

Plant Community Shifts in Response to Fire and Bison in a Restored Tallgrass Prairie

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ABSTRACT

To redress prairie loss, managers seed former agricultural lands and reinstate key ecosystem processes with prescribed fires and reintroduction of native grazers to create restored prairies. Bison (*Bison bison*) were almost hunted to extinction in the late 1800s but are recovering and have recently been reintroduced to restored prairies for their ecosystem engineering roles. The effects bison and fire have on remnant (never-plowed) prairie vegetation are well documented. However, there is little known about how bison will impact plant communities in restored prairies. These effects are most likely driven by reduction of competition from grasses and increased heterogeneity from disturbance. This study aimed to quantify bison impacts on vegetation in a chronosequence of restored prairie with varied burning regimes. We found that plant diversity decreased with restoration age and did not differ among either grazing or fire treatments. However, grazed sites displayed more variation within plant community composition. Older restorations tended to be more similar in species and functional group composition in comparison to younger sites. Although the roles of bison and fire were not as important in these first three years after reintroduction as predicted, changes in composition suggest that bison effects may become more apparent in later years as grazing drives different compositional trajectories.

Index terms: disturbance; grazing; prescribed fire; pyric herbivory; restoration

INTRODUCTION

Tallgrass prairie is a highly diverse North American ecosystem that provides wildlife habitat and ecosystem services such as prevention of soil erosion, water filtration, and C sequestration (Camill et al. 2004; Wan et al. 2005; Rowe et al. 2013). Most tallgrass prairie (82–99% of the historical range) has been converted into other land uses that are more suited for human use, primarily agriculture, and it is now one of the most endangered ecosystems in North America (Samson and Knopf 1994). In Illinois, only 0.01% of remnant tallgrass prairie remains (Anderson 2006), and invasive species, loss of native grazers, and altered fire regimes in these fragments have further exacerbated prairie degradation (Wilcove et al. 1998; Knapp et al. 1999; Fletcher and Koford 2003). Because of this extreme loss and degradation, the only option for preserving the diversity and functioning of tallgrass prairie is through restoration (Rowe 2010), including the reinstatement of historical disturbance regimes via fire and grazing.

Fire regimes (i.e., size, frequency, intensity, season, and extent) are vital for the establishment and persistence of prairie plant species (Leach and Givnish 1996; Archibald et al. 2013). Both lightning strikes and intentional ignitions from Native Americans are the most likely historical sources of fire, while today prescribed fires are ignited by land managers to maintain this historical disturbance regime (Anderson 2006). Fire removes the standing litter, creating more sun exposure that promotes warmer soil temperatures and increased nitrification from cyanobacteria (Anderson 2006; Vogel et al. 2010). However, frequent fires (those

set annually) decrease available soil N due to the volatilization of ammonia (Blair 1997). Effects of fires can last into the following year, but intermediate and low frequencies (3–5 y) can lead to community shifts such as woody encroachment (Ewing and Engle 1988; Briggs et al. 2002). Seed production increases in C₄ grasses following spring fires, helping them compete against the less dominant and commonly nonnative C₃ grasses as well as forbs (Ewing and Engle 1988; Collins et al. 1995; Vogel et al. 2007). Through the promotion of competitively dominant grasses, frequent fires thus reduce plant diversity (Powell 2006). However, another disturbance regime, bison grazing, can moderate this effect through preferential foraging on grasses and other Poales like sedges and rushes (Knapp et al. 1999).

Once ranging between 30 and 60 million individuals, the American bison (*Bison bison*) is thought to be the most influential historical grazer within the tallgrass prairie system (Knapp et al. 1999). Now recovering from the brink of extinction in the late 1800s, bison are being reintroduced for their ecosystem engineering roles (Biondini et al. 1999; Knapp et al. 1999; Eby et al. 2014). Two specific mechanisms, the competitive release hypothesis and the habitat heterogeneity hypothesis, can explain the increase of plant diversity predicted following bison reintroduction (Elson and Hartnett 2017). The competitive release hypothesis states preferential foraging on Poales species reduces biomass and cover of these species, which increases light availability and decreases their ability to compete (McCain et al. 2010; Elson and Hartnett 2017). The habitat heterogeneity hypothesis explains the process in which bison activity (wallow-

ing, trampling, feces and urine deposition) increases patchiness and diversity at a local scale, which increases overall species richness (Hartnett et al. 1996; Knapp et al. 1999; Elson and Hartnett 2017). As bison reduce the competition from grasses and increase patchiness, these mechanisms can work synergistically. In the absence of fire, grazing may drastically decrease grass biomass and cover. However, bison rely on the presence of these largely grass-dominated communities, and the interaction of fire and grazing maintains heterogeneity and diversity.

Patterns of grazing and fire regimes follow a cyclical process in which one is dependent on the other—an interaction termed pyric herbivory (Fuhlendorf et al. 2009; Allred et al. 2011). Fire removes biomass and promotes the growth of grasses, and these accessible fresh shoots attract large herbivores as they emerge (Vogel et al. 2010; Bergmann et al. 2015; Burkepile et al. 2016). Grazing reduces the chance of ignition in the following years until a site is abandoned by the herbivores and the biomass can accumulate and the chance of ignition increases (Fuhlendorf et al. 2009). Bison in prairies are a prime example of this interaction as they preferentially graze in burned areas until the grass abundance is diminished and then they no longer visit the area (Biondini et al. 1999; Knapp et al. 1999; Fuhlendorf et al. 2009; Allred et al. 2011). Bison preferentially graze post-burned sites, which alters future fire regimes. These altered fire regimes shift future grazing patterns and create the patchy mosaic that is iconic to tallgrass prairie.

