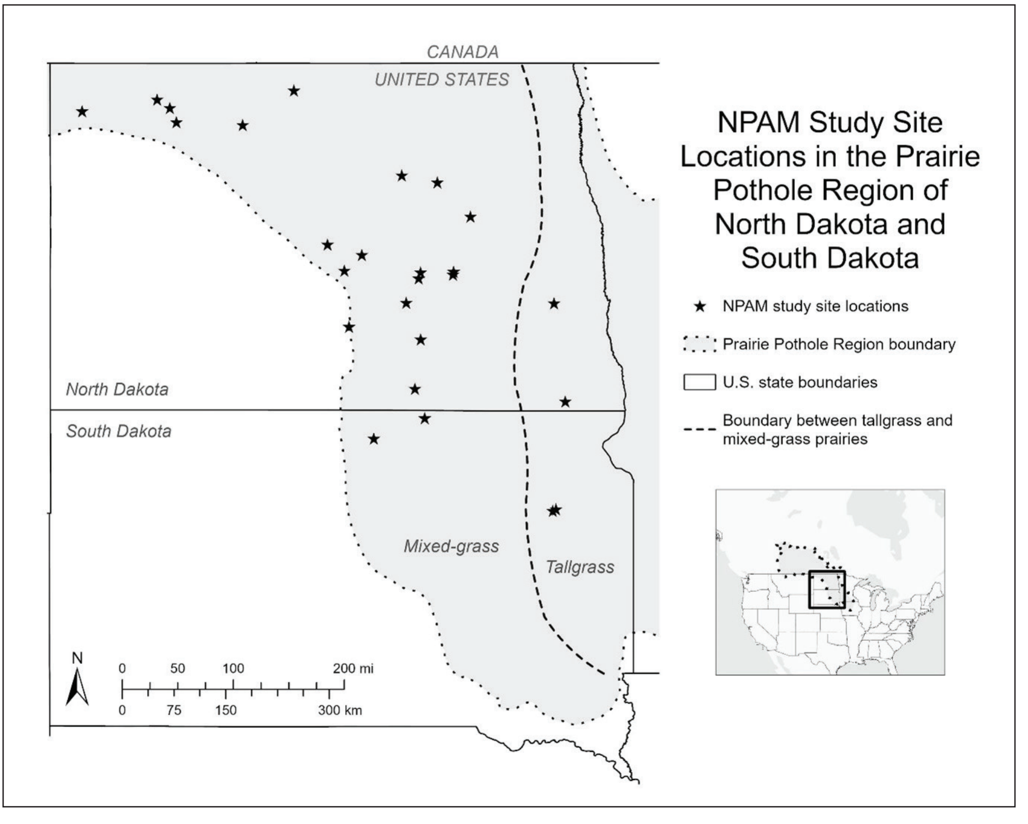

Figure 1. Location of 30 study sites (black stars) enrolled in the NPAM program throughout the Prairie Pothole Region of North Dakota and South Dakota.

Vegetation monitoring and data analysis

We conducted vegetation monitoring between June and September of 2020. We used the Modified-Whittaker sampling method (Supplemental Fig. 1, available online at https://eaglehill.us/prnaonline/suppl-files/prna-039c-DeKeyser-s1.pdf) to measure plant community composition and cover (Stohlgren et al. 1995). The Modified-Whittaker method utilizes a nested frequency design that is useful for comparing land use practices, investigating species-environment relationships, and detecting rare or exotic species (Stohlgren et al. 1995, Stohlgren et al. 1998). When compared with similar vegetation sampling methods, the Modified-Whittaker design reduces spatial autocorrelation and captures the highest species diversity by area (Stohlgren et al. 1995). The plot configuration is non-overlapping subplots of various sizes positioned within a rectangular 20 m x 50 m (1000 m^2) plot (resulting in a total sampling area of 3 hectares). We estimated percent cover for each plant species and ground cover class (litter, bare ground, or rock) in 10 1-m^2 plots. We recorded which species occurred within 2 10-m^2 plots, 1 100-m^2 plot, and 1 1000-m^2 plot. Newly-encountered species were successively recorded at each scale.