The reintroduction of both disturbance regimes has been successful in mitigating prairie degradation within the remnant tallgrass prairies west of the Mississippi River (Knapp et al. 1999; Towne et al. 2005; Houdeshell et al. 2011). Within the prairie peninsula, the ecosystem east of the Mississippi River typified by higher precipitation than western prairies, prescribed fires alone are commonly used to maintain and restore tallgrass prairie systems (Anderson 2006), although this likely reduces heterogeneity (Hartnett et al. 1996). Bison have been absent for >100 y and little is known about how grazing will impact plant communities in the remnants of the prairie peninsula or prairies that have been restored from agriculture. For example, fire has species-specific impacts on invasive species, but bison may alter these interactions by increasing seed dispersal (Fuhlendorf and Engle 2004; Constible et al. 2005; Alba et al. 2015). Bison may forage on N-fixing forbs, an important functional group for nitrogen cycling, during times of nutritional strain within plant communities (Bergmann et al. 2015; Craine et al. 2015). This selection may interact with fire regimes and cause a decrease in N-fixing forbs and consequently plant-available soil N (Craine et al. 2015; Nisi et al. 2015). To complicate the picture further, restored tallgrass prairie plant communities go through successional stages as species establish and compete so bison interactions with these communities may vary (Weber 1999). Despite the limits of our knowledge regarding bison impacts, bison reintroductions are increasingly being used to reinstate grazing regimes in restored tallgrass prairie. Consistent and long-term monitoring of plant community composition will provide insight into whether the reintroductions help to increase plant diversity and create a heterogeneous habitat mosaic as intended.

This research aims to analyze the impacts of a recent bison reintroduction and prescribed fires across a chronosequence of tallgrass prairie restorations. Specifically, we wanted to deter-

mine (1) how recently reintroduced grazing regimes, prescribed burning, and their interaction impact plant community composition and diversity; (2) how plant functional groups (invasive species, N-fixing forbs, forbs, and Poales species) are impacted by reintroduced disturbance regimes; (3) how the impacts of grazing and fire vary in relation to restoration age (time since site was converted from agriculture); and (4) if the competitive release and habitat heterogeneity hypotheses are supported in a restoration setting. We hypothesized we would see evidence of pyric herbivory increasing heterogeneity and plant diversity within sites. We also hypothesized that there would be reduced diversity in sites within later successional stages (older time since restoration), especially those without grazing, and that disturbances would cause more extreme shifts in composition in younger sites as a result of both the competitive release and habitat heterogeneity hypotheses.

METHODS

Study Site and Design

This study took place in the summer of 2016 and 2017 at Nachusa Grasslands, a 1200 ha prairie remnant and restoration site in Franklin Grove, Illinois, owned by The Nature Conservancy (TNC). The area is a mosaic of restored and remnant plant community types including tallgrass prairie and smaller areas of sedge and *Salix*-dominated wetlands, oak savannas, and deciduous broadleaf forests. All community types are managed to increase biodiversity, wildlife habitat, and ecosystem functioning. Total annual precipitation for 2016 measured 702 mm while total annual precipitation for 2017 measured 804 mm, compared to an annual mean of 947 mm.

Nachusa largely consisted of row crops (mostly soy and corn) until restoration began in the 1980s, yielding a chronosequence of restoration ages (Figure 1). All sites were left in row crops until restoration commenced. Practitioners at the site restored sites by planting native seed mixes collected largely from Nachusa remnants and restorations. Following planting, exotic species surveys and subsequent removal through herbicide application and physical methods occurred annually. Additionally, prescribed burns were applied in the year following restorations and reoccurred on a return interval of 1–3 y. This chronosequence of managed restorations provided a unique opportunity to investigate reintroduced disturbance regimes across restoration ages within a natural experiment.

Both fire and grazing regimes have been reintroduced at varying frequencies. In 2014, TNC reintroduced bison to half of the preserve at Nachusa Grasslands (600 ha; hereafter, bison unit). Staff constructed fencing to prevent bison from entering other areas of the preserve while allowing all other herbivores to move freely between units. Herd totals for 2016 and 2017 were 85 and 95 individuals, respectively. The resulting stocking density is ~ 0.15 au ha⁻¹. To define the grazing treatment, we selected eight sites within the bison unit and seven sites outside of the bison unit, each along a chronosequence representing 3–31 y since restoration. One remnant site within each grazing treatment was chosen to compare with restorations. Remnants were never converted for agriculture due to their shallow rocky soils but were originally used as restoration targets by managers. Remnant site