We averaged plant species cover estimates, relativized to total plant cover, across plots at each site. We excluded rare species (those with 2 or fewer occurrences) from the dataset prior to multivariate analyses to ensure the focus of the multivariate analyses was on broad community structure rather than the presence or absence of a few rare species encountered throughout the wide geographic range of this study (McCune and Grace 2002, Peck 2016). Additionally, the relative cover values were transformed using the arcsine square root transformation. Multivariate analysis was conducted using R package VEGAN (Oksanen et al. 2015, R Core Development Team 2010). Univariate analysis was conducted using SAS Enterprise Guide 7.1 (SAS 2017). All species encountered at our sites were retained for univariate analysis of species richness and the calculation of a floristic quality index.

We obtained the USFWS management history for each site between 2010 and 2019. We selected the range of 2010 to 2019 to reflect the maximum period of management influence based on the timing of all sites being enrolled in the NPAM program (2010) and the most recent management year prior to monitoring (2019). We recorded the burn and graze treatment as 2 independent management actions, i.e., sites that received a burn and graze treatment within a single management year had 2 management actions recorded that year.

We used dbRDA to relate plant species composition to explanatory variables because dbRDA has proven useful to ecologists as a robust method for hypothesis testing of complex experimental designs (Jupke and Schafer 2020, Legendre and Anderson 1999, Legendre and Legendre 2012). In addition, dbRDA can be used to test the significance of individual terms and their interactions without requiring distributional assumptions (Legendre and Anderson 1999), rendering the method very useful to ecologists seeking to analyze multivariate datasets, e.g., plant species composition. We used species relative cover as the multivariate response matrix with the Bray-Curtis distance measure. We began with 5 explanatory variables reflecting NPAM management recommendations and site location—the number of times a site was burned between 2010 and 2019; the number of times a site was grazed between 2010 and 2019; the number of years since a site was burned; the number of years since a site was grazed; and the site's Universal Transverse Mercator northing.

We retained explanatory variables in the final model when inclusion increased the explanatory power of the model. We conducted variance partitioning for each variable to determine which explanatory variables were correlated with variation in relative cover. We examined Pearson correlation coefficients (r values) to indicate the strength of species' relationships with ordination axes because of the nature of large datasets, where even very small *r* values are likely to be statistically significant (McCune and Grace 2002, Peck 2016). We retained species possessing *r* values ≥ |0.4| for further interpretation (Jones et al. 2023, McCune and Grace 2002, Smith et al. 2016). The |0.4| threshold was selected a priori to indicate sufficient strength in the relationship between a species and an ordination axis. This threshold was selected to ensure meaningful patterns were detected and interpreted (Jones et al. 2023, McCune and Grace 2002, Smith et al. 2016).

We assigned a coefficient of conservatism value (C value) to each native species and calculated a floristic quality index (FQI) value for each site following the Coefficients of Conservatism for the Vascular Flora of the Dakotas and Adjacent Prairies manual (Northern Great Plains Floristic Quality Assessment Panel 2001). Introduced species are not assigned C values and consequently were not included in the calculation of FQIs. C values range between 0 and 10 with the highest values assigned to species known to be restricted to intact natural areas while lower values reflect species' abilities to survive in degraded areas. The FQI utilizes each native species' C value to provide an estimate of species richness, weighted by the native species' tolerances to site degradation and disturbance.

We used paired *t*-tests to compare 2012 and 2020 estimates of average species richness (all species), native species richness (excluding introduced species), FQI value, and relative cover of certain species and assemblages (i.e., Kentucky Bluegrass; Smooth Brome; all native species; all graminoid species; native warm-season graminoids; native cool-season graminoids; all forb species; all shrub species; and *Melilotus officinalis* [L.] Lam. [Sweetclover]). In addition, we compared 2012 and 2020 relative cover estimates for individual species of special interest to USFWS personnel, including 9 native species selected a priori by USFWS personnel (C. Dixon, USFWS, Woodworth, ND, 2020 pers. comm.) due to their sensitivity to management (i.e., *Andropogon gerardii* Vitman [Big Bluestem]; *Bouteloua curtipendula* [Michx.] Torr. [Sideoats Grama]; *Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths [Blue Grama]; *Calamovilfa longifolia* [Hook.] Scribn. [Prairie Sandreed]; *Hesperostipa commata* [Trin. and Rupr.] Barkworth [Needle and Thread]; *Hesperostipa spartea* [Trin.] Barkworth [Porcupinegrass]; *Nasella viridula* [Trin.] Barkworth [Green Needlegrass]; *Pascopyrum smithii* [Rydb.] A. Love [Western Wheatgrass]; and *Schizachyrium scoparium* [Michx.] Nash [Little Bluestem]).