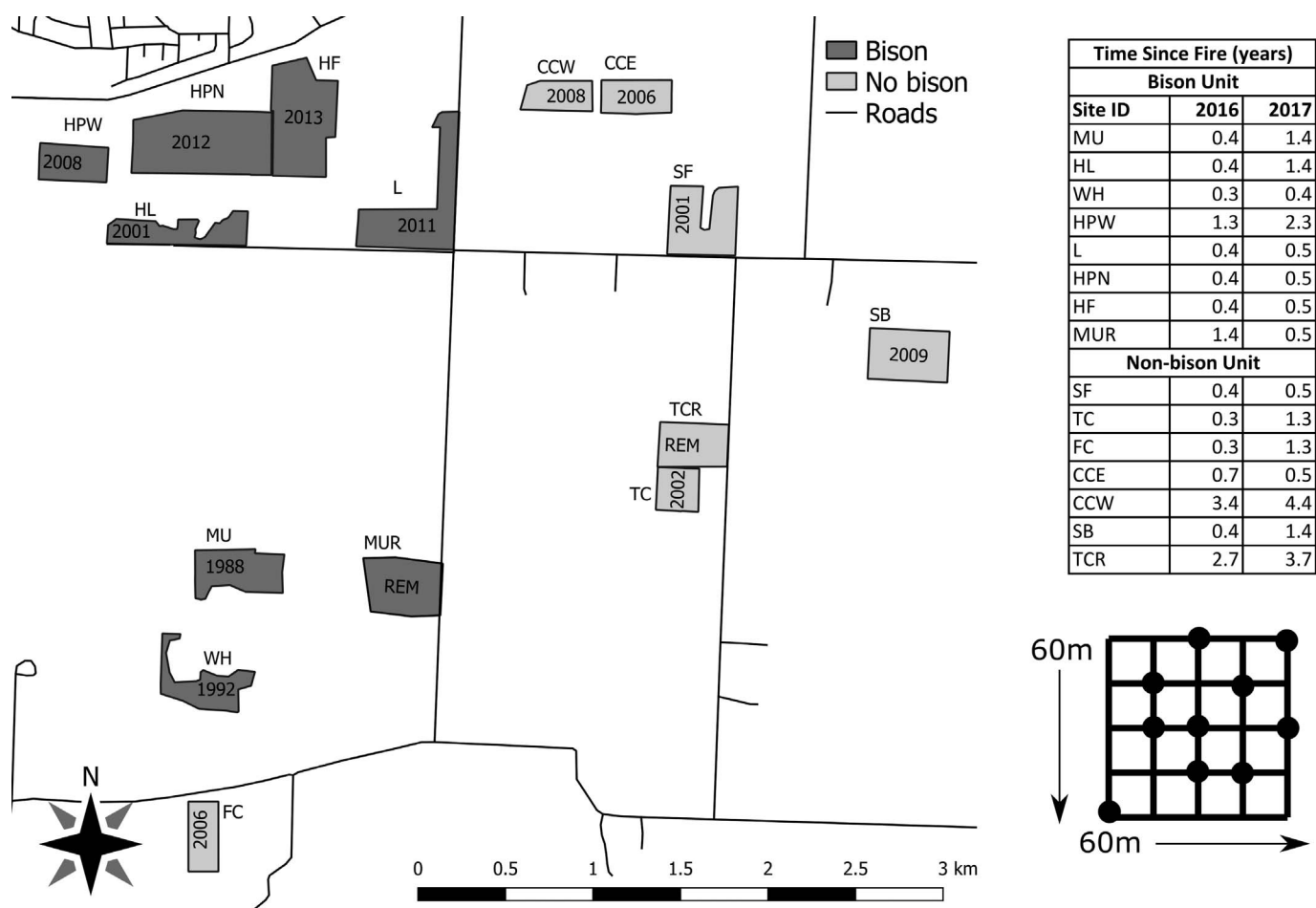


Figure 1.—Study design at Nachusa Grasslands in Franklin Grove, Illinois. Polygons represent individual sites along the chronosequence of restorations and remnants with and without the presence of bison. The year each site was planted is labeled within the polygon, and site IDs are labeled next to polygons. Time since fire for each site is represented for both study years within the table according to site ID. Within each site, one 60 m × 60 m grid was established such as the one represented in the figure. Black dots represent randomly selected locations for quadrat sampling.

characteristics likely drive plant community composition differently than in restorations, so remnants are not considered a restoration goal in this study and were excluded from the analysis. However, we included mean site values on figures for comparison. The time since fires on our sites ranged between 0.3 and 4.4 y. We considered a quadrat to be burned if we were informed a site was burned during that season. The resulting design provided restoration age as a continuous variable, grazing as presence/absence, and time since fire as continuous. Though pyric herbivory was not a discrete treatment, we investigated the presence of this disturbance through the changes in magnitude of grazing impacts given time since fire through their statistical interaction. The study design overall allowed us to observe how bison grazing and prescribed fire impacts interact with one another and change with restoration age.

Data Collection

Within each site, grids (60 m × 60 m) were established with 25 points spaced 15 m apart. We chose 10 points randomly, and permanent plot markers were used to mark each point (Figure 1). A quadrat (0.25 m²) was positioned on the permanent plot markers for a total of 150 quadrats sampled in 2016 and 2017. We

identified vegetation and cover to the species level during August 2016 and August 2017. Cover was estimated between 0 and 100% based on the stem basal area coverage per quadrat. Plants were identified using Williams (2010) and Wilhelm and Rericha (2017). Specimens that were unable to be identified in the field were collected and brought to an expert for consultation.

Data Analysis

All analyses were done within RStudio (R Core Team 2017). We measured the diversity and percent cover in each quadrat with the following response variables:

- Shannon-Weiner Diversity Index (Hill 1973):

$$H = -\sum_{p_i}^S p_i \log p_i$$

where S is the total number of species and p_i is the proportion of species i

Table 1.—Mixed-effect linear model *F*-test results from backwards selection for effects on the Shannon-Weiner diversity index, grass: forb ratio, native:nonnative ratio, and N-fixing forb abundance from restoration age, sampling year, grazing treatment, fire treatment, grazing- restoration age interaction, and pyric herbivory (grazing–fire interaction). Order removed is reported in the column eliminate. Estimates and confidence intervals (CIs) are represented as unit changes for diversity and percent changes for the rest of the response variables due to log transformations. Significance is indicated by (*).