Results

Management effects on plant species composition

We observed a total of 157 plant species (Supplemental Table 1, available online at https://eaglehill.us/prnaonline/suppl-files/prna-039c-DeKeyser-s2.pdf) at our 30 sites in 2020, 36 of which were excluded from dbRDA (due to their occurrence at only 1 or 2 sites). The dbRDA ordination produced a 2-dimensional solution that represented 44.3% of variation in the dataset. The final model indicated latitude, the number of times a site was burned between 2010 and 2019, and the years since a site was most recently grazed were stronger predictors of plant species composition than frequency of grazing or years since last burn (Table 1, Fig. 2). We examined the *r* values correlated with each axis to explore patterns underlying species relationships (Supplemental Table 2, available online at https://eaglehill.us/prnaonline/suppl-files/prna-039c-DeKeyser-s3.pdf). Axis 1 captured 27.6% of variation in the dataset (Fig. 2) and represented a gradient in site latitude and years since a site was grazed. Sites positioned along the negative end of Axis 1 were grazed more recently than sites positioned along the positive end. Species positively correlated with Axis 1 were those that are more abundant in the mixed-grass prairies of northwestern and northcentral North

Dakota (e.g., Needle and Thread). In contrast, species negatively correlated with Axis 1 were those that are more prevalent in the tallgrass prairies of southeastern South Dakota (e.g., Big Bluestem). Axis 2 represented 16.7% of variation in the dataset and was correlated with number of burns (Fig. 2). Positively correlated species were more abundant at sites burned fewer times between 2010 and 2019, while negatively correlated species were more abundant at sites burned more frequently.

Changes in species composition between 2012 and 2020

While overall species richness remained stable, there were shifts in the relative abundance of specific functional groups and individual species. There were no differences in mean total species richness and mean native species richness as sampled at our study sites in 2012 and 2020, while FQI was higher in 2020 than 2012 (Fig. 3, Table 2). There were several differences in species composition based on the relative cover estimates of individual species and species assemblages from 2012 to 2020 (Fig. 3, Table 2). The relative cover of all graminoids decreased ($p = 0.03$) from 2012 to 2020. There was no difference in native warm-season graminoid cover between 2012 and 2020, but native cool-season graminoid cover decreased ($p < 0.01$) and shrub relative cover increased ($p < 0.01$). There were no differences in relative cover estimates for all native species or forbs between 2012 and 2020. Kentucky Bluegrass relative cover decreased ($p < 0.01$) between 2012 and 2020, while Smooth Brome relative cover increased ($p = 0.04$) and Sweetclover relative cover increased ($p = 0.02$). Green Needlegrass relative cover was lower ($p < 0.01$) in 2020 than in 2012. Similarly, Western Wheatgrass relative cover declined ($p = 0.01$) between 2012 and 2020.

Discussion

The NPAM program provides annual recommended management actions for each enrolled site based on the conditions leading up to that point in time, ensuring NPAM guidance is site-specific and responsive (Gannon et al. 2013). Thus, due to differences in

Table 1. Permutational ANOVAs (999 permutations) for the final dbRDA model of relative cover estimates from 30 native tallgrass and mixed-grass prairie sites enrolled in the NPAM program throughout North Dakota and South Dakota. The dbRDA was conducted within the R package VEGAN (Oksanen et al. 2015). Degrees of Freedom (Df), F, and *p*-values are shown with asterisks indicating significant explanatory variables (also in bold).

Overall model	*df*	*F*	*p*
Model	5	2.340	**0.001***
Residuals	24		
Environmental Variables			
Number of burns	1	2.300	**0.009***
Number of grazings	1	1.588	0.087
Years since most recent burn (YSB)	1	0.873	0.579
Years since last grazing (YSG)	1	2.519	**0.003***
Northing	1	4.422	**0.001***

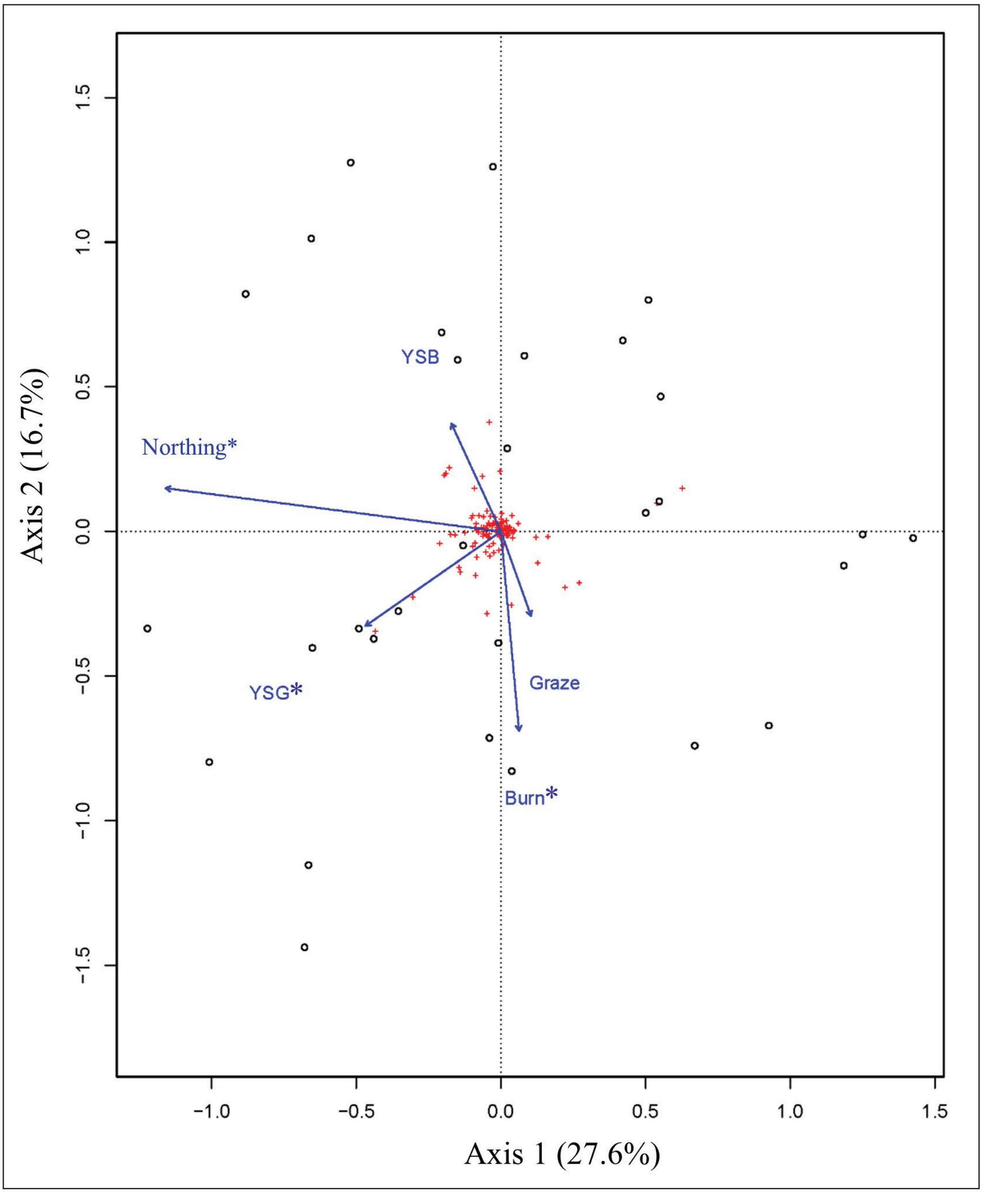

Figure 2. Ordination of plant species and NPAM program sites sampled in 2020 from the distance-based redundancy analysis (dbRDA). Each tallgrass and mixed-grass prairie site (enrolled in the NPAM program and located in North Dakota or South Dakota) is indicated by an open circle, and all plant species included in the analysis are shown as red crosses. Environmental variables are displayed as vectors; significant variables are denoted with an asterisk. The percentages associated with each axis represent the amount of variance in the dataset.