	Diversity				
	Estimate (95% CI)	F	df	p	Eliminated
Rest age	−0.0178 (−0.027, −0.008)	13.117	1, 11.000	0.004014*	—
Year	0.270 (0.185, 0.356)	38.413	1, 251.454	<0.0001*	—
Graze	—	2.032	1, 10.000	0.184	4
Fire	—	0.031	1, 13.972	0.862	3
Graze*Rest	—	0.027	1, 8.471	0.874	1
Graze*Burn	—	1.391	1, 36.104	0.246	2
Poales:Forb					
Rest age	3.0575 (1.265, 4.819)	11.647	1, 11.662	0.005	—
Year	—	2.157	1, 256.264	0.143	5
Graze	—	0.453	1, 10.000	0.516	4
Fire	—	0.896	1, 22.920	0.354	2
Graze*Rest	—	0.658	1, 11.909	0.433	3
Graze*Burn	—	0.112	1, 59.707	0.739	1
Native:Nonnative					
Rest age	—	0.078	1, 10.000	0.786	2
Year	−39.025 (−53.565, −19.933)	12.717	1, 246	0.000	—
Graze	−58.941 (−81.298, −9.859)	4.846	1, 11	0.050	—
Fire	—	—	—	—	—
Graze*Rest	—	0.580	1, 12.527	0.461	1
Graze*Burn	—	—	—	—	—
N-fixing forbs					
Rest age	4.023 (0.838, 7.359)	5.996	1, 11.813	0.031	—
Year	—	0.405	1, 256.435	0.525	5
Graze	—	0.019	1, 9.554	0.893	3
Fire	—	0.694	1, 26.412	0.412	4
Graze*Rest	—	0.017	1, 11.553	0.845	1
Graze*Burn	—	0.148	1, 106.184	0.702	2

- Percent cover ratios of Poales species to forbs and native to nonnative species:

$$\frac{\%Poales}{\%Forbs}; \frac{\%Native}{\%Nonnative}$$

- Percent cover of N-fixing forbs

We tested for differences in the above response variables across treatments by creating linear mixed-effects models using the *lmerTest* package (Kuznetsova et al. 2017). Each quadrat in a restoration was treated as one sampling unit per site ($N = 260$). The Poales:forb ratio, native:nonnative ratio, and the cover of N-fixing forbs were transformed using a natural log function to address issues with non-normality. Restoration age, grazing (bison present or absent), fire (time since fire), the interaction between grazing and fire, and the interaction between grazing and restoration age were all considered fixed factors. We chose to leave fire and the fire–grazing interaction out as fixed effects for the native:nonnative ratio due an unequal sampling design with time since fire >3 y only occurring in ungrazed sites. Year was also treated as a fixed

factor because treating year as a random effect led to issues of model convergence. We treated site as a random factor to account for environmental and management-based differences such as the richness of seed mixes when planting. We evaluated fixed factors using backwards model selection through *F*-tests according to Satterthwaite's degrees of freedom with *step* (Table 1).

We also tested for differences in species composition among sites using a permutational analysis of variance (PERMANOVA) with the *adonis* function in the *vegan* package (Anderson 2001; Oksanen et al. 2017). For multivariate analyses, we totaled species abundance for each site and treated each site as a sampling unit ($N = 26$). We quantified composition using a Hellinger-standardized Bray-Curtis dissimilarity matrix based on overall site abundance of each individual species. Grazing, prescribed fire, and restoration age were considered fixed factors constrained by year. Due to the influence of restoration age on differences between communities, we chose to investigate the influence of grazing and time since fire separately using a Constrained Analysis of Principal Coordinates (CAP) with the *multiconstrained* function in the *BiodiversityR* package (Anderson 2001; Kindt and Coe 2005). Additionally, we calculated convex hull area to make comparisons of site dissimilarity within