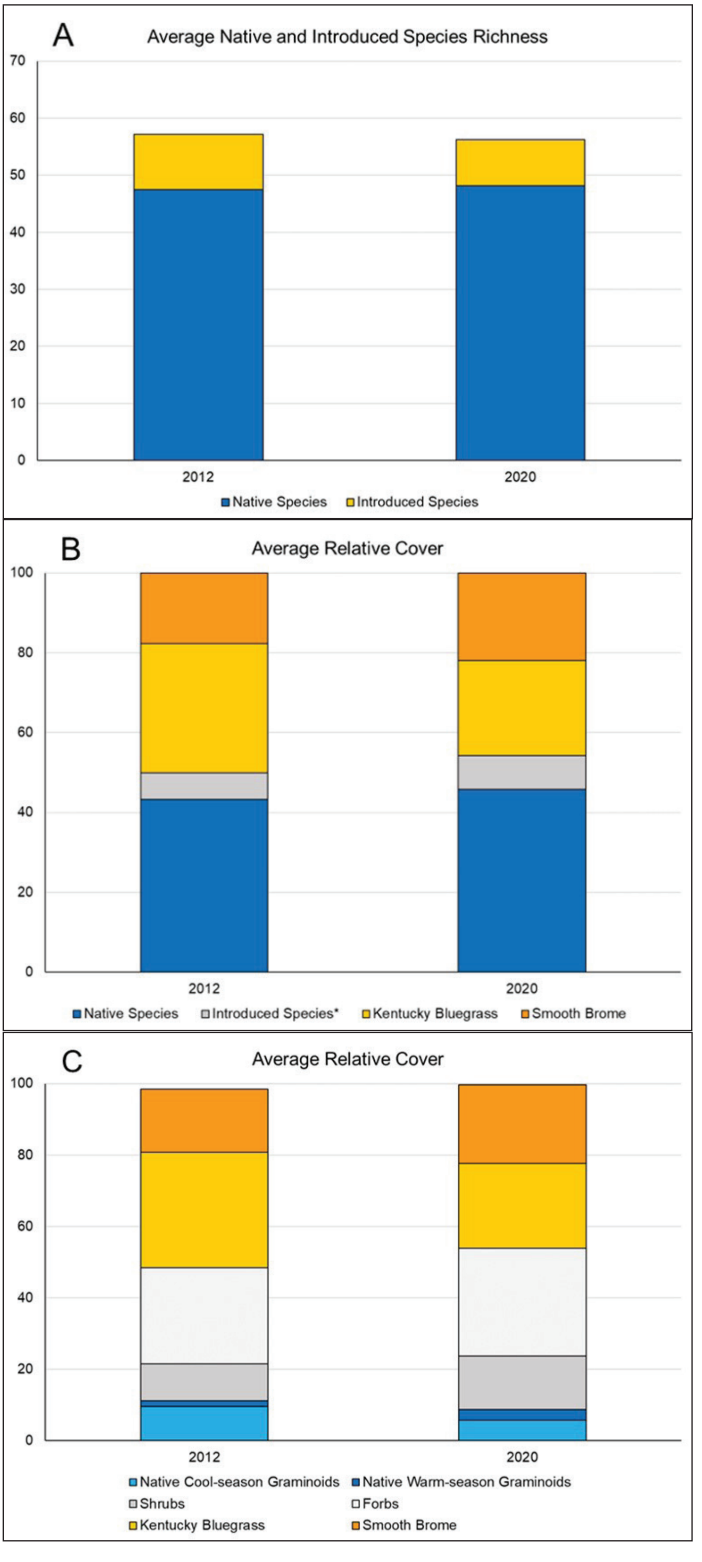

Figure 3. (A) Average 2012 and 2020 native and introduced species richness estimates at native prairie remnants enrolled in the NPAM program. (B) Average 2012 and 2020 relative cover estimates of native species, introduced species (*excluding Kentucky Bluegrass and Smooth Brome), Kentucky Bluegrass, and Smooth Brome. (C) Average 2012 and 2020 relative cover estimates of native cool-season graminoid species, native warm-season graminoid species, shrub species, forb species, Kentucky Bluegrass, and Smooth Brome.

Table 2. Mean and standard deviation for paired t-tests comparing 2012 and 2020 values for community metrics and relative cover estimates of individual species and species assemblages. Degrees of freedom (df), t-value (t), and p-value are included for each paired t-test. Asterisks indicate significant differences in mean values between years and p-values are shown with asterisks indicating significant explanatory variables (also in bold).