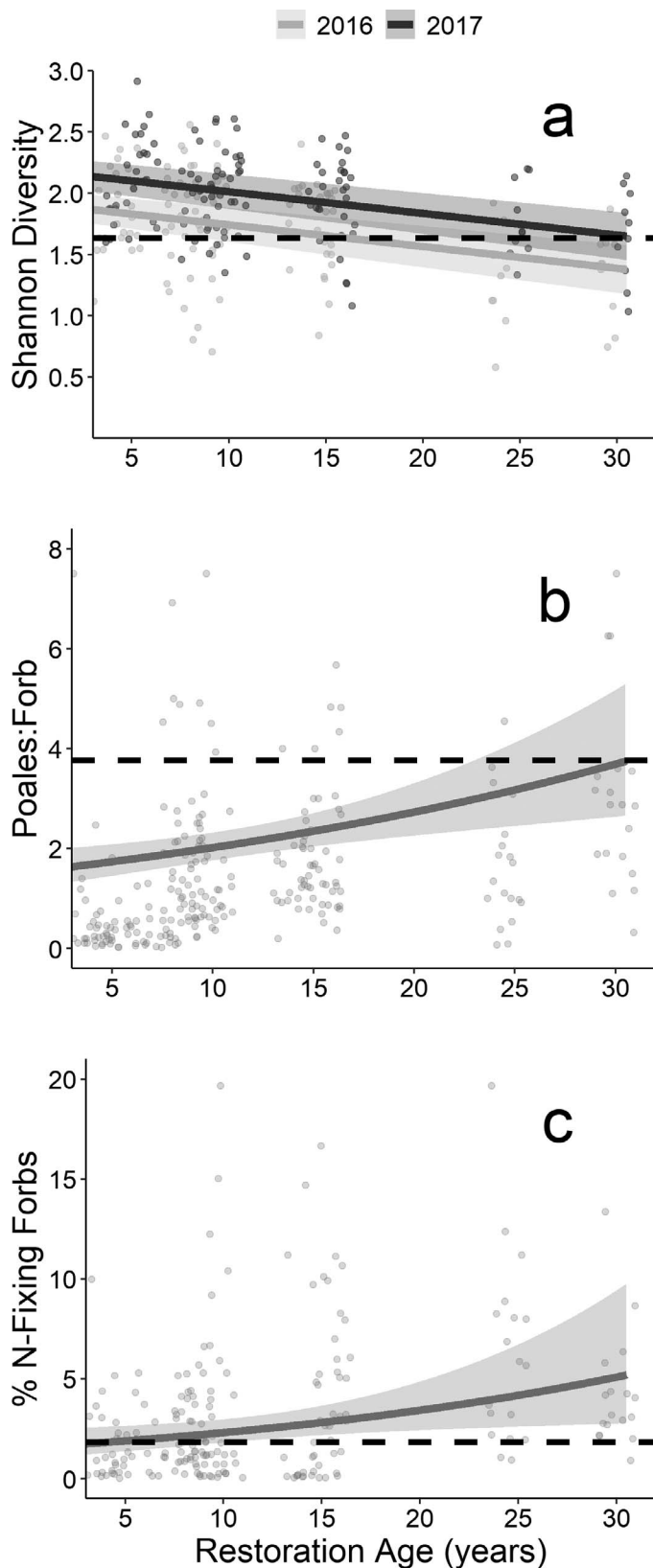


Figure 2.—(a) Model predictions for decreasing diversity with time since restoration. Higher diversity was found in 2017 (dark gray) than 2016 (light gray). (b) Model predictions showing the relationship of increasing grass:forb ratios with time since restoration. (c) Model predictions showing increasing N-fixing forb abundance with time since

bison and non-bison sites. We analyzed data with the same standardized Bray-Curtis dissimilarity matrix. Grazing and time since fire were considered fixed factors while restoration age and year were set as constraints. This allowed us to look for differences within treatments despite differences based on restoration age and the years of sampling. We used this same CAP and PERMANOVA design to examine differences among groups based on functional group (forb, N-fixing forb, C_3 Poales species, and C_4 grasses) abundance data that were transformed and standardized in the same method above into a Bray-Curtis dissimilarity matrix. These functional groups were chosen based on hypothesized influences of bison on community shifts from grass to forb, as well as previously reported responses of N-fixing forbs to fire (Coppedge et al. 1998). To identify which species are driving multivariate patterns, we conducted an Indicator Species Analysis (ISA) using the *multipatt* function in the *indicspecies* package (Cáceres and Legendre 2009). ISA estimates the association of individual species with site groups. For our analysis, we combined 2016 and 2017 surveys and grouped sites by the presence of bison to test for the association of individual species with bison or non-bison sites.

RESULTS

Diversity and Functional Group Response

Shannon-Weiner diversity indices were higher in 2017 than 2016 and decreased with restoration age (Table 1; Figure 2a). However, Shannon-Weiner did not differ based on the disturbance regimes (grazing and fire) or the interaction of the two. Poales:forb ratios and N-fixing forb abundance both increased with restoration age (Table 1; Figure 2b, 2c) but did not vary with grazing, fire, or their interaction. The native:nonnative ratios were lower in 2017 than 2016 and higher within grazed sites (Table 1; Figure 3).

Community Composition and Indicator Species Analysis

Constrained Analysis of Principal Coordinates (CAP) results showed species community composition differing between grazing treatments ($p = 0.001$; $df = 2, 22$; $F = 2.2171$; Figure 4) but not fire. Convex hull area also varied between bison (convex hull area = 2.2) and non-bison (convex hull area = 1.2) sites. Functional group composition did not vary by grazing or fire treatments ($p = 0.431$; $df = 2, 22$; $F = 1.0078$). Permutational analysis of variance (PERMANOVA) results showed species ($p = 0.001$; $R^2 = 0.18632$; $df = 1, 20$; $F = 6.4631$; Figure 5a) and functional group community composition differing by restoration ages ($p < 0.001$; $R^2 = 0.29617$; $df = 1, 20$; $F = 10.4612$; Figure 5b). Indicator Species Analysis (ISA) found three species to be strong indicators of grazing sites and ten species to be strong indicators of non-grazing sites (Table 2).

restoration. Ribbons represent 95% confidence intervals and points represent each quadrat sampled. Data points are slightly repositioned when necessary to prevent overlap. The dashed line represents mean value for remnant sites.