	Mean	SD	df	*t*	*p*-value
Total species richness					
2012	57.1667	11.5999	29	0.33	0.7412
2020	56.2667	13.1567			
Native species richness					
2012	47.4667	10.4510	29	0.29	0.7705
2020	48.1667	12.7849			
FQI score					
2012	33.7492	5.31723	29	2.25	**0.0322***
2020	35.5723	6.78338			
Native species relative cover					
2012	43.2179 %	13.3142 %	29	0.86	0.3956
2020	45.7672 %	17.9503 %			
Graminoids relative cover					
2012	60.8258 %	13.1505 %	29	2.36	**0.0250***
2020	54.3396 %	11.8615 %			
Warm-season graminoids relative cover					
2012	1.6399 %	2.5784 %	29	1.86	0.0735
2020	3.0421 %	4.4887 %			
Cool-season graminoids relative cover					
2012	9.5174 %	9.0430 %	29	3.13	**0.0041***
2020	5.7036 %	6.8025 %			
Forbs relative cover					
2012	26.9220 %	11.0956 %	29	1.41	0.1695
2020	30.1541 %	10.0371 %			
Shrubs relative cover					
2012	10.3608 %	6.8674 %	29	3.78	**0.0007***
2020	14.9274 %	8.6972 %			
Smooth Brome					
2012	17.6742	15.0747	29	2.17	**0.0385***
2020	21.9956	16.0026			
Kentucky Bluegrass					
2012	32.3556	10.0384	29	3.59	**0.0012***
2020	23.8618	11.6606			
Sweetclover					
2012	2.6601	5.3869	29	2.42	**0.0220***
2020	5.1904	9.1086			
Sedge spp. relative cover					
2012	1.1007 %	1.7533 %	29	2.49	**0.0185***
2020	0.4302 %	0.9783 %			

existing plant communities, site histories, past management actions, and any other potential constraints on USFWS personnel or related to a particular site, the management of our 30 study sites was not uniform, making it correspondingly difficult to draw conclusions about the role of individual management actions embedded in NPAM guidance. Instead, we sought to elucidate the role NPAM-guided management plays, in its entirety, across our study area in North Dakota and South Dakota. Our multivariate analysis suggested plant species composition may have been affected by enrollment in the NPAM program, as the number of times a site was burned (between 2010 and 2019) and the amount of time since the last grazing event (prior to 2020 sampling) helped predict plant species composition. While each of these explanatory variables (i.e., the number of times a site was burned and the amount of time since the last grazing event) may provide clues about the effects of NPAM-recommended management actions employed at our tallgrass and mixed-grass study sites, a more detailed analysis would be necessary to draw firm conclusions related to the significance of individual management actions.

Kentucky Bluegrass relative cover decreased nearly 30% from 2012 to 2020 at the tallgrass and mixed-grass prairie remnants sampled in this study. Our observed decline in Kentucky Bluegrass is remarkable as this species is an extremely competitive cool-season grass that has proven difficult to control throughout the Northern Great Plains (Gasch et al. 2020; Grant et al. 2020a, 2020b; Palit et al. 2021; Toledo et al. 2014). Kentucky Bluegrass can be especially difficult to manage when intermixed with native species possessing similar phenological traits, such as the native cool-season grasses that are important components of tallgrass and mixed-grass prairies throughout the PPR (DeKeyser et al. 2015, Palit et al. 2021). Recent reviews suggest management efforts have had varying degrees of success toward reducing Kentucky Bluegrass in the Northern Great Plains (Gasch et al. 2020, Palit et al. 2021).

At our study sites, it appears that the observed reduction in Kentucky Bluegrass cover may have freed resources for Smooth Brome, as Smooth Brome relative cover increased by

Table 2 continued. Mean and standard deviation for paired t-tests comparing 2012 and 2020 values for community metrics and relative cover estimates of individual species and species assemblages. Degrees of freedom (df), *t*-value (*t*), and *p*-value are included for each paired t-test. Asterisks indicate significant differences in mean values between years and *p*-values are shown with asterisks indicating significant explanatory variables (also in bold).

	Mean	SD	df	*t*	*p*-value
Needle and Thread relative cover					
2012	2.5503 %	4.3854 %	29	0.06	0.9498
2020	2.5927 %	5.5104 %			
Porcupinegrass relative cover					
2012	0.1164 %	0.3841 %	29	1.30	0.2023
2020	0.3013 %	0.9072 %			
Green Needlegrass relative cover					
2012	2.8171 %	3.1439 %	29	4.45	**0.0001***
2020	0.4022 %	0.7773 %			
Western Wheatgrass					
2012	1.9851	2.8935	29	2.72	**0.0108***
2020	0.8579	1.4314			

almost 20% from 2012 to 2020. Smooth Brome is an aggressive competitor, able to establish and spread across a wide range of conditions encountered throughout the PPR (Murphy and Grant 2005, Otfinowski et al. 2007, Preister et al. 2019, Vinton and Goergen 2006). Smooth Brome invasion has impacted tallgrass and mixed-grass prairies throughout our study area (DeKeyser et al. 2009; Fink and Wilson 2011; Grant et al. 2020a, 2020b; Murphy and Grant 2005). The effects of Smooth Brome's proliferation in the Northern Great Plains are widespread, with negative implications for the preservation of the region's ecological integrity and ecosystem services (Toledo et al. 2014).