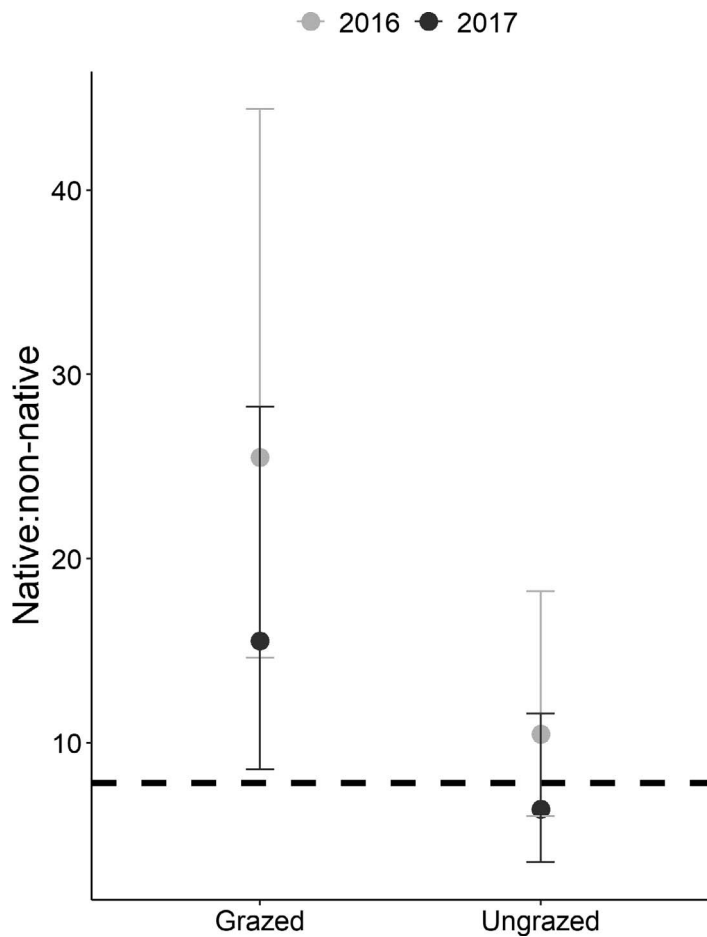


Figure 3.—Model predictions showing the increase in the native:non-native ratio in bison sites and the decrease between years. The bars represent standard error of predictions. The dashed line represents mean value for remnant sites.

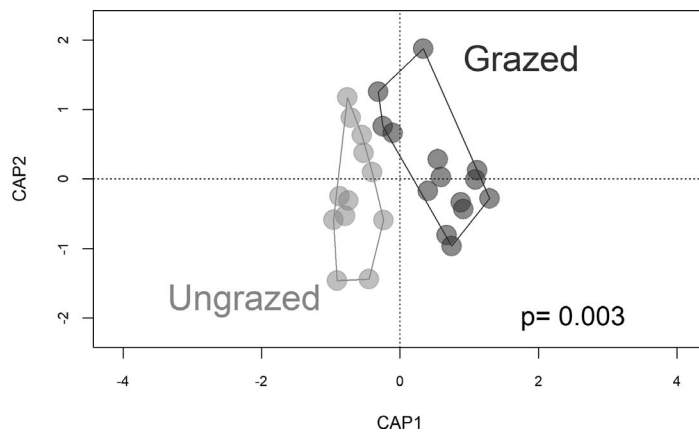


Figure 4.—CAP ordination plot representing the Bray-Curtis dissimilarities of plant community composition between sites (circles). Sites with bison (dark gray) have more complex or various plant assemblages than those without bison (light gray). Convex hulls were calculated around bison (convex hull area = 2.2) and non-bison sites (convex hull area = 1.2).

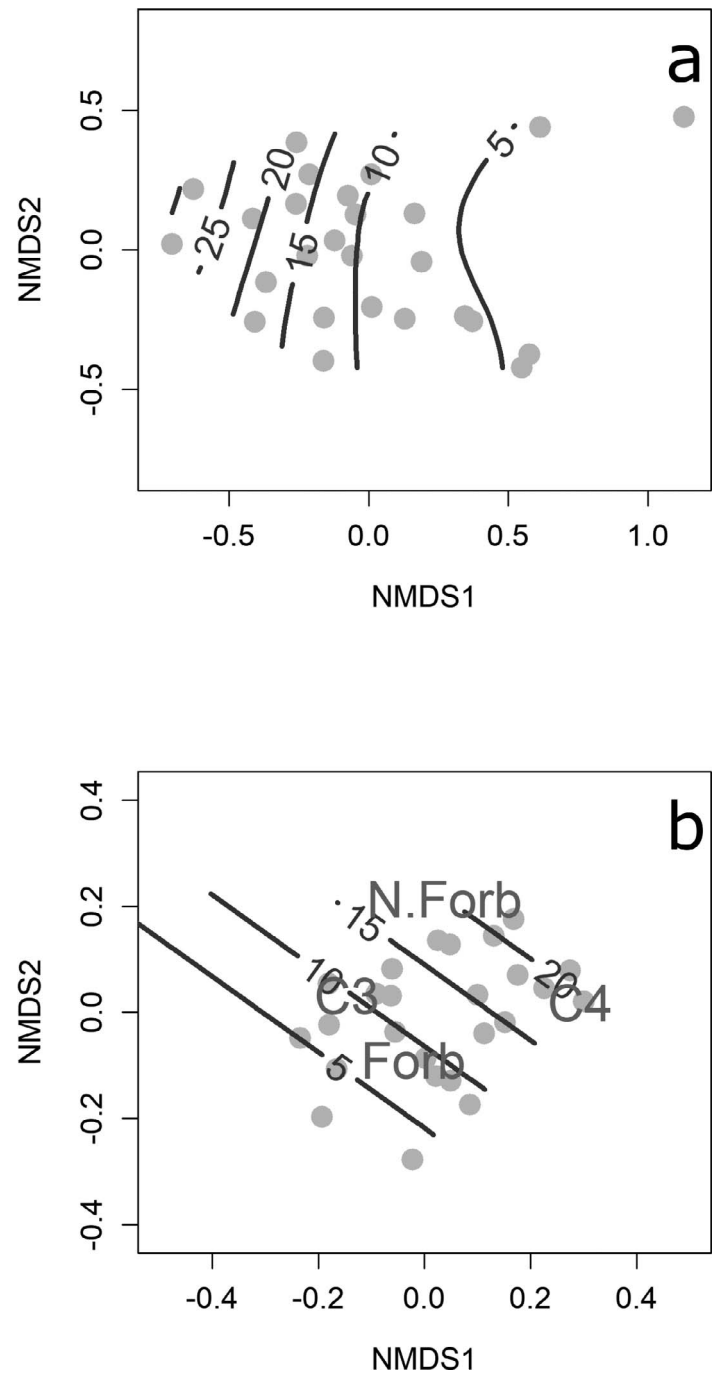


Figure 5.—Non-metric multidimensional scaling plot representing the Bray-Curtis dissimilarities of plant species community composition between sites (gray circles) across the gradient of time since restoration (lines). Numbers represent years since restoration and the space in between lines represents 5 y. (a) Communities based on species abundance become more similar as they age. (b) Functional groups are displayed in text to visualize functional group community transitions. Communities based on functional group abundance become more similar as they age.

Table 2.—Significant ($p > 0.05$) Indicator Species Analysis results for bison and non-bison sites. The indicator value (IV) is the square root of the product of A and B. A represents the probability a site belongs to the group given the species if found and B represents the probability of finding the species given you are in a site belonging to the group (bison or non-bison). All species values can be found in Supplemental Table 2.

Bison sites				
Species	A	B	IV	<i>p</i>
<i>Solidago nemoralis</i>	0.8042	0.7143	0.758	0.018
<i>Helianthus occidentalis</i>	0.7221	0.7857	0.753	0.047
<i>Symphyotrichum sericeum</i>	1	0.3571	0.598	0.048
Non-bison sites				
Species	A	B	IV	<i>p</i>
<i>Anemone cylindrica</i>	0.7583	1	0.871	0.001
<i>Ratibida pinnata</i>	0.6709	1	0.819	0.005
<i>Monarda fistulosa</i>	0.6373	1	0.798	0.023
<i>Poa pratensis</i>	0.693	0.9167	0.797	0.03
<i>Pycnanthemum virginianum</i>	0.8336	0.75	0.791	0.006
<i>Achillea millefolium</i>	0.6656	0.9167	0.781	0.028
<i>Poa compressa</i>	0.7572	0.75	0.754	0.014
<i>Taraxacum officinale</i>	0.7293	0.75	0.74	0.03
<i>Helianthus grosseserratus</i>	0.8637	0.5833	0.71	0.012
<i>Bromus inermis</i>	0.8292	0.5833	0.696	0.024

DISCUSSION

Grazing and Fire

Although our understanding of grazing and fire regimes in remnant tallgrass prairies west of the Mississippi River is well developed (Knapp et al. 1999; Anderson 2006; Fuhlendorf et al. 2009), the impacts of reintroduced grazing regimes and their interactions with fire on restored tallgrass prairie within the prairie peninsula are unknown. Higher precipitation and varying successional stages of plant communities as restorations age make these prairies unique, which contributes to the difficulty of predicting potential impacts of bison reintroduction. In this study, we found that although recently reintroduced bison have not caused changes in diversity or most functional group abundances, they are associated with changes in plant community composition and the ratio of native to nonnative plants.

Species associations with the presence of bison provide context into potential impacts of bison on plant community composition. The three most important indicator species within bison sites included *Solidago nemoralis*, *Helianthus occidentalis*, and *Symphyotrichum sericeum*. Grazing reduces the amount of biomass and competition for sunlight for species closer to the ground (McCain et al. 2010; Elson and Hartnett 2017). Both *S. nemoralis* and *H. occidentalis* have a majority of their photosynthetic tissues closer to the ground and *S. sericeum* has been associated with grazed areas elsewhere (Werner 1979; Brudvig et al. 2007; Wilhelm and Rericha 2017). The ten indicator species found within the non-bison sites most notably included three nonnative C_3 grasses. *Poa pratensis*, *Poa compressa*, and *Bromus inermis* are all nonnative grasses that are common among most restored sites. *P. pratensis* specifically has been found to decrease in areas with bison (Vinton et al. 1993). Both *Bromus* and *Poa* species are known to remain photosynthetically active after C_4 grasses senesce and so may provide a food source to bison in the early spring and late fall (Vinton et al. 1993; Steuter et al. 1995). This is also in line with our findings that sites with bison present have increased native plant

dominance. These associations indicate that bison may be reducing nonnative C_3 grasses and competition for light allowing forb species to benefit.

Although our results found no direct evidence of the proposed competitive release and habitat heterogeneity hypotheses, they do provide insight into the possibility of these conditions occurring after prolonged exposure to disturbance regimes. The recorded dissimilarity and resulting convex hull areas provide evidence for increases in heterogeneity resulting from bison reintroduction hinting that the habitat heterogeneity hypothesis could be responsible (Figure 4). Although the direct causes such as grazing, digestive excretion, and wallowing are unknown, we can say bison are shifting plant communities to more distinct assemblages in comparison to one another. Results from western remnant prairies with bison have shown that this is an important mechanism driving bison impacts and restored prairies appear to be reflecting the same pattern (Hartnett et al. 1996; Knapp et al. 1999; Elson and Hartnett 2017). We did not find any differences in grass cover or diversity between sites with or without bison, indicating the competitive release hypothesis is not supported in our study system. However, previous work in bison grazed communities and experimental plots shows that the competitive release hypothesis causes increases in richness and shifts in community composition (Jutla and Grace 2002; Elson and Hartnett 2017). The surprising paucity of initial bison impacts in our study may be a result of the relatively low stocking density (0.15 au ha^{-1}) and short period of time since reintroduction. Communities with a large amount of perennial herbaceous species, such as our study sites, have been shown to take longer ($>3 \text{ y}$) to respond to grazing in comparison to annual communities (Belsky 1992). Additionally, other measures such as biomass have been used to indicate decreases in grass production and increases in forb performance, which support the competitive release hypothesis (Elson and Hartnett 2017). The indicator species we found within the grazed sites hints that this may be occurring (Table 2). Further investigation into the resource acquisition of forbs and grasses at Nachusa Grasslands

would help tease out any changes in competitive pressures from bison that may be taking place.