A previous assessment of our tallgrass and mixed-grass study sites found lower Smooth Brome relative cover on sites where prescribed burns were conducted more frequently over a 4-year period following NPAM enrollment (Kobiela et al. 2017). This outcome was interpreted as a hopeful indication that following NPAM management recommendations had the potential to measurably improve plant community composition on prairie remnants managed by the USFWS. The disparity between our current results and what was reported by Kobiela et al. in 2017 suggests that the effects of NPAM-recommended management on Smooth Brome relative cover may be highly variable. NPAM management recommendations for tallgrass units are timed to defoliate (via prescribed burning and/or spring grazing; Gannon et al. 2013) during the period when Smooth Brome is theoretically most vulnerable to defoliation, i.e., during Smooth Brome's elongation window (Willson and Stubbendieck 1997, 2000). However, recent research suggests that the timing of burning on tallgrass NPAM units may not be optimal for targeting Smooth Brome, based on development stages such as leaf stage suggested by Willson and Stubbendieck (1997, 2000) or elongation stage suggested by Priester et al. (2019; Preister et al. 2021; Vacek et al. 2023, unpublished data). Additional research is necessary to evaluate and improve the NPAM program's management recommendations' potential for controlling Smooth Brome. For example, other studies of Smooth Brome patterns of occurrence in the PPR indicate that extended periods of annual moderate- to high-intensity grazing (>1.8 AUM) may be effective for combatting Smooth Brome invasion (Coleman 2022, Coleman et al. 2023, Murphy and Grant 2005). Plant communities where Smooth Brome is the dominant invader may benefit from repeat grazing, though changes may not be apparent over short periods (Dornbusch et al. 2020, Hendrickson et al. 2020).

Our observed increase in FQI scores from 2012 to 2020 suggested a potential improvement in the native plant component of tallgrass and mixed-grass prairie remnants enrolled in NPAM. It is possible that the NPAM program's management recommendations are promoting native plant species that are well-adapted to the local environment, in turn leading to higher FQIs in 2020 after a longer time under NPAM guidance. However, it is unknown whether the improvement in FQI scores was caused by NPAM program management due to the lack of controls for comparison. We posit that the increase in FQI at our study sites may be related to NPAM guidance, as the management actions recommended by the NPAM program include prescribed burning and grazing intended to promote native plant species diversity and target introduced species (Gannon et al. 2013). Burning and grazing have been shown to promote plant species with higher conservation values in native prairie (Manning et al. 2017).

A related research project (Coleman et al. 2023) compared plant community composition of NPAM enrolled sites to nearby remnant prairie sites under private ownership to elucidate potential effects of long-term management. Coleman et al. (2023) determined that sites under private ownership were managed with more frequent grazing than the USFWS historically employed and the privately-owned sites possessed higher quality native plant communities. Higher FQIs were found at privately managed prairie sites associated with a long-term history of grazing, in contrast to the USFWS-managed sites that were left idle for decades prior to NPAM enrollment. Plant communities with high floristic quality may be indicative of broader ecological integrity (Klopf et al. 2017). Thus, we are hopeful that the observed increase in FQI at NPAM sites in 2020 may be an early indication that the management recommendations produced by the NPAM program have the potential to improve prairie plant communities, but we realize future research projects tracking changes in FQI at comparable sites that are not enrolled in NPAM will be necessary to draw firm conclusions.

Our multivariate analysis indicated plant species composition varied with site latitude (UTM northing). While we limited site selection to loamy ecosites to counteract the large geographic extent of our study, all our tallgrass prairie remnants were located in the southern extent of our study area, and mixed-grass remnants occurred in the central and northern portions of the study area. While loamy ecosites throughout our entire study area are expected to possess broadly comparable plant communities (Sedivec and Printz 2012; USDA-NRCS 2022b, 2022c, 2022d), it is not entirely surprising that there would be certain differences attributable to site latitude given the broad geographic extent of the current study. In addition, in the southern extent of our study area, the landscape was dominated by croplands and restored grasslands while land use was more evenly mixed between croplands and rangelands in the central and northern portions. Fragmented landscapes can provide corridors for introduced species to spread and are associated with higher prevalence of introduced species in the Northern Great Plains (Grant et al. 2020b, Palit et al. 2021, Seabloom and van der Valk 2003, Van Riper and Larson 2009).