Fire is a driving force in tallgrass prairie plant communities, and the changes within fire regimes (frequency, season, and intensity) may have differing impacts on the biotic and abiotic conditions of the site (Ewing and Engle 1988; Blair 1997; Anderson 2006; Vogel et al. 2007). Our study was unable to detect any differences between plant communities experiencing different lengths of time since fire (Table 1). However, variation in time since fire across the sites is somewhat limited, with sites on average burned within the previous year (mean = 0.996, SD = 1.006). Prescribed fire impacts on plant composition can persist past the burn year into the second subsequent growing season (Ewing and Engle 1988), so fires within our study sites may have occurred too recently to detect differential fire impacts. That is, essentially all sites are high-frequency-fire communities, which is a common prairie management approach in the region to help control exotic weeds. This likely creates a fairly homogeneous landscape in relation to the effects of fire. Other research has shown that fire may be duplicating some effects of grazing, resulting in a smaller individual impact by either fire or grazing (Belsky 1992).

We hypothesized that pyric herbivory would modify plant communities and create a more heterogeneous landscape overall. However, we did not record any evidence of such pyric herbivory (tested through grazing and fire interaction; Table 1), which may be due again to the continuation of prescribed burning effects, the relatively low stocking density, and the short time period of study following bison reintroduction. There was observational evidence of pyric herbivory occurring during our sampling season (we saw lots of bison in recently burned sites), but we still did not find an interaction between grazing and fire in our data. Pyric herbivory may be driving some effects measured in the community analyses but limitations in the ability to test interactions prevented investigation into such possibilities. Looking at areas that we know were grazed or including variables for bison presence and grazing intensity may help future work determine why there is no evidence of pyric herbivory altering plant communities in our study area.

Restoration Age

We have shown that time since restoration is the main factor explaining diversity, functional group abundance, and community composition at this study site. As restorations mature through time, both species and functional community composition become more similar between restorations (Figure 5). This supports the idea of successional stages as restorations progress; however, the early stages of restoration can vary greatly in functional groups and species composition from one another (Weber 1999). This change in composition through time is also seen as diversity begins to decrease while the ratio of *Poales* to forbs and N-fixing forb abundance increases as restorations age (Figure 2). This supports the hypothesis that grasses outcompete forbs (particularly non-nitrogen-fixing forbs) as restorations mature and as a result diversity declines. This is concerning because the projected diversity declined below the remnant communities in 2016, which coincides with other findings (Sluis 2002; Polley et al. 2005; Dickson and Busby 2009). However, in

2017 diversity seems to have increased and no longer fell below the average remnant diversity. This increase may be a result of higher precipitation in 2017.

The decrease in diversity and increase in the *Poales* to forb ratio with age do not explain the increased establishment of N-fixing forbs within older restorations. Because N-fixing forbs can obtain nitrogen through fixation, they may not experience the same competitive pressures as non-N-fixing forbs. Frequent prescribed burning can reduce soil N, and soil C:N increases resulting from increases in carbon as restorations age (Blair 1997; Klopff et al. 2017). N-fixing forbs are better competitors than other non-N-fixing forbs in high fire frequency environments (Towne and Knapp 1996). Further, most problematic invasives are N-fixing forbs, but our data show that invasive forbs are not increasing in abundance and are not driving this change (Table 1). N-fixing forbs also increase usable soil nitrogen, potentially facilitating other species (Craine et al. 2015; Nisi et al. 2015). Restorations managed for higher diversity through establishment from species rich seed mixes and maintained through invasive species removal and frequent fire regimes, such as Nachusa Grasslands, have lower amounts of N to lose so increased N-fixing forb abundance may be stabilizing plant-available N (Barber et al. 2017; Klopff et al. 2017). Long-term grazing pressures may begin to decrease grass abundance and allow the non-N-fixing forbs to take advantage of the available N from N-fixing forbs. Further studies are needed to clarify these interactive effects of N-fixing forbs, pyric herbivory, and restoration age on soil N availability.

Restoration Implications

Decreasing plant diversity through time, especially to levels below remnant diversity, is counter to the desired goals of restoration. Although it is not certain that bison will eventually counteract this decrease in diversity, we show that bison are creating more heterogeneous plant communities. Continued grazing may suppress grasses at local scales and increase the overall diversity of older restorations. However, potential negative impacts including invasive species dispersal and increased grazing pressures on native N-fixing forbs may still occur after prolonged exposure to bison grazing. This study looked at the impacts of bison after 2–3 y of reintroduction, which is likely too short of a time frame for the full magnitude of bison impacts to occur. Nonetheless, our study on the short-term impacts of bison is important for managers to predict changes in restored prairies following bison reintroduction, especially given the increase in bison reintroduction throughout the prairie peninsula. Our results provide some optimistic signs of potential bison impacts, but continued monitoring of these plant communities is needed to clarify long-term impacts.

Across our study, all sites had been burned recently (time since fire <5 y). Nachusa Grasslands aims to maintain a fire return interval of 1–3 y, although the average return interval in our study sites was at the low end of this range. These conditions may have lasting impacts on plant communities that persist into years when restorations are not burned (Ewing and Engle 1988). Our results for community composition did not show a difference between time since fire, so frequent fire may be

homogenizing the landscape. Reduction in prescribed fire return intervals may increase heterogeneity of these plantings and reduce competitive pressures from grasses. If high-frequency fires are continued, stable N availability due to abundant N-fixing forbs may continue. However, if bison grazing results in patchier fire effects (Fuhlendorf et al. 2009), then grazing regimes may allow high-frequency fires to continue while still promoting community heterogeneity.

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