Sweetclover, an introduced forb species, may be responding positively to NPAM-guided management as its relative cover increased from 2012 to 2020 at our study sites. Sweetcover is a biennial leguminous species that thrives in disturbed areas and produces seed which may remain viable for years (Kline 1986, Ogle et al. 2008, Whitson et al. 2006). Sweetclover's germination is stimulated by fire and seedling density may increase for several years post-fire (Heitlinger 1975). While consecutive multi-year spring burning may target Sweetcover (Heitlinger 1975, Kline 1986), infrequent burning may promote its expansion by opening areas for seedling establishment (Kline 1986, Ogle et al. 2008). Sweetclover may be sensitive to heavy grazing in the late summer and fall, but as a biennial species with a steady supply of viable seeds, it is hard to eliminate once established (Ogle et al. 2008). Thus, the timing and intensity of the grazing and/or prescribed burning, as included in the NPAM program, may do little to reduce Sweetclover relative cover as the timing and intensity of the management actions may not be optimal to target Sweetclover. However, the increase we observed in 2020 from 2012 may be little more than a reflection of Sweetclover's ability as a biennial to respond with increased biomass production following management actions that open areas for Sweetclover seedlings (Ogle et al. 2008).

The NPAM program's management recommendations were expected to reduce the abundance of native shrub species, as many native shrub species are noted to proliferate following periods of fire suppression (Grant and Murphy 2005, Murphy and Grant 2005) and prescribed burning is recommended to control shrub encroachment in herbaceous communities (Bailey et al. 1990, Romo et al. 1993). Our observations were not consistent with these studies—shrub relative cover increased from 2012 to 2020 across our study sites. Once shrubs are established in an area, reintroducing fire through occasional prescribed burning may not be effective for controlling shrub expansion (Briggs et al. 2005). A study of shrub expansion in the central tallgrass prairie observed comparable increases in shrub cover at sites burned every 4 years and sites burned once in a 20-year period (Heisler et al.

2003). This study and ours indicate that factors aside from prescribed burn frequency play roles in shrub encroachment in prairie remnants. In addition to fire suppression, increased atmospheric CO_2 concentrations, climate change, and nitrogen deposition are implicated as potential causes of woody encroachment (Ratajczak et al. 2012). Increases in shrub cover are associated with changes in plant community composition and reduced species richness (Ratajczak et al. 2012, Van Auken 2000). Woody species may facilitate secondary invasion by Kentucky Bluegrass and Smooth Brome by altering nutrient and moisture conditions in shrub understories (Lett and Knapp 2003). Indeed, an assessment of floristic composition on USFWS lands in North Dakota and South Dakota showed that shrub understories were more frequently dominated by Kentucky Bluegrass and Smooth Brome than native species assemblages (Grant et al. 2020a). Our analysis suggests that the NPAM program's management recommendations may not be counteracting shrub expansion on remnant tallgrass and mixed-grass prairie, but additional analysis would be required to draw firm conclusions about the factors impacting shrub populations across the region or the role of specific management actions.

The principal goal of the NPAM program is to increase the abundance of native species while minimizing the cost of controlling Kentucky Bluegrass and Smooth Brome. In this study, native species, as well as the non-native species Kentucky Bluegrass, Smooth Brome, and Sweetclover, exhibited different responses to the NPAM program's management recommendations. Our results point to the inherent difficulty of improving native plant species composition within a highly-invaded ecosystem where individual species have differing responses to management actions and the timing of growth of introduced species overlaps with native species (e.g., Green Needlegrass and Western Wheatgrass; Grant et al. 2020b; Toledo et al. 2014). Predicting management outcomes may be improved by understanding the mechanisms and ecological processes driving changes in species composition on remnant prairies (Dixon et al. 2019). Given the relatively short period since implementation of the NPAM program, it is quite possible that the impacts of the program's management recommendations on plant community composition are not fully apparent. A long-term commitment to restoring ecological processes may be required to increase and maintain native species abundance on remnant prairies in the PPR.

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